CHAPTER TWO

How Agricultural Intensification Affects Biodiversity and Ecosystem Services

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- Abstract

As the world's population continues to grow, the demand for food, fodder, fibre and bioenergy will increase. In Europe, the Common Agricultural Policy (CAP) has driven the intensification of agriculture, promoting the simplification and specialization of agroecosystems through the decline in landscape heterogeneity, the increased use of chemicals per unit area, and the abandonment of less fertile areas. In combination, these processes have eroded the quantity and quality of habitat for many plants and animals, and hence decreased biodiversity and the abundance of species across a hierarchy of trophic levels and spatial scales within Europe. This biodiversity loss has led to profound changes in the functioning of European agroecosystems over the last 50 years. Here, we synthesize the findings from a large-scale pan-European investigation of the combined effects of agricultural intensification on a range of agroecosystem services. These include (1) the persistence of high conservation value species; (2) the level of biological control of agricultural pests and (3) the functional diversity of a number of taxonomic groups, including birds, beetles and arable weeds. The study encompasses a gradient of geography-bioclimate and agricultural intensification that enables the large-scale measurement of ecological impacts of agricultural intensification across European agroecosystems. We provide an overview of the role of the CAP as a driver of agricultural intensification in the European Union, and we demonstrate compelling negative relationships between the application of pesticides and the various components of biodiversity studied on a pan-European scale.

1. INTRODUCTION

The world's population is predicted to grow from 7 to at least 9 billion by 2050, whilst simultaneously the climate is predicted get warmer globally and the frequency of extreme climate events to increase. At the same time, crop production is not increasing and as a consequence of economic and global climatic changes is even declining in major agricultural regions despite technological advances (Ray et al., 2012). This combination has the potential to create a global food crisis (Global Food Security, 2011; Godfray et al., 2010; Lennon, 2015; Poppy et al., 2014).

Farmlands are the most extensive habitat for biodiversity in Europe, harbouring, for example more than one half (250 species) of European bird species, of which 50% are either threatened or have suffered steep population declines (Chamberlain et al., 2000; Donald et al., 2001, 2006;

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Krebs et al., 1999; Robinson and Sutherland, 2002). There were 10.8 million farms across the EU-28 in 2013, working 174.4 million ha of land (the utilized agricultural area or UAA), which represents roughly 40% of the total land area of the EU-28 (Eurostat, 2015). Nearly 60% of the UAA was used as arable land (104.2 million ha), including 57.6 million ha being used for cereal production. A large proportion of the production of crops such as cereals is not used for direct human consumption, but rather is fed to livestock (Foley et al., 2011), and estimates show that in 2011 around 6.1 million ha of agricultural land (3.4% of the total UAA) were directly and increasingly devoted to the production of biomass and energy crops (Eurostat, 2015).

Until recently in Europe, the Common Agricultural Policy (CAP) drove the intensification of agriculture in order to meet increased demands for food and fodder starting in the 1950s. European farmed landscapes have traditionally consisted of complex mosaics of extensive crops that sustained high levels of biodiversity (Potter, 1997; Walk and Warner, 2000). Over the last 50 years, however, the farmlands of western European countries have experienced dramatic changes, mainly through the intensification of farming techniques (Björklund et al., 1999; Robinson and Sutherland, 2002; Siriwardena et al., 2000). For example, the yield of cereals has increased steadily (Liira et al., 2008a), although the total application of fertilizers has dropped by 30% since the 1980s (Eurostat, 2015; Liira et al., 2008a; see Fig. 1). The loss of biodiversity driven by agricultural intensification (AI) is judged to be similar in scale to that expected from climate change (Tilman et al., 2001).

AI occurs at multiple spatial scales, with particular focus on local and landscape scales (Benton et al., 2003; Firbank et al., 2008). On the one hand, crop yield and revenue optimization lead to an increased impact by agricultural activities, at the cost of noncultivated components of the field and its immediate surroundings, and thereby, severe losses of wild plant and animal populations (Firbank et al., 2008; Haberl et al., 2004). On the other hand, large-scale field-level intensification leads to landscape simplification and homogenization, which further reduces habitat availability for wild species (Tscharntke et al., 2005). At regional scales that incorporate several landscapes, specialization, focused on particular monocultures, can occur, e.g. on fertile alluvial soils. In contrast, some regions can experience land abandonment, for example in less productive areas such as mountainous regions (Benton et al., 2003; Tivy, 1990) or forest-dominated regions in northern Europe (Wretenberg et al., 2007). In summary, AI operates primarily at

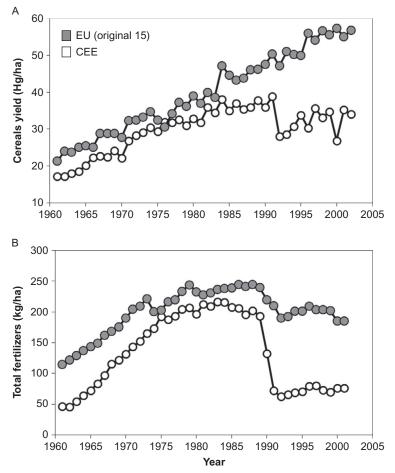


Fig. 1 Long-term trends of cereal yield per hectare (A) and application of total fertilizers (active substances) per hectare (B) in early (western) members of European Union (EU(15)) and in countries of Central- and Eastern Europe (CEE). Source: FAOSTAT, 2004. Agricultural data; see details in Liira, J., Aavik, T., Parrest, O., Zobel, M., 2008a. Agricultural sector, rural environment and biodiversity in the central and eastern European EU member states. Acta Geograph. Debrecina Landsc. Environ. Ser. 2, 46–64.

the field level (increased fertilizers, pesticides, employment of machinery, increased sowing density, ploughing depth, etc.), but may also dominate whole landscapes and regions, thereby contributing to biodiversity declines and homogenization of agricultural ecosystems at larger scales (Flohre et al., 2011a).

In contrast, many management decisions made by farmers do not concern particular fields, but rather the entire farm. Such decisions often affect the production mode and sequence of crop rotations, for example the decision to manage conventionally vs organic farming techniques, and may generate a certain degree of spatial aggregation of farming types in the landscape, particularly in regions where the agrarian property is spatially concentrated, e.g. Western Europe. Therefore, farm-level measures of intensification might often be required in some regions, and field-level measures in others.

The increased human demand of food and energy crops is predicted to contribute to the continuing intensification of European agriculture, but it also poses an environmental and sustainability problem (Godfray et al., 2010). The intensive management practices that prevail in agricultural ecosystems have the potential to affect a wide range of plant and animal species, as well as ecosystem processes underpinning agricultural production, at local to very large spatial scales (Oliver et al., 2015). For example, over the last 50 years, AI has led to marked declines of numerous species of European flora and fauna at local, national and regional scales (Donald et al., 2001; Kleijn et al., 2009; Stoate et al., 2001; Tilman et al., 2001). This decline is reflected in the National Biodiversity Indices (SCBD, 2001) of old EU states (15) subject to AI, relative to new EU member states that have significantly higher indices of biodiversity (Liira et al., 2008a).

Agricultural ecosystems harbour part of a wide ecological network of interacting organisms from arable and nonarable habitats that form the ecological context for food production. This ecological network comprises the biodiversity elements that confer a range of beneficial ecosystem services underpinning the production of food and other commodities in agroecosystems. At large spatial scales, there are clines in species richness and biodiversity that reflect underlying spatial variation in the physical environment, e.g. patterns in precipitation, temperature and soil conditions that in combination comprise the bioclimate of a region.

The physical environment, including bioclimate and human management activities that modify the physical environment, creates a range of different environmental contexts that are intimately associated with the presence and relative abundance of species, and therefore drive large and fine scale patterns in biodiversity. In addition, the environmental context can affect the physical attributes or traits of species that in turn can alter the way in which species interact within their ecological networks (Poisot et al., 2012; Woodward et al., 2005). For example, changes in body mass can alter the relative strength of trophic or competitive interactions among species (Vucic-Pestic et al., 2010). Changing patterns of interactions can affect the flow of energy and nutrients and alter the resilience and functioning of an ecosystem.

1.1 General Objective and Goals

How AI processes drive habitat degradation and the loss of biodiversity and associated ecosystem services is the focus of this chapter. Since the impacts of AI manifest at different spatial scales and can affect biodiversity and ecosystem service delivery in unique ways, we pay particular attention to the relationships between biodiversity and AI factors operating at local and landscape scales. To manage agroecosystems for secure and sustainable food production requires that we understand how the different components of agricultural management practices affect biodiversity and ecosystem functioning. To achieve this, we first provide an overview of the role of the CAP as a driver of AI in the European Union. We then review and synthesize evidence quantifying where and how AI has had impacts on the taxonomic and functional diversity (FD) of agricultural ecosystems, and the provision of biological control of pests, a key ecosystem service for the sustainability of food production.

We draw predominantly, but not exclusively, on the results of AGRIPOPES (AGRIcultural POlicy-Induced landscaPe changes: effects on biodiversity and Ecosystem Services), a large-scale pan-European research project focused on quantifying agricultural policy-induced landscape changes and their effects on taxonomic and FD and the associated delivery of biological pest control. Our goal is to use the results obtained within AGRIPOPES that address the impacts of AI on biodiversity in farmed landscapes, but we highlight and review evidence from the relevant literature that is far broader than the AGRIPOPES project in scope. We focus on the three processes that are understood to drive biodiversity loss through AI: (1) increased use of farm chemicals, like fertilizers, herbicides and pesticides; (2) mechanization and crop and husbandry specialization and (3) simplification of farmed landscapes leading to loss of landscape diversity. Initially, we provide a historical background of the CAP as the main driver of agricultural change and AI over recent decades in Europe, and we present the general methodology of AGRIPOPES. We then review the evidence for impacts of AI on biodiversity throughout Europe and

beyond. We have concentrated on agricultural areas dominated by cereals, since they alone comprise more than 13% of EU-28 land area, that is, more than 57 million ha, which amounts to one-third of the total area devoted to agriculture in Europe (Eurostat, 2015).

2. THE CAP AND AI

2.1 CAP as a Driver of Agriculture in Europe

The CAP is frequently considered the main instrument behind the dual process of intensification and abandonment observed in agricultural systems in the European Union over the last few decades. Paradoxically, the CAP is also now expected to play a role in the environmental conservation of these systems (Pe'er et al., 2014). This apparent contradiction is explained by considering the founding principles and evolution of one of the oldest policies of the European Union, which has been strongly rooted in the European integration project since its effective inception in 1962.

The original priority of the CAP was to increase agricultural production in order to stabilize agricultural markets and farmers incomes, this was enshrined in the Treaty of Rome, which came into effect in 1957. The core mechanisms were based on (1) price support, i.e. maintaining prices to producers above world levels through intervention, e.g. buying food; (2) import levies, i.e. raising the price of imports above world prices; and (3) export subsidies, i.e. compensating producers selling at lower world market prices. The economic environment provided by the security of commodity prices offered by the CAP also stimulated scientific research and development aimed at increasing crop and animal yields, much of it financed by public funds (Robson, 1997). In this way the CAP incentivised the intensive use of farm chemicals (e.g. fertilizers, pesticides and herbicides) and machinery, and so increased the yields of all supported commodities. Originally these were cereals, milk and livestock, but the list increased as the European Community expanded in subsequent years. Further, the CAP also promoted capital-intensive operations, such as drainage, land consolidation and irrigation expansion, and was often supported by National governments that reinforced the trend towards greater intensity and scale of agricultural production (Robson, 1997).

The resulting multivariate process of change is embodied in the term 'Agricultural Intensification', which from an agronomic and economic

view, is related to the increase of production output, i.e. yield, per unit of area or time (Turner and Doolittle, 1978) or per unit of inputs (FAO, 2004). Agricultural production can be intensified by increasing inputs of capital, such as machinery, energy and biotechnology, or by increasing inputs of manual labour (Börjeson, 2010). The continued decrease of agricultural labour input in Western Europe over the last decades (4.2% of total EU-15 employment in 1999 to 2.9% in 2013; Eurostat, 2015; Eastern Europe ca. 12% in 2013) indicates that AI in the EU has been based on high inputs of entrants and capital investment per unit land area.

Biodiversity declines are more likely to be related to inputs than to yield per se. Therefore, in the ecological domain, AI refers to the increased use per unit area of fertilizers, pesticides, water and machinery for crop production and high-density housing systems for animals. Broadly, the concept of AI also relates to the landscape-scale consequences of these and other changes, such as reduced crop rotations, or loss of noncrop features (e.g. Donald et al., 2001; Kleijn et al., 2009; Stoate et al., 2001). These variables are often used as surrogate measures of intensity (Herzog et al., 2006), an approach that was adopted in the AGRIPOPES project.

The changes observed in agricultural landscapes and the declines in biodiversity during CAP implementation are well documented (Lefebvre et al., 2012; Meeus, 1993; Tscharntke et al., 2005; Wretenberg et al., 2007). Whilst the CAP played a major role in transforming the rural landscape of Europe, other drivers were also important. It is likely that the observed patterns of agricultural change would have taken place even without government interventions, since they are ultimately related to the processes of technological development (supporting advanced use of machinery, chemicals, biology and information-related developments) and social and demographic change, including industrialization, urbanization, migration to cities and the ageing of rural populations, processes that have been ongoing since the beginning of the 20th century (Brouwer and Lowe, 2000; Buckwell, 1990). It is likely, however, that the financial support under the CAP played a major role in determining the profitability of the adoption and diffusion of novel crops, livestock and techniques in the agricultural sector, thus creating the conditions for their general adoption (Potter, 1997). Therefore the confluence between capacity (technical progress) and opportunity (farm support) has in the long run brought about the changes in the structure, pattern and practice of farming now recognized to have had profound environmental effects (Benton et al., 2003).

The CAP has evolved and has undergone numerous reforms throughout its 54-year history. These modifications to the CAP reflect attempts at remediating unforeseen consequences of varied internal (e.g. production surpluses, budget deficits, environmental concerns) and external problems (e.g. trade conflicts) that arose because of legislation embodied in the CAP (Robson, 1997). Initiatives to reform the CAP were developed in the early 1970s, although the major shift came with the 'MacSharry reform', adopted in 1992. This included replacement of price support with direct aid payments per hectare and the introduction of compulsory set aside, and the formal introduction of environmental objectives in the CAP, i.e. promoting the adoption of environmentally friendly farming methods. Since then, Agri-Environmental Schemes (AESs) represent the most prominent instrument available to achieve alignment between agricultural practices and nature conservation policies (Hodge et al., 2015). These measures provide economic incentives to compensate for the additional costs and income foregone resulting from the voluntary adoption by farmers of practices that protect the environment. These practices include the reduction of agrochemical inputs, adoption of organic farming, and extensive forms of production, based on longer rotations and allowing the presence of fallows and unploughed landscape features (hedgerows, trees, small woods, ponds, wetlands, field borders), as well as reduced livestock density. Expenditure on these schemes and area covered by their prescriptions has steadily increased across the EU, but they have had only partial success in the environmental enhancement of the targeted systems, due to unclear objectives, inadequate design, or low uptake (see Batáry et al., 2015 and references herein). Although several studies have assessed the effectiveness of these schemes in different countries (Concepción et al., 2012; Kleijn et al., 2001; Tuck et al., 2014), the lack of continuous and homogeneously applied monitoring schemes may have limited their efficacy.

The Agenda 2000 reform subsequently recognized the multifunctionality of European agricultural systems, and the 2003 reform of the CAP removed the link between the receipt of a direct payment and the production of a specific commodity (known as 'decoupling'). These reforms also introduced 'cross-compliance', as a series of rules that the farmer had to respect in order to receive direct payments. These rules were related to the environment, the protection of water resources, and the condition in which farmland was maintained. In 2007, AESs were further reinforced with the creation of the European Agricultural Fund for Rural Development as the second pillar of the CAP. Direct payments to farmers and market management measures continued in the so-called first pillar, but with a budget close to four times the size of that of pillar 2 in the last programming period 2007–2013. Decoupling was completed by the 'health check' of the CAP, a range of streamlining measures introduced in 2008 that also included the abolition of arable set aside, new cross-compliance requirements, and a reduction of direct payments to farmers with the money transferred to the Rural Development Fund instead.

With the CAP reform in 2013, covering the period 2014–2020, new so-called 'greening measures' were introduced affecting direct payments to farmers. These measures made 30% of the payment conditional upon the maintenance of permanent pastures, the diversification of crops, and the establishment of 'ecological focus areas'. However, the new environmental prescriptions are so diluted—only applying to roughly 50% of EU farmland, and with most farmers exempted from deploying them—that they are unlikely to be of benefit to biodiversity (Pe'er et al., 2014). For example, in the AGRIPOPES data, only around 12% of the farms grew less than three crops, the majority of those were in Spain.

2.2 How Does CAP Affect AI?

In a European context, AI is therefore a multifactorial process that leads to increased yields (Donald et al., 2006; Herzog et al., 2006; Matson et al., 1997). Crop and livestock specialization, increased synthetic inputs and soildisrupting operations or removal of semi-natural elements and landscape features are all components acting at field and landscape levels which have interacted jointly to modify the agricultural ecosystems of Europe over the last decades (Chamberlain et al., 2000). Two related processes acting at different scales underlie increased AI: (1) intensification of management practices at the field level through the increased use of farm chemicals (herbicides, pesticides and fertilizers) per unit area (see Fig. 1) and soildisrupting operations (ploughing, refining) and (2) simplification of landscape diversity through crop specialization, removal of landscape elements, conversion of permanent pastures into arable land, and land abandonment on less fertile areas and expansion of early successional, homogeneous shrub replacing the landscape mosaic landscape typical of extensive farmland. These processes in combination have led to a degradation of habitat quality and an overall decline in the diversity and total biomass of a wide range of species. These species make up the biological matrix within which agricultural ecosystems are nested. Ultimately, the processes underpinning AI have

led to similar rates of local species loss for several taxonomic groups across European agricultural landscapes (Robinson and Sutherland, 2002). The massive use of entrants also has additional detrimental effects like soil and water eutrophication and contamination, whilst soil-disrupting operations favour erosion (Stoate et al., 2001).

2.3 How Does CAP Affect Biodiversity and Ecosystem Services Through AI?

AI is considered to be the main process driving the generalized decline of farmland biodiversity observed in Europe over the last decades. Such declines affect organisms from different taxa, including birds (e.g. Donald et al., 2001, 2006), vascular plants (Marshall et al., 2003; Storkey, 2012), invertebrates (e.g. Aebischer, 1990; Östman et al., 2001a; Weibull et al., 2000) and soil organisms (Kladivko, 2001).

Arguably, species loss in European agricultural landscapes is driven by changes in food web, and more generally, ecological network structure, e.g. plant–pollinator networks (Ings et al., 2009). Structural habitat modification and changes in the supply and diversity of the species' resource base have altered the availability of food and shelter, which has in turn driven changes in the abundance and diversity of species. The simplification of agricultural landscapes has also affected ecosystem services, i.e. the benefits for human society provided by different ecological processes, produced by subsets of biodiversity, for example biological control of agricultural pests (Östman et al., 2001b, 2003; Thies and Tscharntke, 1999) and pollination (Garibaldi et al., 2011; Kennedy et al., 2013). However, the documentation of changes in biodiversity and ecosystem services at a European-wide scale is largely lacking.

Plants, insects and especially birds have all declined in European farmland at the community and landscape level (Billeter et al., 2008; Chamberlain et al., 2000; Pain and Dixon, 1997; Wretenberg et al., 2007). Different local and country scale studies have shown that AI and landscape homogenization can induce biodiversity loss (e.g. Benton et al., 2003; Robinson and Sutherland, 2002; Tuck et al., 2014). For example, the study by Wretenberg et al. (2007) showed that changes in farmland bird population trends in Sweden were directly linked to changes in agricultural intensity caused by corresponding changes in agricultural policies between 1970 and 2000. That study also showed that these relationships were partly dependent on landscape heterogeneity. However, until recently, there were limited data available to support the statement that intensification led directly to biodiversity loss at the European scale. The lack of such supporting evidence was the basis of much of the work summarized here in the context of the AGRIPOPES project.

2.4 The AGRIPOPES Project—Examining the Multiple Effects of AI on Biodiversity and Ecosystem Services

The AGRIPOPES project was developed within the EuroDiversity programme of the European Science Foundation during the years 2006–2009. A consortium of nine research teams, representing a latitudinal gradient and two different land intensification histories (east-west) from eight European countries (Sweden, Estonia, Poland, the Netherlands, Germany (two areas: close to Göttingen, reflecting West Germany, and Jena, reflecting East Germany), France, Spain and Ireland), examined multiple aspects of the intensification of agriculture associated with the CAP and its consequences for the biodiversity and the ecosystem services associated with cereal agroecosystems. Three major issues were addressed: the persistence of taxonomic diversity, the responses to AI of FD of a number of taxa and the prevalence of sustained biological control of important agricultural pests. The design of the project used the double gradient of geography or bioclimate, and AI from Northern and Eastern Europe (Sweden, Estonia) through Germany, the Netherlands, Ireland and France to Mediterranean climate in Spain, which made it possible to assess large-scale ecological impacts of AI across European cereal-dominated agroecosystems (Fig. 2).

The project aimed to quantify the effects of AI on landscape composition and the taxonomic and FD of selected vertebrate (birds), insect (carabid beetles) and wild plant groups in European agroecosystems. AGRIPOPES also examined the effects of AI on the potential for biological control of pests on common crops, in relation to local and regional landscape composition. The main working hypotheses formulated at the start of the project were (1) AI leads to a loss of biodiversity and decrease in density in many organisms associated with the agricultural landscape, and this effect across Europe is similar to that found when examining regions within a country and (2) the loss of biodiversity due to AI leads to a simplification of food webs associated with biological control of insect pests, consequently entailing less efficient biological control.

The eight study areas were all agricultural regions where winter cereal was the dominant crop. Hence we chose winter wheat as a standard crop and were careful to standardize measurements of biodiversity and biological

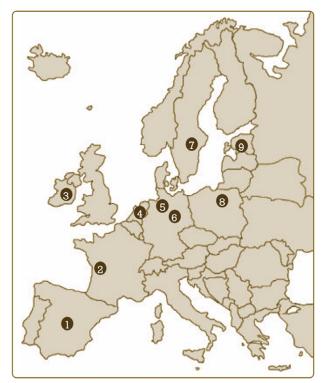


Fig. 2 Location of the 9 AGRIPOPES European study sites. All sites are named after the corresponding country, except for Germany, where two sites were located. 1: Spain; 2: France; 3: Ireland; 4: the Netherlands; 5: West Germany (Göttingen); 6: East Germany (Jenna); 7: Sweden; 8: Poland; 9: Estonia.

control potential across all field sites, whilst allowing landscape composition and AI to vary within, as well as between countries.

2.4.1 General Methodology

2.4.1.1 Selection of Farms and Fields

Given the diversity of agricultural structures in the different countries involved in AGRIPOPES, a farm was considered the ecological unit under study and was recognized as a set of one or more fields, separated by a distance of not more than 1 km, which were cultivated by the same farmer (owned or leased), and occupying an area not exceeding 1 km².

In each sampling area (one per country, except in the case of Germany, see Fig. 2), 30 farms separated by at least 1 km were selected, and considered to be representative of a gradient of regional AI. These farms were situated in regions between 30×30 and 50×50 km² in area, in order to limit variation

in within-region species pools and β diversity, and to avoid an excessive heterogeneity of landscapes and soil types within each study area. Farms were selected so that the range of cereal productivity in the sample was as large as possible, based on information obtained from the farmers on cereal yields in the years preceding the study, and with a representative and even distribution across the gradient of productivity in each area.

On selected farms (which could be conventional or organic agriculture farms) cereal had to be grown during biodiversity sampling, mainly winter wheat (80% of the fields). Only cereal crops were sampled on each farm. Sampled fields were never smaller than 1 ha in size nor irrigated. To assess the gradient of regional AI, the average cereal yield in the three previous years to sampling (2004–2006) was used. Sampling took place during spring and summer 2007 and was synchronized using the phenological stages of winter wheat in each study area. Winter wheat passes through well-recognized growth stages that are used by farmers to assess crop development. We timed the sampling of biodiversity components, i.e. plants, invertebrates and birds to coincide with the different growth stages of winter wheat (see Section 2.4.1.2 for details of each taxonomic group).

2.4.1.2 Selection of Points for Biodiversity Sampling

For each farm unit, five points distributed over no more than five arable fields were selected for sampling wild plants and carabids and estimating the biological control potential. Sampling points were located, whenever possible, in five different fields of the same farm and, when possible, always on winter wheat. When this was not feasible (less than 20% of all studied fields), winter barley was used instead. When there were fewer than five fields available, the points were stratified in proportion to size of sampled fields. Sampling points were placed parallel to an herbaceous (not woody) field edge and at 10 m distance from the edge towards the centre of the field. When more than one sampling point was placed in the same field, they were placed at opposite sides of the field. For the survey of breeding birds, one area of $500 \times 500 \text{ m}^2$ was selected around one of the sampled fields on each farm.

Plants were sampled in three $2 \times 2 \text{ m}^2$ plots parallel to the edge of the field and separated from each other by a distance of 5 m. In each plot, information on presence and abundance of all present species was collected. Sampling was performed once during the flowering to the milk-ripening stage of winter wheat. To further avoid phenological effects of sampling regionally, the sequence of farm surveys was randomized over the AI gradient within each study area.

Carabids were sampled using two pitfall traps per sampling point located in the middle of the two outer vegetation plots. The traps were protected with a covered with a plastic lid, suspended 1 cm above the ground by 100 mm nails, to avoid the effect of precipitation. Each pitfall trap was filled with 150 ml of ethylene glycol at 50%. Traps were opened during two periods of 7 days. The first sampling period occurred 1 week after the appearance of spikes of winter wheat and the second coincided with the milk-ripening stage of winter wheat. Specimens caught in pitfall traps were stored in 70% ethanol, and all the species caught in one trap randomly selected from each pair of traps were identified.

A modified version of the British Trust for Ornithology's Common Bird Census (Bibby et al., 1992) was used for the bird surveys. Given their mobility characteristics, birds were sampled over a $500 \times 500 \text{ m}^2$ square centred on the largest field of each sampled farm, in such a way that each spot within the quadrat was no more than 100 m from the surveyor's route. Surveys were conducted three times, at intervals of 3 weeks during the spring and summer 2007 (March-June) to cover the breeding time of farmland birds. Based on local information on the phenology of breeding birds, this meant that the start and end of the surveys varied from south to north reflecting local information on timing of known breeding seasons, e.g. in Spain surveys began in March, whilst in Sweden they started in April. Individuals of all ground-nesting farmland species showing some activity inside the square sample were counted. Breeding bird territories were determined considering the three visits and applying the following three categories, depending on species detectability and reproductive behaviour, and the number of visits in which they were recorded (see Geiger et al., 2010a for details):

- Category A: Easily detectable species, present throughout the spring, detected in at least two visits as showing territorial behaviour (song, call and defence of territory) in the same location.
- Category B: Species difficult to detect and species that were less likely to be detected during the three visits (e.g. long distance migrant species and strictly summer visitors), detected at least once showing territorial behaviour.
- Category C: Direct evidence was required of breeding activities to confirm a territory of these species.

2.4.1.3 Biological Control Potential

During the emergence of the first inflorescence of winter wheat, biological control potential was estimated by a 2-day experiment, which was repeated

once within 8 days (Ostman et al., 2001b). In the morning of the first day, three live pea aphids (Acyrthosiphon pisum) of the third or fourth instar were glued to plastic labels by at least two of their legs and part of their abdomen using odourless superglue. At noon, three labels were placed on the ground along the diagonal of each plot, at three of the five sampling points per farm. The labels were bent and placed, so the aphids were on the lower surface, protected from rain. Hence, at each farm there were 27 labels, with 81 aphids in total. The labels were checked at the start of the experiment and four more times over a 30 h interval: around 6 p.m. of the first day, at 8 a.m., 1 p.m. and about 6 p.m. on the following day, the exact time varying depending on the study area. The labels with the remaining aphids after the last counts were taken to the lab to check under stereomicroscopes whether remaining aphids could not have been removed by predators because they were covered with glue. The data from one or both of the rounds from each study area were used for the analyses, depending on whether the measurements were reliable or interrupted by, for example heavy rains.

2.4.1.4 Field-Level Intensification Variables

AI variables at the field scale were obtained through questionnaires conducted by personal interviews with all farmers owning the fields or responsible for their management. Spatial measures were obtained using digital maps processed in a Geographic Information System. The farmers' response rate was 98%, and information about yields and farming practices (pesticide and fertilizer use, ploughing and mechanical weed control regime) and farm layout (number of crops, percentage land covered by AES, field size) was collected.

2.4.1.5 Landscape-Level Intensification Variables

Four variables reflecting landscape structure and composition were estimated from aerial photographs with ArcView Patch Analyst 3.12 tool (Rempel et al., 1999) from 500 m radius circles around each sampling point and coinciding with the centre of the bird survey area: mean field size and its standard deviation, the percentage of land planted with arable crops within the area, and the Shannon habitat diversity index. For the latter, the following habitat classes were used (according to the definitions from the European Topic Centre on Land Use and Spatial Information; Büttner et al., 2000): continuous urban fabrics, discontinuous urban fabrics, cultivated arable lands, fallow lands under rotation systems, permanent crops, pastures, forests, transitional woodland-scrub and water (Table 1).

Response					
	Vascular plant species richness	Number of plant species detected in five sampling points (three $2 \times 2 \text{ m}^2$ plots each) distributed over focal fields within $1 \times 1 \text{ km}^2$ squares			
	Carabid richness	Number of carabid species detected in five sampling points (one pitfall traps each) distributed over focal fields within $1 \times 1 \text{ km}^2$ squares			
	Bird species richness	Number of wintering bird species detected in $500 \times 500 \text{ m}^2$ squares centred on focal fields			
Explanatory	/				
Field level	Focal field size	Size of each surveyed plot's focal field (ha)			
	Yield	Cereal grain obtained in focal field (tons/ha)			
	Amount of herbicide	Total amount of herbicide active ingredients applied on focal field (g/ha)			
	Frequency of herbicide	Number of herbicide applications on focal field during the previous agricultural year			
	Amount of insecticide	Total amount of insecticide active ingredients applied on focal field (g/ha)			
	Frequency of insecticide	Number of insecticide applications on focal field during the previous agricultural year			
	Amount of fungicide	Total amount of fungicide active ingredients applied on focal field (g/ha)			
	Frequency of fungicide	Number of fungicide applications on focal field during the previous agricultural year			
	N fertilizer	Total amount of nitrogen applied on focal field (kg/ha)			
	Frequency of tillage	Number of soil-disrupting operations carried out on focal field during the previous agricultural year			
Landscape level	Mean field size	Mean size of fields with arable crops within a 500 m radius circle centred on focal field (ha)			
	Substrate diversity	Shannon–Wiener index of agricultural, natural and artificial substrates within a 500 m radius circle centred on focal field			
	Percentage cover of arable crops	Percentage area of arable crops within a 500-m radius circle centred on focal field			
-					

 Table 1
 Main Response and Explanatory Variables Considered in AGRIPOPES

 Variable
 Description

Farm level	Area under AES	Percentage area of a particular farm under Agri-Environmental Schemes
	Number of crops	Number of different crop types in the farm
	Organic vs conventional	Whether a particular farm is under organic farming or not

 Table 1
 Main Response and Explanatory Variables Considered in AGRIPOPES—cont'd

 Variable
 Description

Explanatory variables are classified as field, landscape or farm-level variables.

3. LOCAL-LEVEL AND LANDSCAPE-LEVEL EFFECTS OF AI

Most studies quantifying AI effects on biodiversity and ecosystem functions have measured variables at several spatial scales. At the field scale, yield has been frequently used as a main output variable summarizing the effects of management practices such as agrochemical applications (Donald et al., 2006; Geiger et al., 2010a; Tilman et al., 2002). At the landscape scale, metrics describing heterogeneity due to configuration and composition are usually employed (Fahrig et al., 2011; Hiron et al., 2015; Teillard et al., 2014). The heterogeneity of configuration can be measured by mean field size or the total length of borders (Benton et al., 2003; Teillard et al., 2014). Landscape composition indices like Shannon–Wiener H' or the proportion of arable land are commonly employed (Chiron et al., 2010; Ekroos et al., 2010; Filippi-Codaccioni et al., 2010). However, configurational and compositional heterogeneity components are usually strongly correlated (Fahrig et al., 2011), which may confound landscape effects on biodiversity. In fact, few studies have attempted to disentangle the effects of the two types of heterogeneity (Hiron et al., 2015; Teillard et al., 2014), and further research would help designing more targeted landscape management prescriptions. As an example, Table 1 summarizes the variables measured to cover both field and landscape-scale components of AI, as well as farm-level intensification measures, in the AGRIPOPES project.

3.1 Local (Field)-Level Components of AI and Their Effect on Biodiversity

Field-level AI is associated with an increase in the amount and frequency of application of pesticides and synthetic fertilizers, which allows for an increase

in the density of sown cereal crops. The result is a significant increase in yields and a concomitant loss of spatiotemporal heterogeneity of crops. In turn, higher field productivity allows the abandonment of crop rotation systems, leading to landscape simplification (e.g. Benton et al., 2003).

Among the field-level intensification variables measured in AGRIPOPES (Table 1), yield and those related to pesticide application accounted most for variation in the various measures of biodiversity studied and are discussed later, although results on other important field-level factors like fertilizer input, tillage and sowing density are important and are also summarized.

In all study sites, winter cereal crops were the dominant land use. However there were important differences between the sites in their level of AI, which are reflected in the average values of the different intensification components considered (Figs. 3 and 4). At the field scale, the Irish study site was the most intensively managed one according to both yield and entrants such as nitrogen fertilizer and insecticides, followed by the East German site (Jena), which was the most intensively managed when considered from the perspective of herbicides (Fig. 3). Spain was situated at the opposite end of the continental intensification gradient with the lowest average values of yield and synthetic inputs. Consistently, sites with low entrant levels showed a much higher degree of other intensification practices at the field scale that allows for some compensation. This can be seen in the high frequency of tillage operations (an alternative to weed elimination through herbicide application) and sowing density shown not only by the Spanish area but also by the Swedish and Polish areas, where entrants were also relatively low.

With regard to landscape-scale intensification, Jena and Estonia had the largest field and farm sizes (Fig. 4). Along with the Dutch and Polish sites, they also contained the largest proportions of arable land in the landscape, as well as the greatest diversity of crops. The Polish, Spanish and Irish sites had the smallest field size, which probably suggests lower historical intensification levels and indicates a very strong intensification process per unit area in the case of Ireland. Finally, Spain had the lowest crop diversity, as expected for a continental Mediterranean region where soil and rainfall are particularly limiting for crops other than cereals.

3.1.1 Relationships with Yield

As a fundamental output variable in AGRIPOPES, yield was used as a proxy for AI. Yield had a strong negative influence on wild vascular plant, carabid beetle and ground-nesting farmland bird species richness across all study sites (Wald tests: plants: $\chi_1^2 = 141.42$, p < 0.001; carabids $\chi_1^2 = 23.33$, p < 0.001;

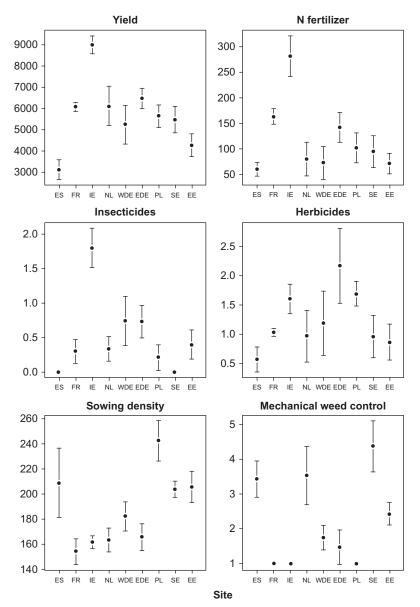


Fig. 3 Differences between study areas in the mean values of the field-level intensification variables measured in the AGRIPOPES project (see Table 1 for descriptions). Error bars indicate 95% confidence intervals. *ES*, Spain; *FR*, France; *IE*, Ireland; *NL*, Netherlands; *WDE*, West Germany (Göttingen); *EDE*, East Germany (Jena); *PL*, Poland; *SE*, Sweden; *EE*, Estonia.

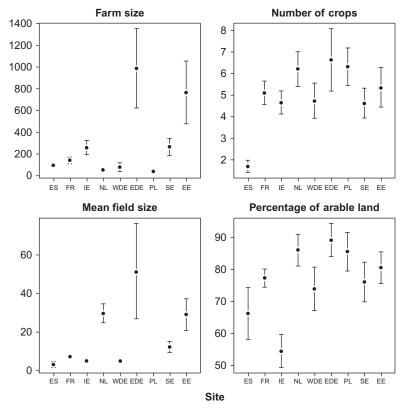


Fig. 4 Differences between study areas in the mean values of the landscape-level intensification variables measured in the AGRIPOPES project (see Table 1 for descriptions). Error bars indicate 95% confidence intervals. *ES*, Spain; *FR*, France; *IE*, Ireland; *NL*, Netherlands; *WDE*, West Germany (Göttingen); *EDE*, East Germany (Jena); *PL*, Poland; *SE*, Sweden; *EE*, Estonia.

birds: $\chi_1^2 = 7.33$, p = 0.007; regional landscape differences were controlled for by treating them as random factors using General Linear Mixed Model analyses; see Fig. 4). On average, an increase in cereal yield from 4 to 8 ton/ha resulted in the loss of five of nine plant species, two of seven carabid species and one of three bird species (Fig. 5A–C).

The overall negative relationships between yield and different components of biodiversity were not always consistent and these varied with country and taxa, i.e. wild plants and carabid beetles (yield×study area interaction: $\chi_8^2 = 36.87$, p < 0.001; $\chi_8^2 = 24.35$, p = 0.002; respectively). Comparison of the yield effects among study areas revealed that in some countries, yield had negative effects, but in other countries there was no

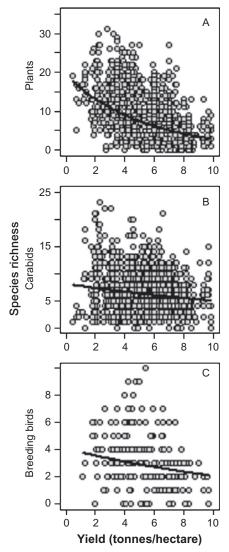


Fig. 5 Effects of cereal yield (tons/ha) on (A) wild plant species richness per sampling point (in three plots of 4 m²), (B) carabid species richness per sampling point (per pitfall trap during two sampling periods) and (C) ground-nesting bird species richness per farm (one survey plot of 500×500 m²). Trend lines were calculated using GLMM including the two surrounding landscape variables as covariates and field, farm and study area as nested random effects. *Based on Geiger et al. (2010a)*.

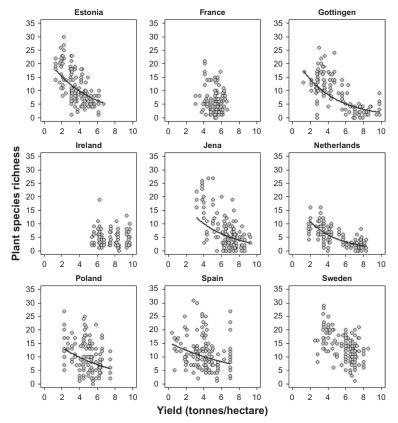


Fig. 6 Effects of cereal yield (tons/ha) on the number of wild plant species per sampling point (in three plots of 4 m²) in each of the study areas. Trend lines were calculated using GLMM including the two surrounding landscape variables as covariates and field, farm and study area as nested random effects (see Section 2.4.1). Trend lines were only plotted when the relationship was significant (p < 0.05). Based on Geiger, F., Bengtsson, J., Berendse, F., Weisser, W.W., Emmerson, M., Morales, M.B., Ceryngier, P., Liira, J., Tscharntke, T., Winqvist, C., Eggers, S., Bommarco, R., Pärt, T., Bretagnolle, V., Plantegenest, M., Clement, L.W., Dennis, C., Palmer, C., Oñate, J.J., Guerrero, I., Hawro, V., Aavik, T., Thies, C., Flohre, A., Hänke, S., Fischer, C., Goedhart, P.W., Inchausti, P., 2010a. Persistent negative effects of pesticides on biodiversity and biological control potential on European farmland. Basic Appl. Ecol. 11, 97–105.

relationship (Fig. 6). In two of the three study areas where no relationship was found, the variation in yield among fields and farms was much smaller than in the other countries, which probably explains the lack of significant effects.

Yield also had a negative effect on farmland bird FD (quantified using diet type, nesting behaviour, and foraging and migration strategy, see

Guerrero et al., 2011 for details of methodologies employed), and individual and breeding pair abundance across the continent (Guerrero et al., 2012). In the case of carabid beetles, their total abundance decreased with yield, but species richness and the abundance of some functional groups (small and medium-sized beetles and wingless carabids) did not show any response (Winqvist et al., 2014).

Species richness and abundance of overwintering birds was also negatively associated with yield (Geiger et al., 2010b), which indicates that AI might limit the resources available for birds in this particularly constrained period of the year, with direct impacts on survival and future reproductive performance (Newton, 1998). Notably, when these relationships were examined on a national basis, it was found that species richness in some instances increased with yield, e.g. wintering birds in Spain. This suggests that fields with higher yields sometimes could provide a larger resource base to overwintering birds (Morales et al., 2015). The Spanish study area contained some of the least intensively managed fields measured by the metrics of intensification used in AGRIPOPES (see Figs. 3 and 4), suggesting that higher yielding fields in relatively less intensified areas still provide sufficient and beneficial resources to overwintering birds. For example, the stubble remaining after harvesting of higher yielding fields might provide greater quantities of waste or spilt cereal seeds to species that rely on them during winter, such as skylarks and corn buntings (Morales et al., 2015).

The impacts of increased yield on the delivery of biocontrol were also negative. Here, the survival time of tethered aphids increased with increased yield ($\chi_1^2 = 6.85$; p = 0.009, see Fig. 7) and was therefore inversely related to predation. However, the effect of yield on aphid survival time was not consistent geographically, and differed among study areas (yield × study area interaction: $\chi_6^2 = 17.84$, p = 0.007).

Our results support the suitability of yield as a general measure of intensification and demonstrate its overall negative effect on biodiversity components. However, the individual effects of the different intensification factors summarized by yield are complex and warrant further examination. These intensification factors are measured through variables that describe field-scale management activities (see Table 1 and Figs. 3 and 4). To disentangle these effects, the importance of 13 variables considered as relevant components of AI were investigated (see Table 2). Here, we present and explore their main effects and discuss them in a broader context.

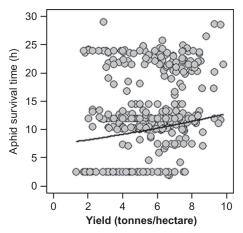


Fig. 7 Effects of cereal yield (tons/ha) on the median survival time of aphids (h). The trend line was calculated using GLMM including the two surrounding landscape variables as covariates and field, farm and study area as nested random effects. Based on Geiger, F., Bengtsson, J., Berendse, F., Weisser, W.W., Emmerson, M., Morales, M.B., Ceryngier, P., Liira, J., Tscharntke, T., Winqvist, C., Eggers, S., Bommarco, R., Pärt, T., Bretagnolle, V., Plantegenest, M., Clement, L.W., Dennis, C., Palmer, C., Oñate, J.J., Guerrero, I., Hawro, V., Aavik, T., Thies, C., Flohre, A., Hänke, S., Fischer, C., Goedhart, P.W., Inchausti, P., 2010a. Persistent negative effects of pesticides on biodiversity and biological control potential on European farmland. Basic Appl. Ecol. 11, 97–105.

3.1.2 Effects of Pesticides

Pesticides had consistently negative effects on the studied components of farmland biodiversity (see Table 2; Geiger et al., 2010a). Wild plant species richness declined as the frequency of herbicide and insecticide applications and the amounts of active ingredients of fungicides increased. Carabid species richness was negatively associated with the amounts of active ingredients of insecticide applied, whilst bird species richness declined with increasing frequency of fungicide application. Fungicide application rate is strongly correlated with the frequency of insecticide applications (Pearson's correlation coefficient r=0.732; p<0.001), and consequently it was difficult to disentangle their relative effects. In terms of ecosystem services, the predation rate of aphids measured in the field significantly declined as the amounts of insecticide applied increased, suggesting reduced activity or abundance of natural predators such as beetles and spiders.

The dominant effect of pesticides on species diversity and biological control potential was one of the key results emerging from the analysis of the field data collected in the AGRIPOPES project (Geiger et al., 2010a).

Response Variable	Explanatory Variable	Standardized Effect	χ²	<i>p</i> -Value
Number of plant	Mean field size	-0.094	6.09	0.014
species	% of land under AES	0.149	12.23	< 0.001
	Frequency of herbicide applications	-0.106	8.88	0.003
	Frequency of insecticide applications	-0.105	6.15	0.013
	Applied amounts of a.i. of fungicides	-0.262	31.45	< 0.001
Number of carabid	% of land under AES	0.062	6.31	0.012
species	Applied amounts of a.i. of insecticides	-0.061	10.87	0.001
Number of breeding bird species	Frequency of fungicide applications	-0.127	5.71	0.017
Median survival time	% of land under AES	-0.144	9.43	0.002
of aphids	Applied amounts of a.i. of insecticides	0.114	11.17	0.001

Table 2 Effects of Different Components of Agricultural Intensification on the Number

 of Plant, Carabid and Bird Species and Median Aphid Survival Time

The models were selected after considering 13 intensification variables using forward selection (backward selection produced identical models). All models included two landscape variables (mean field size and percentage of land planted with arable crops within a radius of 500 m), even if these had no significant effects (nonsignificant effects are not shown). Intensification variables were only included, if they had significant effects using the Wald test (p < 0.05). *AES*, Agri-Environmental Schemes; *amount of a.i.*, amount of active ingredients.

After Geiger, F., Bengtsson, J., Berendse, F., Weisser, W.W., Emmerson, M., Morales, M.B., Ceryngier, P., Liira, J., Tscharntke, T., Winqvist, C., Eggers, S., Bommarco, R., Pärt, T., Bretagnolle, V., Plantegenest, M., Clement, L.W., Dennis, C., Palmer, C., Oñate, J.J., Guerrero, I., Hawro, V., Aavik, T., Thies, C., Flohre, A., Hänke, S., Fischer, C., Goedhart, P.W., Inchausti, P., 2010a. Persistent negative effects of pesticides on biodiversity and biological control potential on European farmland. Basic Appl. Ecol. 11, 97–105.

The result was novel in that whilst it might be unsurprising to find negative effects of pesticides on biodiversity, they were found consistently at a pan-European scale, and despite decades of policy implementation regulating their controlled use.

In the particular case of birds, the application of fungicides was significantly and negatively associated with the total (combined) abundance of all breeding birds surveyed. In four breeding bird species—Yellow Wagtail, Whinchat, Corn Bunting and Quail—significant negative effects of the application of fungicides were found, and these were also strongly correlated to the application of insecticides.

The numbers of overwintering birds in the surveyed areas were also assessed (Geiger et al., 2010b). Notably, pesticides did not have any associations with the abundance of birds during winter. Similar results were obtained when the Spanish wintering bird data alone were analyzed (Morales et al., 2015). This suggests that the most important effect of insecticides or fungicides on the abundance of breeding birds acts through their impacts on food supply during the period in which most species feed their nestlings with insects. However, a potential effect of pesticide-coated seeds on seed-eating wintering birds cannot be discounted (López-Antia et al., 2015).

Organic farms and AESs had positive effects on plant and carabid diversity, but not on breeding birds. It is unclear why birds were not positively affected. Organic farming, whilst not intensive by measures relevant to AI, is an intensive, yet benign, form of management, and it is possible that breeding birds are disturbed by some organic management practices. Alternatively, a possible explanation is the large spatial scale at which pesticide pollution occurs, which inevitably leads to negative effects—even in areas where the application of these chemicals has ceased locally. Such large-scale impacts are especially relevant for highly mobile organisms such as birds, bees and butterflies (Clough et al., 2007; Rundlöf et al., 2008).

In Western Europe many birds of prey such as Kestrel, Sparrow Hawk and Buzzard showed large-scale declines between 1950 and 1970. After banning most of the responsible pesticides such as DDT and dieldrin, many of these species recovered rather quickly, whilst others with much slower life cycles, such as White-tailed Eagle, needed several decades (Newton, 1998). In the subsequent years the European Union developed policies to restrict the negative effects of pesticides, resulting in the EU's Sustainable Pesticides Directive in 2009. There were therefore good reasons to assume that the pesticide load of European agricultural landscapes had been substantially reduced. However, the results reported here and others recently published (e.g. Hallmann et al., 2014) do not support such an assumption.

3.1.2.1 Pending Questions in Pesticide Research

Although the results from AGRIPOPES are correlational and thus do not necessarily reflect cause–effect relationships, they consistently reveal a negative association, suggesting that the pesticide load on European farmland continues to impact biodiversity and relevant ecosystem services such as the biological control of harmful organisms. Therefore, landscape-wide experiments are needed to stringently test potential cause–effect relationships.

European farmers apply a large variety of chemicals to protect their crops against herbivorous insects, aphids and pathogenic fungi. An important, yet unanswered question concerns the identity of the active ingredients that were responsible for the observed negative relations between pesticides and biodiversity components. The most important groups of compounds are organophosphates, carbamates, pyrethroids and the recently introduced neonicotinoids. The last group of chemicals has recently received much attention and been the subject of intense scientific and societal debate.

The debate regarding the effects of neonicotinoids on biodiversity and ecosystem services is illustrated by the contrasting results of two reviews that appeared in 2014. Godfray et al. (2014) reviewed 259 peer-reviewed papers and concluded that the evidence for negative impacts on honeybee colonies was not yet convincing. In contrast, Van der Sluijs et al. (2015) reviewed 800 scientific studies and concluded that there was sufficient evidence for direct toxic effects on honeybees and for sublethal effects of concentrations that overlap with concentrations measured in nectar and pollen in the field (see also Rundlöf et al., 2015).

In 2014 the European Commission asked the European Academy of Sciences (EASAC) to analyse these contrasting views and to review the most recent scientific evidence on the use of neonicotinoids (EASAC, 2015). The resulting report reached some conclusions relevant in the context of this review. First, the existing debate was focussed almost completely on the survival of honeybee colonies. It is true that honeybees are extremely important pollinators, accounting for about 50% of crop pollination. However, wild solitary bees, bumblebees and hover flies perform the other 50% (Kleijn et al., 2015). The honeybee forms large colonies that provide a resilient buffer against forager losses, which explains the absence of net negative results on this exceptional species. However, bumblebees have much smaller colonies and solitary bees lack any form of buffering capacity to ensure pollination potential. Therefore, honeybee colonies do not provide a useful model system to assess the impacts on the broader group of wild crop pollinators.

Secondly, the EASAC (2015) report noted that the different approaches applied in the assessment (laboratory studies, field correlational studies and field experiments) had their own specific weaknesses, concluding that such weaknesses are inherent to the scientific analysis of complex ecological problems. Reviewing the combined evidence generated by the different studies, the report concluded that an increasing body of evidence supports the severe negative effects of the prophylactic use of neonicotinoids on non-target organisms (see also Gibbons et al., 2015). Furthermore, there was clear evidence for sublethal effects of very low concentrations over long periods.

These conclusions were supported by recent studies. Rundlöf et al. (2015) showed experimentally that neonicotinoids strongly affected solitary bees and bumblebee colonies, whilst honeybee colonies did not respond (probably due to colony resilience). Williams et al. (2015) demonstrated significant effects on honeybee queen reproductive organs resulting in decreased fertility (e.g. Hallmann et al., 2014). Therefore, the scientific evidence that neonicotinoids can have dramatic effects on nontarget insects and on insectivorous organisms such as birds or bats is increasing rapidly. However, similar information about the impacts of the other pesticides commonly applied in the European agricultural landscapes is still lacking. An assessment of these impacts using large-scale field experiments, longer time scales and including a broad variety of nontarget organisms is urgently required.

3.1.3 Effects of Fertilization

Inorganic fertilizer input is one of the main components of AI (Firbank et al., 2008; Tivy, 1990) with a number of potential direct and indirect effects on biodiversity (Robinson and Sutherland, 2002). Although artificial fertilization clearly contributes to the monopolization of primary production by agriculture, it also increases the global productivity of the system, and thus some mixed responses of biodiversity components might be expected. Geiger et al. (2010a) did not demonstrate any significant effect of inorganic fertilizers on the species richness of vascular plants, carabid beetles or birds. However, Guerrero et al. (2011) focused on the FD of birds using the AGRIPOPES data and showed a positive relationship between the diversity of some functional groups, such as diet type and nesting strategy, and the amount of N fertilizers probably related to the increased productivity of agroecosystems.

Studies at particular sites also provided mixed results. Aavik and Liira (2009, 2010) found in Estonian farmland that higher fertilization rates negatively affected small-scale plant species richness among taxa with a high tolerance to agriculture, but also among less tolerant ones (more associated with natural habitats). Such responses could be explained by the enhanced growth of cultivated cereals due to fertilizers, which in turn could favour

their ability to monopolize other resources such as light and water, outcompeting weeds and other wild plants. Guerrero et al. (2010) did not find such effects in the Spanish study area, where no response of arable weeds to the application of N, P and K was observed. These differences might be explained by the high prevalence of agricultural weeds at the Spanish sites, and these species are well adapted to local crop conditions. It is also likely that farmers apply fertilizers more intensively when sowing at higher density, so that the negative effect of sowing density (see in the following section) might mask the influence of fertilizers. Guerrero et al. (2010) found that carabid species richness was negatively influenced by inorganic N input, but positively affected by applied P. Previous studies on organic farming have indicated a negative effect of synthetic fertilizers on this group, possibly mediated by decreased prey abundance (e.g. Bengtsson et al., 2005), although the influence of different inorganic nutrients was not examined. The positive effect of P found by Guerrero et al. (2010) could result from an indirect relationship of P with other factors affecting carabids such as sward structure or microclimate (Holland, 2002). In summary, the effect of inorganic fertilizers on biodiversity components is less consistent across taxa and geography than that of other inputs such pesticides, which probably results from differences in local management and landscape configuration.

3.1.4 Effects of Tillage

Field ploughing and other mechanical operations cause soil disruption, thus becoming a source of disturbance for plants growing in fields. Ploughing was the traditional technique used to eliminate weeds until the use of herbicides was generalized (Tivy, 1990). In regions where 1 year rotation is still frequent, it continues to be the dominant procedure of weed control. For example, in central Spain fallow fields used to be employed in a 3-year rotation cycle, where fallow fields were kept as bare terrain until sown with a legume crop in the second year and then a cereal crop on the third (Suárez et al., 1997). As a result of AI, fallow fields are frequently ploughed and treated with herbicides throughout the agrarian season and then followed directly by the cereal crop. Such treatment not only eliminates plants but reduces resources for other organisms, such as food and cover for insects and birds (Robinson and Sutherland, 1999; Suárez et al., 1997). The retention of unploughed winter stubbles as an agrienvironmental measure, is extensively applied in different European countries (Suárez et al., 1997) and has benefited farmland birds in many regions (Wakeham-Dawson and Aebischer, 1998; Wilson et al., 1996). Despite the

positive effects of such measures, the frequency of ploughing and other mechanical operations, per se, was not significantly associated to the biodiversity components considered across the areas studied in AGRIPOPES (Geiger et al., 2010a), possibly due to the correlational structure of data. However, when the frequency of soil disruption was integrated with pesticide and fertilizer inputs to define an index of AI, it was found that there was a negative correlation with the species richness of plants and birds (but not carabids) at local, landscape and regional scales (Flohre et al., 2011a).

In the particular case of wintering birds (Geiger et al., 2010b), mechanical weed control did negatively affect species richness, though not abundance, presumably due to food reduction. Guerrero et al. (2010) found no significant relationship between mechanical weed control and plant, bird or carabid species richness in central Spain, which suggests that the frequent ploughing typical of this area, which exerts important deleterious effects on fallow-nesting birds (Morales et al., 2013), might be a spurious control measure of weed abundance.

3.1.5 Effects of Sowing Density

Field-level intensification, through the use of increasingly efficient machinery and the application of inorganic fertilizer, has allowed for an increase in the density of sown grains, and, subsequently, of yields (Firbank et al., 2008; Tivy, 1990). As humans increasingly monopolize the primary production in agroecosystems, increased sowing densities generate denser and more homogeneous sward structures (Benton et al., 2003; Robinson and Sutherland, 2002), sequestering resources and modifying habitats for plants, invertebrates and birds. At the European scale, the influence of sowing density on total bird abundance, the number of nesting territories, skylark abundance and the number of skylark nesting territories was examined along with other field and landscape-scale intensification components (Guerrero et al., 2012). Sowing density did not have a significant influence on the bird response variables, and its importance relative to that of other intensification components was minor. Crop vegetation structure has proved to be a relevant component of habitat suitability for farmland birds (Chamberlain et al., 1999; Donald, 2004; Donald et al., 2001; Eggers et al., 2011; Morales et al., 2008), yet these results were not supported by the AGRIPOPES findings. It should also be noted that not all sward structure features are directly determined by sowing density. For example, crop height, which is key for many ground-nesting birds, may vary with management, the wind and rain, and factors such as date of sowing (e.g. Eggers et al., 2011). Alternatively, the lack

of sowing density effects presented by Guerrero et al. (2012) might only indicate that this measure has poor explanatory capacity compared to other intensification factors considered, particularly yield as the main surrogate of the process. At local scales, sowing density negatively affected breeding bird and weed abundances at the Spanish study sites, consistent with expectations and results of previous studies.

3.2 Landscape-Level Components of AI and Their Effect of Biodiversity

Practices that lead to AI include a range of activities that occur in the landscape, that is, farmers specializing on one or few (arable) crops instead of mixed farming, converting perennial habitat (grassland) to arable fields, destroying edge habitats (e.g. hedges, field boundaries, buffer zones along creeks) and reallocating land to increase field size and make farms more compact. These activities further simplify landscapes by limiting the spatial and temporal variety of land-use types, ultimately increasing landscape homogeneity (Tscharntke et al., 2005).

In the AGRIPOPES project, several studies focused on how landscape context affected local biodiversity and community composition, and how those effects might impact upon the ecosystem service of biological control.

Flohre et al. (2011a) analyzed the diversity of vascular plants, carabid beetles and birds in agricultural landscapes in cereal crop fields at the field (n=1350), farm (n=270) and European region (n=9) scales, and partitioned diversity into its additive components, the alpha, beta and gamma diversity at each spatial scale. AI negatively affected the species richness of plants and birds at all spatial scales, but not carabid beetles (see Fig. 8). Local AI was closely correlated to beta diversity at larger scales up to the farm and region level and was hence a good indicator of farm- and region-wide biodiversity losses.

Winqvist et al. (2011) found that landscape simplification from 20% to 100% arable land reduced plant species richness by about 16% and cover by 14% in organic fields, and by 33% and 5.5% in conventional fields. For birds, landscape simplification reduced species richness and abundance by 34% and 32% in organic fields and by 45.5% and 39% in conventional fields. In contrast, ground beetles were more abundant in simple landscapes but were unaffected by farming practice. This Europe-wide study suggested that organic farming enhanced the biodiversity of plants and birds in all landscapes, but only improved the potential for biological control in heterogeneous landscapes.

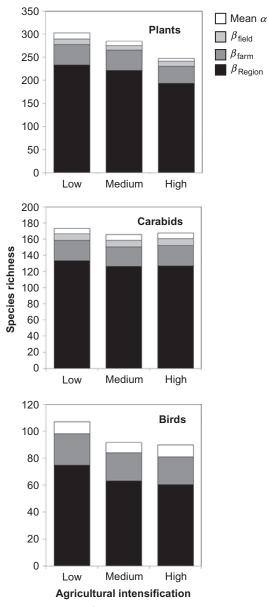


Fig. 8 Effect of agricultural intensification (AI) level (low, medium and high) on species richness of plants, carabids and birds, separating (α) diversity in the field and (β) diversity between fields, farms and regions. *Based on Flohre, A., Hänke, S., Fischer, C., Geiger, F., Bengtsson, J., Berendse, F., Weisser, W.W., Emmerson, M., Ceryngier, P., Liira, J., Tscharntke, T., Winqvist, C., Eggers, S., Bommarco, R., Pärt, T., Bretagnolle, V., Plantegenest, M., Clement, L.W., Dennis, C., Palmer, C., Morales, M.B., Oñate, J.J., Guerrero, I., Hawro, V., Aavik, T., Thies, C., Inchausti, P., 2011a. Agricultural intensification and biodiversity partitioning in European landscapes comparing plants, carabids, and birds. Ecol. Appl. 21, 1772–1781; Flohre, A., Rudnick, M., Traserc, G., Tscharntke, T., Eggers, T., 2011b. Does soil biota benefit from organic farming in complex vs. simple landscapes? Agric. Ecosyst. Environ. 141, 210–214.*

Guerrero et al. (2012) studied the response of ground-nesting farmland birds to AI in six European countries and found that landscape factors accounted for most of the variation of ground-nesting farmland bird breeding pair densities. In the case of breeding Skylarks, field factors were found to be more important. These results suggest that landscape management for farmland bird conservation is most important, but that field-level practices are also relevant, as crop yield and bird densities were negatively related.

Although belowground biodiversity is an important part of the agroecosystem, studies focussed on the interacting effects of local and landscape intensification on the belowground detritivore community, including bacteria, fungi, collembola and earthworms are rare. Flohre et al. (2011b) found that landscape context plays a significant role in shaping the effects of organic vs conventional farming on soil biota. Earthworm species richness in simple landscapes, where predation pressure is reduced, was enhanced by organic farming, whereas in complex landscapes conventional farming enhanced earthworm species richness. As the same pattern has been found for microbial carbon biomass, earthworms might play a role in enhancing microbial biomass.

The impacts of the various components differ considerably among bird species. Many species are affected by mean field size in the area around the sampled field. Mean field size had negative effects on the abundance of Skylark, Yellowhammer, Whinchat and Marsh Warbler (Guerrero et al., 2012), illustrating the important role of field margins and less intensively exploited areas in-between the fields. Field size had positive effects on lapwing densities, probably due to the preference of this species for open areas (Klomp, 1954).

In conclusion, AESs need to expand the view from the local field and farm to the landscape and region level to improve their effectiveness. Taxonspecific responses also need to be considered in conservation efforts.

3.3 Farm-Level Components of AI

As mentioned earlier, the farm scale represents an administrative and decision-making level that translates into specific types of field management as well as landscape features. For example, a farmer's decision to consolidate land, thus enlarging fields, to convert to organic farming with its more diverse crop rotations, or to devote a certain surface area to AES generates changes both at field and landscape scales. The response of biodiversity and ecosystem functioning to the application of organic instead of conventional

farming is discussed in Section 4 later. Here, we discuss farm-level responses of biodiversity components to field-scale intensification.

Flohre et al. (2011a) addressed this question by partitioning diversity of plants, birds and carabids across European sites. They found that field-level intensification explained 12.83–20.52% of the variation in farm-level beta diversity of the three groups, which indicated important differences in environmental conditions between farms. The response of beta diversity to local intensification was even stronger when the regional scale (i.e. study area) was considered. In the case of birds and carabids, beta diversity increased at the farm-scale with increased field-level intensification. Therefore, and contrary to initial expectations, field-level intensification did not necessarily homogenize local communities. Rather, these communities retained their compositional differences, and it is likely that this is due to the relative heterogeneity of farm-scale management practices. It is thus necessary to better understand intensification effects on biodiversity patterns of different groups and at multiple spatial scales so that more efficient AES can be designed.

3.4 Comparing the Importance of Local- vs Landscape-Level Components of AI on Biodiversity and Ecosystem Services

Our results clearly support the negative influence of landscape-level intensification factors on biodiversity and ecosystem function, as well as the effects of landscape structure on biodiversity responses shown by other authors (Concepción et al., 2012; Tscharntke et al., 2005; Whitthingham, 2007). However, they also highlight the importance of field-level management. Therefore, the question of how biodiversity and associated ecosystem services change in response to the relative importance of intensification at each scale remains pertinent. Different studies carried out in the AGRIPOPES context have specifically addressed this question.

Guerrero et al. (2012) employed a PCA and variance partitioning analysis, and showed that field-level factors explained a smaller amount of variation when the overall abundance of ground-nesting farmland birds was considered (2.9%) than when the density of breeding territories was examined (13.1%). However, landscape-scale factors always explained more variation (11.3% and 20.1%, respectively). This effect was stronger in the particular case of the skylark (from 12.9% to 18%), for which field-level intensification outweighed landscape-scale factors (11.2%). These results indicate that the influence of field-level intensification on farmland birds is particularly important for open or simplified habitat specialists, like the skylark, which rely on the arable area of fields for both foraging and breeding.

In their study of wintering birds across Europe, Geiger et al. (2010b) also found an important influence of landscape-scale intensification: farmland bird abundance was higher in areas with more stubble pasture and green manure crops, as well as in heterogeneous landscapes comprising arable crops as well as grasslands, whilst species richness was higher in areas with more pasture. This is consistent with later results of Morales et al. (2015) for the Spanish study site, where landscape-scale factors explained 70.79% of the variation in wintering bird community composition vs the 29.21% explained by field-level intensification.

In contrast, field-level intensification was particularly important for plant FD in Spain (Guerrero et al., 2014). Plant species richness decreased linearly with field-level intensification, but showed no response to landscape-level intensification. Community-weighted mean and diversity of the different functional traits considered (plant height, specific leaf area, seed mass and flowering onset) were affected by intensification at the field scale in nonlinear ways, but no influence of landscape-level intensification was found. More specifically, the diversity of all functional traits decreased with AI at the field scale, although specific leaf area and seed mass followed marked nonlinear relationships, showing the strongest decreases at medium to high intensification levels, and an increase at low values. In contrast, the greatest loss of species was not accompanied by similar changes in FD and vice versa (Carmona et al., 2016). In the lowest levels of field-scale intensification, species were lost without a decrease in FD, which implies a reduction in functional redundancy of communities, and thus in their resistance to environmental change (Mouillot et al., 2013). At intermediate levels, FD decreased rapidly with the loss of few species, that is, the community had become more functionally vulnerable due to reduced redundancy. At the highest end of the field-level intensification gradient, no important FD reductions were observed, which suggests that these poorer communities were characterized by intensification-resistant species and traits. Similarly, functional vulnerability of arable plant communities due to species loss showed a nonlinear positive relationship with field-level intensification, whilst no landscape-scale effect was found (Carmona et al., 2016).

Winqvist et al. (2014) also addressed the influence of scale on FD, in this case for carabid beetles. They showed that functional traits (size, diet and type of dispersal) in these ground beetles responded differently to local and landscape management. Field-scale intensification (yield) reduced

overall carabid abundance, although it did not affect abundance of small and medium-sized beetles, or that of wingless carabids. Species richness was not affected either, although the increased proportion of arable land in the landscape increased overall carabid abundance, an effect that was driven by an increase of omnivorous beetles. Total carabid species richness did not increase with the proportion of arable land, although richness of wingless beetles did increase with that variable.

These results support the view that landscape-scale factors are the main drivers of biodiversity responses in highly mobile groups like birds and carabids, but that this influence may be relatively reduced by field-level factors, e.g. for birds that rely on the crop field for both foraging and nesting (Butler et al., 2007; Guerrero et al., 2012). However, for sessile organisms like arable plants, field-level management seems to be the key factor influencing their populations, community structure and FD.

4. ORGANIC-CONVENTIONAL COMPARISONS

Comparing conventional farming to organic practices provides an approach to quantify the effects of agricultural management intensity on the diversity of farmland systems, because organic farming is often regarded as less intensive. AESs in Europe differ between countries, but organic farming is a more uniformly understood agri-environmental measure, as insecticides, herbicides and synthetic fertilizers are forbidden. Organic farming combines the best environmental practices expected to preserve a high level of biodiversity and natural resources, thereby also contributing to human welfare (e.g. Council Regulation (EC) No. 834/2007). Consequently, various AES, and organic farming in particular, have been widely advertised and supported (Bengtsson et al., 2005; Gibson et al., 2007; Kleijn et al., 2006, 2009). Some reports have shown, however, that organic farming practices might not be effective (Kleijn et al., 2001, 2006), or that the effects vary among organism groups and landscapes (Hiron et al., 2013; Tuck et al., 2014). For example, organic farming appeared to be more efficient in conserving aboveground than belowground species diversity (Tuck et al., 2014). Other studies contend that the overall benefit of organic farming for biodiversity compared to the costs related to lower yields is ambiguous, and the cost efficiency is not properly linked with the reality of ecological processes (Gabriel et al., 2013; Kremen, 2015). In AGRIPOPES, we examined the biodiversity of 151 farms occurring across a subset of five study regions (Sweden, Estonia, the Netherlands, Western Germany and Eastern Germany), reflecting the high prevalence of organic farms in these regions (33%). Among the 151 farms studied, 51 were organically managed. We found that environmental conditions and associated biodiversity responses of our focal groups did not always differ between organic vs conventional farms, although there were positive effects of AES, which included organic farming, on diversity of plants, carabids and biocontrol potential across the nine study regions (Geiger et al., 2010a). Winqvist et al. (2011) found that organic farming had higher levels of species richness in plants and birds, whilst carabids showed no response to farming system, and biological control potential only increased with organic farming in heterogeneous landscapes. These results show that a detailed analysis of various organism groups at different trophic levels and delivering a range of ecosystem services in organic farming should include several other factors, such as landscape context and taxon-specific responses, to accurately estimate the potential advantages of organic practices over other types of farming.

4.1 Landscape Context

In addition to the intensive application of agrochemicals, contemporary agricultural landscapes have experienced a severe loss of the area and connectivity of natural and semi-natural habitats, which impose another major pressure on biodiversity (Benton et al., 2003; Fahrig, 2003; Liira et al., 2008a). One of the main challenges in evaluating the effect of organic farming relative to conventional farming practices is the frequent correlation between these two groups of factors of farming practices and landscape characteristics. Conventional farming systems and related land-use intensity are often accompanied by larger fields and homogeneous landscapes, whilst organic fields are smaller and located in remote areas with an increased representation of natural habitats around (e.g. Bengtsson et al., 2005; Hole et al., 2005; Norton et al., 2009). In AGRIPOPES, the aim was to avoid potentially confounding effects of farming practice and landscape characteristics by examining biodiversity patterns and biocontrol potential in organic and conventional farms along a gradient of landscape complexity (Geiger et al., 2010a; Winqvist et al., 2011).

The relative benefits of organic farming on biodiversity have been found to be highest in simple homogeneous landscapes characterized by a high proportion of croplands (Batáry et al., 2011; Tuck et al., 2014). Indeed, such an interactive effect of landscape structure and farming practices has also been observed for plants (Roschewitz et al., 2005), birds (Dänhardt et al., 2010; Hiron et al., 2013) and various insect groups (Holzschuh et al., 2007; Rundlöf et al., 2008). Nevertheless, the analysis of the pan-European biodiversity dataset within the AGRIPOPES framework revealed that positive effects of organic farming on the diversity of plants and birds did not differ between complex and simple landscapes (Geiger et al., 2010a), whereas the species richness of ground beetles did not depend on landscape characteristics nor land-use practices (Winqvist et al., 2011). Furthermore, biocontrol potential was highest in the organic farms of complex landscapes. In contrast, in homogeneous landscapes biological control potential was higher in conventional fields (Thies et al., 2011; Winqvist et al., 2011). These mixed effects of organic farming in simple and complex landscapes suggest that biodiversity and related ecosystem services, such as biocontrol, may in fact show a differential response to land-use and landscape structure depending on the studied ecosystems. Future AES and related monitoring programmes should therefore place more emphasis on enhancing and evaluating the potential of ecosystem services in addition to biodiversity per se, in order to maximize the outcome of environmentally sound management practices. The relative role of farming practices on biodiversity is also location-specific at the field scale. For example, the positive influence of organic farming on plants has been most evident and widely reported at the field scale (Gabriel et al., 2013; Gibson et al., 2007; Hole et al., 2005), a result consistent with the findings observed in AGRIPOPES (Geiger et al., 2010b; Winqvist et al., 2011). Hiron et al. (2013) also found a positive field-scale response of birds to organic farming. Conventional farming tends to have impacts in habitats adjacent to focal fields, e.g. due to leaching of agrochemicals (de Snoo and Van der Poll, 1999; Kleijn and Snoeijing, 1997), whilst the effects of organic farming on plant species richness in field boundaries and in other habitats adjacent to agricultural land have been less apparent (Clough et al., 2007; Gibson et al., 2007). Indeed, the analysis of field margin vegetation (Aavik and Liira, 2009, 2010; Aavik et al., 2008) showed that large- and local-scale landscape structure and the presence and abundance of source habitats for species were the main determinants of species richness and composition, whilst only a relatively low amount of variation in species patterns was explained by farming type (organic and conventional). Nevertheless, as the results of AGRIPOPES have shown, focusing only on species richness might not provide sufficient detail regarding the effects of land-use intensification on biodiversity in and around agricultural land. In contrast, in-depth analyses within groups of species with different traits and conservation value would significantly advance our understanding of agriculturerelated drivers of biodiversity change.

4.2 Functional and Taxon-Specific Responses of Biodiversity to Farming Practices

A recent meta-analysis concluded that organic farming increases overall species richness approximately by 30% (Tuck et al., 2014), but that different organisms vary in their responses to organic practices. In accordance with this, various studies of bird (Birkhofer et al., 2014), insect (Birkhofer et al., 2014), plant (Boutin et al., 2008; Gabriel and Tscharntke, 2007; Petersen et al., 2006) and microbial (Hartmann et al., 2015) communities in agricultural systems show that responses of biodiversity to farming practices are largely taxonspecific and/or varies among functional groups (see also Section 3.1). Indeed, such taxon-specific responses of biodiversity to organic and conventional farming systems were also observed in AGRIPOPES, as described earlier.

Plants, whose habitat conditions are directly influenced by the application of agrochemicals, show a clearly different response to AI depending on the functional group considered. Enhanced nitrogen and phosphorus concentrations facilitate the growth of competitive plants, and herbicides affect large-sized species, so that resulting communities mainly consist of grasses and other generalists, as well as fast-growing ruderal plants (Marshall and Moonen, 2002). Indeed, boundaries of organic fields may support a higher diversity of hemerophobic and habitat specialist species at local scales (Aavik and Liira, 2009, 2010; Manhoudt et al., 2007), whilst species tolerating agricultural management, such as nitrophilous and disturbance-tolerant species persist in the boundaries of all farming types (Aavik and Liira, 2009). In an analysis of landscape-scale vegetation, Liira et al. (2008b) showed that landuse intensity decreased the species richness of two growth forms-sedges and pteridophytes. However, in the same study, Liira et al. (2008b) showed that an increased number of crops caused an increase in the richness of annuals and a decrease in the richness of perennials. Thus, the responses of different plant functional groups to organic and conventional farming are highly complex and depend on the scale (local vs landscape) of the study.

Changes in plant productivity and plant species composition induced by intensive agricultural practices are expected to covary with the composition of species at other trophic levels due to altered interactions among species groups, e.g. plant–pollinator interactions (Gabriel and Tscharntke, 2007). Nevertheless, whilst the cover, species richness and functional group composition of plants were observed to vary between farming systems with contrasting management (Aavik and Liira, 2010; Geiger et al., 2010a; Winqvist et al., 2011), Winqvist et al. (2014) observed no trait-specific response of ground beetles to organic and conventional farming. Instead, continuous variables describing farm-level land-use intensity, such as yield, were significantly better predictors of the trait composition of ground beetles.

The results obtained from a large-scale comparison of organic and conventional farming systems within the framework of AGRIPOPES suggest that whilst organic methods often benefit biodiversity and related ecosystem services, the relative effects of farming system may also depend on landscape context. In addition, the oversimplification of evaluating only species richness may lead to underestimation of the role of land-use intensification on biodiversity. More in-depth analyses of species responses within different functional groups may help to target future AES towards species groups with higher conservation needs and/or to related ecosystem services.

5. LINKING AI TO BIODIVERSITY AND ECOSYSTEM SERVICES

5.1 General Model

Using structural equation modelling (SEM), it was possible to examine the respective contributions of agricultural land use, plant diversity and predator (carabid) diversity on the biological control potential measures presented in Geiger et al. (2010a). The SEM method makes it possible to disentangle the indirect pathways leading to biological control (Fig. 9).

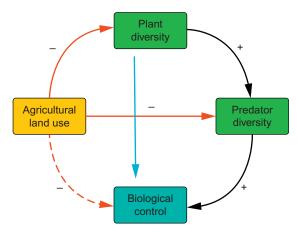


Fig. 9 General model for predicting the influence of agricultural land use on biological pest control. Biological control can be affected directly by predator diversity, which in turn may be affected by agricultural land use (AI), either through changes in plant diversity or through other unknown mechanisms (direct path). There may also be a direct effect of plant diversity (independent of predator diversity).

5.2 Study Area, Biodiversity Surveys and Biocontrol Experiment

Using a subset of AGRIPOPES data from six regions (FR, IR, JE, NL, PL, SW) with 90 sampling points per region, we assessed the relative importance of agricultural land use, plant diversity and predatory carabid diversity on aphid survival rates. We excluded Estonian and Göttingen data due to extremely high predation rates (nearly all aphids were gone after 36 h). Given our study design, the SEM approach requires seven variables per sampling point represented as nodes (Fig. 10A and B). These consisted of four variables reflecting measures of AI: three local intensification variables (the application of mineral fertilizer measured as N kg/ha, the frequency of herbicide use and the frequency of insecticide use) and one landscape-scale variable (the percentage of arable land measured in a 1000 m buffer area). We also included two variables characterizing biodiversity at the field scale (mean plant and carabid species richness per sampling point). Aphid survival was treated as a binomial response variable, i.e. the number of aphids predated as a proportion of the number provided at the start of the experiment. Sampling points where any of the seven required data records were missing were excluded, resulting in a dataset of 436 sampling points.

5.3 Structural Equation Modelling

The initial full SEM contained all possible paths (including correlations among AI variables) with the exception of the effect of herbicide application frequency on biocontrol, which was the least justifiable relationship. Both initial full and the simplified SEMs consisted of three models analyzed together with the piecewise SEM (Lefcheck, 2016) in R (R Development Core Team, 2015):

- (1) mean plant species richness per sampling point analyzed with a General Linear Mixed Model based on a normal distribution with the nlme package (Pinheiro et al., 2015);
- (2) carabid species richness per sampling point analyzed with a General Linear Mixed Model based on a normal distribution with the nlme package;
- (3) aphid survival per sampling point analyzed with a Generalized Linear Mixed Model based on a binomial distribution with the lme4 package (Bates et al., 2014).

In all three models, we used the following hierarchical random structure: sampling points were nested in fields, fields were nested in farms and farms

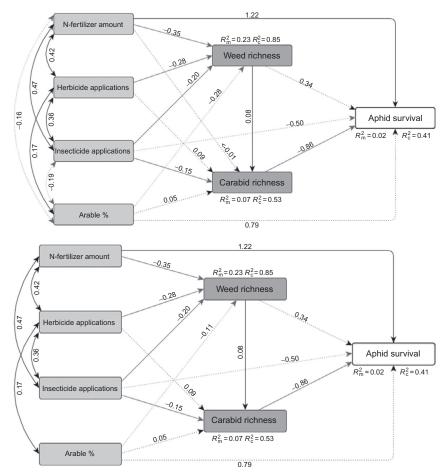


Fig. 10 Initial full (A) and final fitted (B) SEM models for aphid survival (Fisher's C statistic for initial full and final fitted models: $C_2 = 3.04$, p = 0.218; $C_6 = 8.86$, p = 0.181, respectively). Standardized path coefficients are presented for richness models (*grey*), unstandardized path coefficients for binomial aphid survival model (*white*) and Pearson's *r* correlation coefficients for correlations among agricultural intensification variables (*light grey*). For all three models per SEM marginal (R_m^2) and conditional (R_c^2) *R*-squared are shown. Negative path *arrows* are in *dark grey*, and *dotted lines* mean non-significant effects.

were nested in regions. The fixed effects and correlations that were tested are shown in Fig. 10A and B. The initial full SEM was simplified with manual backward selection by excluding the least significant variable considering all model coefficients until reaching the minimal SEM based on AIC (Shipley, 2013).

5.4 Results and Discussion of SEM

Aphid survival was negatively affected by predator diversity, which was in turn (weakly) affected by plant species richness. The number of plant species was negatively affected by local AI variables and by AI at the landscape scale (percentage arable land) (Geiger et al., 2010a). The negative effect of insecticide applications on the predators indicates a mechanism by which AI decreased biological control potential, i.e. that insecticide use reduced the diversity of carabid beetles (Fig 10A and B; cf. Geiger et al., 2010a). Among the direct effects of AI variables on aphid survival retained in the reduced model, the amount of N fertilizer was significantly positive, whilst application of insecticides (negative) and percentage of arable land in the surroundings (positive) were nonsignificant. The synthetic inputs (pesticides, herbicides and fertilizer) affected the measure of pest control indirectly via the number of plant species in the field or via the diversity of carabids in the field (insecticide input). Insecticide applications may also have affected other invertebrates that are prey for carabid beetles, additionally decreasing carabid richness and indirectly enhancing aphid survival. Thus the spectrum of prey and also its abundance is reduced in fields managed by using insecticides.

Although the focal variables (percentage of surviving aphids survived and median survival time of aphids) were highly correlated ($R^2 = 0.58$, p < 0.001), there were some differences in interpreting the outcomes of our experiment. The number of surviving aphids is a general measure for the effectiveness of the aphidophagous predators in the field and for the attractiveness of the glued aphids. The time when half of the aphids where removed, or the median survival time of aphids, is a measure of the predators' detection rate of the aphids. The shorter this period then the faster the aphids were found and consumed.

Our results show that biological pest control of aphids was more than the simple effects of land use on pest control. It is a multitrophic system where different stages are affected by land use in a range of different ways. The decrease in biological control potential with AI was mediated by decreases in predator diversity related to increased insecticide use, and to lower weed richness because of herbicide and fertilizer applications. In turn, more ground-dwelling predators reduced the number of aphids in our experiment, as indicated by the effect of predator diversity. The number of weed species seemed to be an important part of the system because of its mediating position in our model. Many of our AI measures influenced biological control of cereal aphids indirectly via weeds and their positive effect on carabids. These findings seem to be repeatable at a European scale, which makes them relevant for a general understanding of biological control in agricultural landscapes altered by the agricultural policy of the European Community.

6. CONCLUSIONS

AI has been related to biodiversity declines both globally and notably within the agroecosystems of the European Union, where biodiversity has developed and been shaped by agricultural land-use history. Such biological impoverishment may compromise the delivery of ecosystem services important for human welfare. However, a comprehensive review of the response of different components of biodiversity and ecosystem services to the AI process resulting from the European Union agricultural policy has remained lacking.

In this chapter, we have synthesized the findings from a large-scale pan-European study investigating the combined effects of AI and large-scale climatic gradients on taxonomic and functional biodiversity of key taxa (birds, carabid beetles, arable plants), as well the biological pest control ecosystem service provided by biodiversity in European agroecosystems.

We found that the three-service providing taxa studied (birds, carabid beetles, plants) were negatively related to AI when measured in terms of yield, but when these effects were examined in different regions across Europe the results were variable. Diversity often had negative relationships to yield, but in some regions there was no relationship, probably because intensification has coevolved with developments of varieties and technologies. On the other hand, and for some individual (input) measures such as fertilizers, we even found positive effects. However, diversity was generally distinctly negatively related to the use of pesticides (herbicides, insecticides or fungicides) and fertilizer application, although the relationships varied extensively between organism groups and regions. Notably, we also found clear negative effects of AI on the biological control potential of aphids, an important pest of cereals. Using a SEM model, we linked the decrease in biological control potential to a decrease in diversity of predatory insects (carabid beetles) and to pesticide use.

With regard to landscape-wide impacts, AI clearly had negative relationships with plant and bird diversity from farm to landscape scales, whilst relationships with beetles were more ambiguous. Notably, communities were not homogenized in intensively farmed landscapes, which may be attributed to variation in farming practices among farms in such landscapes. The effects of AI varied not just with region and taxa, but were further complicated when large-scale comparisons of organic and conventional farming systems were taken into consideration. Whilst organic methods and other AESs generally seem to benefit biodiversity and related ecosystem services, such as biological pest control, the relative effects of especially organic farming varied from none to large and depended on, for example the organisms studied and landscape context.

Several policy-relevant results have emerged from the project. Most important is that AESs, which mainly target single sites and are uncoordinated among farmers and landowners, need to expand from the local field and farm to the landscape (several neighbouring farms) and regional levels to be effective conservation tools. Also, the results strongly suggest that AESs need to be more taxon specific, as different components of biodiversity react differently to such measures. Finally, the large-scale results highlight that the CAP-supported AI not only has affected many components of biodiversity negatively but also has had negative effects on a critical ecosystem service like biological pest control, on which sustainable farming relies. Conventionally, pesticides are used to help produce food by controlling a range of pest species that have economic impacts on food production. Prevailing wisdom considers their use to be essential, yet here we have shown pervasive and compelling evidence demonstrating that pesticides have detrimental impacts on a range of biodiversity components at a pan-European scale. Recently, there have been calls to halt the *routine* and *indiscriminate* use of antibiotics in agriculture (Neff et al., 2015); our results indicate that it would be of particular importance to substantially decrease or halt the *routine* and *indiscriminate* use of pesticides in many European agricultural landscapes as well.

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