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Reconciling food production and biodiversity in farmlands: the role of agricultural intensity and its spatial allocation

Concilier production agricole et biodiversité : le rôle de l'intensité et de son allocation spatiale

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Articles

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Teillard F, Allaire G, Cahuzac E, Léger F, Maigné E, Tichit M (2012). A novel method for mapping agricultural intensity reveals its spatial aggregation : Implications for conservation policies. *Agriculture, Ecosystem and Environment*, 149, 135-143. (Chapter V).

Tichit M, Puillet L, Sabatier R, **Teillard F** (2011). Multicriteria performance and sustainability in livestock farming systems: functional diversity matters. *Livestock Science*, 139, 161-171.

In preparation

Teillard F, Jiguet F, Tichit M (Resubmitted to *Journal of Applied Ecology*). The response of farmland bird communities to agricultural intensity as mediated by intensity aggregation. (Chapter VII).

Teillard F, Jiguet F, Tichit M (In revision in *Biological Conservation*) Mixed benefits of compositional and configurational heterogeneity on farmland birds according to their habitat specialization. (Chapter VI).

Teillard F, Tichit M (In preparation) Optimal targeting of agricultural intensity allocation to reconcile production, economy and biodiversity at the countrywide scale. (Chapter VIII).

Teillard F, Sabatier R, Doyen L, Tichit M (In preparation). Multi-dimensional assessment of a grassland based livestock farming system: trade-off between production and wildlife conservation.

Participation to conferences

Oral communications

Teillard F, Allaire G, Cahuzac E, Léger F, Maigné E, Tichit M (2011). The spatial aggregation of agricultural intensity. What opportunities for policy targeting? Farming System Design /

World Congress on Conservation Agriculture, Brisbane (Australia). Article in the conference proceedings.

Teillard F, Jiguet F, Allaire G, Doyen L, Tichit M (2010). Production intensity and biodiversity? Bird abundances along an intensity gradient of dairy livestock farming system. Annual Meeting of the European Association for Animal Production, Heraklion, Greece. Book of abstracts.

Teillard F, Allaire G, Jiguet F, Tichit M (2010). Biodiversity in agro-landscapes: measuring bird response to intensity with simple vs. aggregated intensity indicators. Innovation and Sustainable Development in Agriculture and Food, Montpellier, France. Book of abstracts.

Future (accepted) oral communications

Teillard F, Tichit M (August 2012). Planning production intensity and its spatial allocation for reconciling livestock production and biodiversity – a model-based scenario approach. Annual Meeting of the European Association for Animal Production, Bratislava, Slovakia.

Teillard F, Jiguet F, Tichit M (September 2012). The land sparing strategy influences the relationship between biodiversity and agricultural intensity in European farmlands. EcoSummit, Colombus, USA.

Posters

Teillard F, Sabatier R and Tichit M (2009) Modeling trade-offs between agricultural production and bird conservation in grassland farms. Ecological Engineering from Concept to Applications international congress, Paris, France.

Teillard F, Sabatier R and Tichit M (2009) Coviability between farming and avifauna in a grassland agro-landscape. Farming System Design international symposium, Monterey, USA.

Communication articles

Teillard F, Muriel T (In press) Elevage et biodiversité : une relation complexe arbitrée par l'intensité de production. Ethnozoothechnie.

Organization of the manuscript

This thesis is organized in two Parts.

- The Part A is a general presentation of the work that I conducted during my Ph.D. It describes the scientific literature background, which leads to the statement of the research question (Chapter I). Then, I present the case study and general methodological aspects of the work (Chapter II). Chapter III summarizes the main results and brings basic interpretations. The limitation, implications and perspective of the results are finally discussed (Chapter IV).
- Part B is formed of four scientific articles (Chapters V to VIII). They contain further methodological details, the complete results of the Ph.D., and specific elements of comparison and discussion in relation to the literature.

Part A

General Presentation

Chapter I

Introduction

1 Agricultural intensity and the trade-off between production and biodiversity

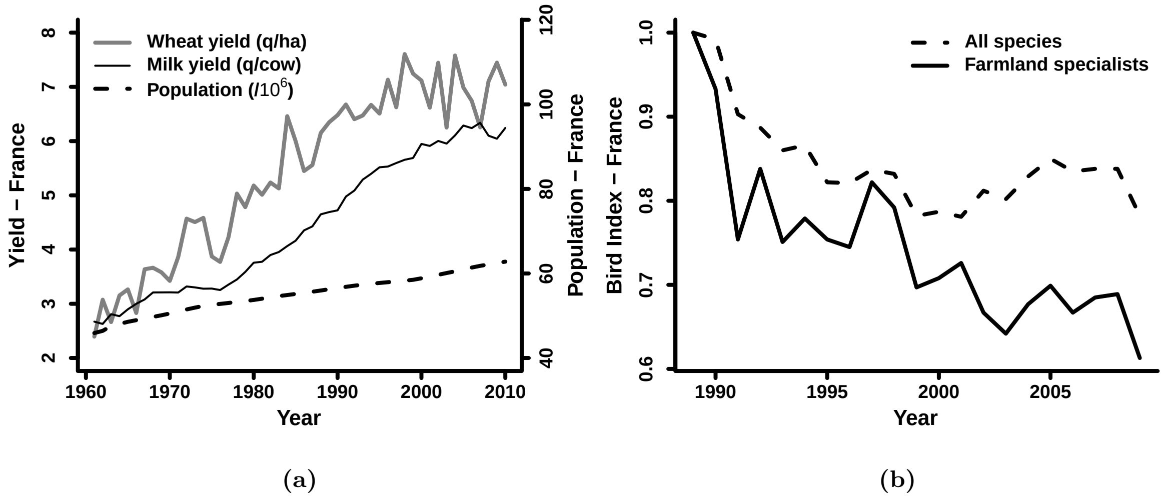
1.1 Two conflicting objectives

The consequences of agricultural intensification over several decades reveal how agricultural intensity affects the trade-off between food production and biodiversity conservation. *Intensification* is the process of agricultural change (that has occurred during the past half-century) that increases *intensity*, *i.e.* production or utilization *per* unit of cultivated land.

Intensification led to very significant yield improvements, worldwide, for both crop and livestock. It increased *per-capita* production, reduced hunger, and improved nutrition (Tilman *et al.*, 2002; FAO, 2011). In France, wheat and milk yields increased threefold from the 1960s to today (Fig. I.1a), yet the French population has only grown by a factor 1.4. The adoption of new varieties and technologies increased yield, high yielding crop varieties reached full potential with the greater use of inputs (*e.g.*, fertilizers, pesticides) and irrigation, and agricultural works gained efficiency with mechanization (Tilman *et al.*, 2002). At the landscape level, unproductive and low productive land uses have been converted, and spatial structure has been homogenized to permit easier machinery use (Tscharntke *et al.*, 2005).

All the changes related to agricultural intensification have produced major environmental damage (Matson, 1997). Agricultural intensification has been an important cause of biodiversity erosion through habitat destruction and alteration. In tropical regions, agricultural conversion led to the loss and fragmentation of pristine forest, habitat that hosts most of the region's endemic biodiversity (Fearnside, 2005; Nepstad *et al.*, 2009). In Europe, intensification of existing agricultural landscapes altered habitats and caused direct negative impacts on biodiversity (McLaughlin & Mineau, 1995; Firbank *et al.*, 2008). The large scale monitoring of bird populations is evidence of this decline, showing how specialists of the farmland habitat have been particularly affected (Fig. I.1b, for France; Gregory *et al.* 2005 for the UK). Biodiversity is not the only threat of agricultural intensification to the environment. Livestock are among the main causes of anthropogenic greenhouse gas emissions (Steinfeld *et al.*, 2006); the concentration of farming activities involves large amounts of chemical inputs and wastes that cause air and water pollution (Vitousek *et al.*, 1997; Carpenter *et al.*, 1998). To address the general question of the impact of agriculture on natural ecosystems, biodiversity is an interesting focus because it drives the ecosystems dynamics.

Past intensification of agriculture focused on, and successfully achieved, increased production. Now, the challenge for agriculture is to improve its sustainability: satisfying the food demand, while mitigating its harm to biodiversity. This challenge is magnified by the rising food demand caused by worldwide human population growth (Alexandratos, 1999). Moreover, increase in the global *per-capita* income leads to dietary shifts toward higher consumption of animal products, which needs more resources to be farmed (McMichael *et al.*, 2007; Wirsenius *et al.*, 2010). Such pressure to increase food production may further promote intensification; however, the rate of yield increases have recently been dropping in developed countries (Fig. I.1a). The intensification model itself shows several limitations, such as pesticide resistance and dependence on oil. Most importantly, further intensification will likely accentuate the production/biodiversity conflict whereas these two objectives are mutually dependent (Le Roux *et al.*, 2008).



(a) (b)

Figure I.1: An illustration of how past agricultural intensity drives the trade-off between production and biodiversity. (I.1a) Evolution of wheat yield, milk yield, and population in France, between 1960 and 2010. Yield data: FAO (2011); population data: INSEE (2011). (I.1b) Evolution of bird population indices between 1989 and 2009. Index values were set to 1.0 in 1989. Data: French Breeding Bird Survey (see Jiguet *et al.* 2011).

1.2 Two mutually dependent objectives

About 40% of the global land area is currently dedicated to agriculture (Ramankutty *et al.*, 2008). It represents a substantial area of semi-natural habitat for wildlife species that cannot be ignored. Conversely, biodiversity benefits agriculture through ecosystem services[1]. This mutual dependency means agricultural lands must be involved in biodiversity conservation along with natural reserves (Rosenzweig, 2003).

In Europe, the conservation value of farmland has long been understood. Farming is historically old, which provided the time for a large pool of species to adapt and specialize to agricultural land uses (Benton *et al.*, 2002). Extensively managed, permanent grasslands are among the habitats with high biodiversity levels (Baldock *et al.*, 1993; Bignal & McCracken, 1996). Extensive agricultural use (*e.g.*, moderate grazing, mowing) positively affects biodiversity (Watkinson & Ormerod, 2001) and it is necessary to maintain grassland habitats, otherwise lost by ecological succession. In certain countries of Eastern Europe, the abandonment of agricultural activities is as equally threatening to biodiversity as agricultural intensification (Verhulst *et al.*, 2004). To achieve conservation in tropical regions, focus is on mitigating the detrimental effects of agricultural expansion and obtaining minimally-impacted reserve areas. Recent studies, however, advocate for more research that addresses conservation in human-modified landscapes (Chazdon *et al.*, 2009). Some ancient production systems can sustain many species associated with native forests (Ranganathan *et al.*, 2008). In return, biodiversity could benefit agriculture.

High biodiversity is needed for the health and resilience of ecosystems. It also contributes to the capacity of ecosystems to sustain services (Loreau *et al.*, 2001; Tilman *et al.*, 2001). As an agroecosystem, agriculture is a provider of ecosystem services (*e.g.*, provisioning of food, fiber, and fuel). As a human activity, agriculture is also a user of ecosystem services (Zhang *et al.*, 2007). Several ecosystem services are essential to agricultural production: soil structure and fertility, nitrogen fixation (supporting services), pollination, and pest control (regulating services). Past models of agricultural intensification overlook the importance of ecosystem services and rely on technologies to fulfill some of their function (*e.g.*, pesticides instead of natural predation or parasitoidism). Intensive agriculture degrades biodiversity and has negative impacts on ecosystem services (Giller, 1997; Kremen *et al.*, 2002; Bianchi *et al.*, 2007). Substituting some of the impacted services by technology, like soil fertility and pollination, would have a tremendous economic cost (*e.g.*, manual pollination, hydroponic crop production).

Agricultural intensification may be able to keep increasing production to satisfy food demand in the short-term. Its detrimental effects on biodiversity and ecosystems, however, would ultimately undermine ecosystem services and threaten production in the long-term (Foley *et al.*,

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[1] Ecosystem services are defined as the direct or indirect benefits of ecosystems for human societies and they can be categorized into supporting, provisioning, regulating and cultural services (MEA, 2005)

2005; Rockström *et al.*, 2009; Foley *et al.*, 2011). A biodiversity collapse could occur in the future, causing, in turn, a collapse in production. Solutions to reconcile the production and biodiversity objectives are thereby crucial.

1.3 What are the solutions for reconciliation?

Two general visions on how to solve the conflict between agricultural production and biodiversity exist. *Sustainable intensification* seeks to improve water and nutrient use efficiency, in order to keep increasing yield, while limiting environmental damages (Cassman, 1999; The Royal Society, 2009; Godfray *et al.*, 2010). *Agroecology* relies on ecosystem services to partially achieve the functions that are currently fulfilled by chemical inputs (Altieri, 2002). Both options are likely to be adequate, either in combination or according to agroecosystem type and intensity context. Agroecology principles are effective in certain tropical agroforested systems (Perfecto *et al.*, 1996). In Europe, however, agricultural systems are more intensive and artificial, needing bigger transformations to restore functional agroecosystems. European agriculture, however, has a powerful means for transformation: agricultural policy.

The Common Agricultural Policy (CAP) of the European Union (EU) historically only supported production. To meet the sustainability challenge, Agri-Environment Schemes (AESs) were introduced in the CAP in 1992. AESs propose subsidies to farmers, based on voluntary compliance, for adoption of management practices that reduce environmental pollution, and preserve biodiversity and landscapes. These practices correspond to extensification at local and landscape scales, such as reduced fertilization, reduced stocking rates in grasslands, use of hedgerows, and strip maintenance. In 1999, the CAP added a second “pillar” (in addition to production support) that was dedicated to rural development. AESs have not managed to elicit extensification through significant changes in agricultural practices, yet they permitted to limit further intensification (CNASEA *et al.*, 2008). Although a significant budget increase occurred after 1992, the effectiveness of AESs at reversing the biodiversity decline in farmland is debatable (Kleijn *et al.*, 2006; Le Roux *et al.*, 2008; Princé *et al.*, 2012). This lack of effectiveness may be explained by uptake rates of AESs that are too low and too spatially diffuse to elicit biodiversity benefits on a large scale (Kleijn & Sutherland, 2003; Whittingham, 2007). Most schemes are not well adapted to the agro-ecological context because they have large application gradients where their effects on species can vary (Whittingham *et al.*, 2007). Spatial targeting has been suggested as a way to improve the effectiveness of AESs, which adapts and concentrates measures at points where they are expected to yield the highest environmental benefits (Piorr *et al.*, 2009; Uthes *et al.*, 2010).

2 Adjusting intensity and its allocation to meet production and conservation objectives

Because it drives the trade-off between production and biodiversity, agricultural intensity is a variable that should be adjusted in space to reconcile two objectives. A quantitative description of the effects of agricultural intensity and its spatial allocation on biodiversity is needed for effective reconciliation; it will help to determine the intensity range that should be targeted by conservation policies and the intensity allocation strategy that should be adopted.

2.1 The land sparing/land sharing framework

A debate has been ongoing in the literature about two contrasting intensity allocation strategies aimed at reconciling production and biodiversity: land sparing and land sharing (also called wildlife-friendly farming) (Cassman, 1999; Trewavas, 2001; Fischer *et al.*, 2008; Perfecto & Vandermeer, 2008). Green *et al.* (2005) formalized this debate by developing a theoretical model that answers the following question: *for a given level of agricultural production, what allocation of area to different land uses maximizes biodiversity level?* This model relies on the shape of the relationship between biodiversity and agricultural yield (Fig. I.2). A convex relationship hypothesis (full curve) means that biodiversity exponentially decreases with yield (*i.e.*, loss of either unfarmed or very extensively managed habitats is the most detrimental to biodiversity). Under this hypothesis, land sparing would be the best strategy. Part of a region would be spared at nul or very low intensity to fulfill conservation objectives, while the remaining area would compensate for the loss of productive land with high yielding intensive farming. On the other hand, a concave relationship hypothesis (dashed curve) means that biodiversity declines slowly, as intensity starts to increase, but becomes severely impacted at high intensity levels. Under this hypothesis, land sharing would be the best strategy. The entire region would be farmed at moderate intensities because they could achieve satisfying performances for both production and biodiversity criteria.

Land sparing follows a logic of segregation for production and biodiversity objectives, while land sharing follows a logic of integration. The two strategies can also be linked to reconciliation visions described in Section 1.3. Land sparing requires sustainable intensification that mitigates negative externalities, such as pollution outside cultivated areas (*e.g.*, nitrogen runoff, eutrophication) and global impacts (*e.g.*, greenhouse gas emissions, climate change). Conversely, land sharing creates opportunity to reintegrate biodiversity and ecological processes into agroecosystems, as suggested by the principle of agroecology and multifunctionality.

Empirical evidence about the shape of the relationship between biodiversity and intensity is still limited. In Ghana and India, Phalan *et al.* (2011b) found most bird and tree species displayed convex negative relationships with yield. In Europe, Kleijn *et al.* (2009) found more

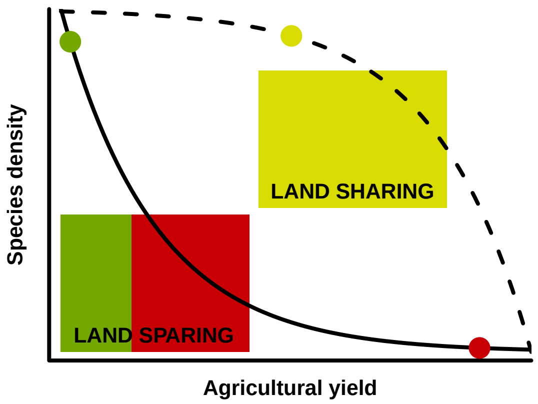


Figure I.2: Consequences of the shape of the biodiversity/intensity relationship for sustainable intensity allocation (adapted from Green *et al.* 2005). Under the hypothesis of a convex relationship (full curve), the land sparing strategy (segregation of the intensity extremes) is best. Under the hypothesis of a concave relationship (dashed curve), the land sharing strategy (the entire region at moderate intensity) is best.

convex negative relationships between plant species richness and nitrogen input intensity. Relying on the Green *et al.* (2005) model, several authors concluded, from these convex relationships, that land sparing would be the best land use allocation strategy (Gabriel *et al.*, 2009; Phalan *et al.*, 2011a; Godfray, 2011). The Green *et al.* (2005) model is a good starting point to explore sustainable intensity allocation strategies, yet it could benefit from some important improvements. In particular, the spatial arrangement of agricultural intensity is likely to have an effect on biodiversity, which has not been tested in previous studies that address the biodiversity/intensity relationship.

2.2 The importance of intensity spatial arrangement

Allocation strategies, as considered by the Green *et al.* (2005) model, only include intensity levels and their relative proportions. The model does not account for spatial arrangement. Land sparing, however, corresponds to an aggregated arrangement because the two intensity extremes are segregated in space. Several studies show that mobile species are impacted by neighbor land uses, and, thus, by the spatial arrangement of land uses and their intensity. Two main mechanisms, taking place at different scales, can explain this effect.

The first mechanism concerns the role of different land uses of the agricultural landscape during the life cycle of a species. For some species, different land uses are needed to fulfill essential, complementary requirements (*e.g.*, nesting and foraging habitats, Blomqvist & Johansson 1995). Other land uses produce resources with different qualities, such as food resources with different levels of availability (*i.e.*, Brotons *et al.* 2005). In both cases, complex spatial arrangement provides species access to different resources within their habitat range (Dunning *et al.*, 1992). Conversely, some land uses can be dangerous to species, and their scattered distribution within a complex spatial arrangement is detrimental (Fahrig *et al.*, 2011). They include land uses with either high predation risk or intensive land uses, where input use has a direct negative impact on non-targeted organisms (Freemark, 1995; Bradbury & Kirby, 2006). The impact of spatial arrangement of resources, and dangers, takes place on a relatively short time scale (one reproductive season) and, thus, at a relatively small spatial scale (the individual habitat range).

The second mechanism concerns the impact of different land uses during species metapopulation dynamics (Macarthur *et al.*, 1962; Levins, 1969). Agricultural landscapes can be striking examples of the metapopulation conceptual framework, such as when cultivated land has fragmented the original, natural habitat (Andrén, 1994; Verboom *et al.*, 1991). Some species can only persist in patches of semi-natural habitats: their metapopulation dynamics consist of local population dynamics within these patches and spatial dynamics of migrations and colonizations amongst them. For such species, the most important properties of land use spatial allocation are when large enough patches, to sustain local populations, and patches close enough, to sustain the metapopulation dynamics, are available (Hanski, 1994; Steffan-Dewenter, 2000). Even for species persisting in spared patches of semi-natural habitats, the intensity of the surrounding agricultural matrix impacts their dispersal abilities and their metapopulation dynamics (Sutcliffe *et al.*, 2003; Donald & Evans, 2006). Furthermore, this agricultural matrix can be used as lower quality habitat in some cases (Baillie *et al.*, 2000; Perfecto & Vandermeer, 2002). When this occurs, a source-sink dynamic exists between semi-natural and agricultural habitats, and the quality of the agricultural matrix also becomes important (Foppen *et al.*, 2000). The land sparing allocation strategy confines biodiversity objectives to natural habitats that serve as reserves. For species having metapopulation dynamics, however, the intensity of the surrounding agricultural matrix also has great impact on their viability. The impact of spatial arrangement, through metapopulation dynamics, occurs over several generations and, therefore, involves larger spatial scales (Devictor & Jiguet, 2007).

2.3 Policy targeting to influence intensity allocation

A corollary question of the land sparing/sharing model is: *how can policy measures effectively promote the production/biodiversity reconciliation and influence land use allocation?* Knowing the shape of the biodiversity/intensity relationship and the effect of intensity spatial arrangement is necessary to determine the intensity level that should be targeted by conservation measures and, therefore, be most effective. Policy targeting could also be a way to adjust the spatial allocation of intensity.

Under the hypothesis of a convex relationship, conservation policies promoting less intensive practices will elicit higher biodiversity benefits within extensively managed areas (Fig. I.3). Measures targeted at extensive areas may be more effective because they reinforce the quality

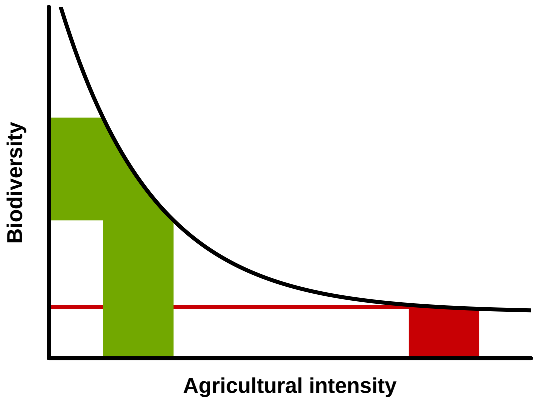


Figure I.3: Consequences of the shape of the biodiversity/intensity relationship to determine the effectiveness of conservation policies (adapted from Kleijn & Sutherland 2003). Under the hypothesis of a convex relationship, policies promoting extensification are more effective at improving biodiversity in extensive areas than in intensive areas.

of areas that already have high biodiversity and resource potential (Kleijn & Sutherland, 2003; Whittingham, 2007). Conversely, measures could seek to improve the quality of agroecosystems in intensive areas where negative impacts on biodiversity are most severe (Primdahl *et al.*, 2003). Whether extensive or intensive areas are the most suitable for policy targeting will remain unanswered as long as the biodiversity/intensity relationship is unknown. Moreover, the effects of the spatial arrangement of intensity need to be understood to achieve effective policy targeting. At the landscape scale, local conservation measures that promote extensive management practices often yield higher biodiversity benefits when the surrounding landscape is intensive (Tscharntke *et al.*, 2005; Concepción *et al.*, 2008). However, this effect can vary between cropland and grassland landscapes (Batáry *et al.*, 2011a). At larger scales, conservation measures seem more effective when the surrounding small region (Gabriel *et al.*, 2010) or country (Kohler *et al.*, 2007; Batáry *et al.*, 2010) is less intensive.

Most AESs use untargeted measures; therefore, the distribution of their uptake in space cannot be controlled. Uptake is based on voluntary compliance results in a rather random distribution, although some bias is observed. In particular, uptake tends to be higher where the adaptation cost for the measure is lower (Osterburg *et al.*, 2001; Kleijn & Sutherland, 2003). Conversely, the spatial targeting of conservation measures could be a way to adjust the spatial allocation of intensity in order to promote either the segregation of extreme intensities (land sparing) or more heterogeneity with moderate intensities (land sharing). Knowing the spatial distribution of agricultural intensity is, therefore, important for targeting policies and modulating intensity allocations. For instance, Gabriel *et al.* (2009) mapped the proportion of organic farms in the UK and found that land sparing allocation at the country scale could be achieved by targeting the measures that endorse organic conversion in the areas where it is already aggregated.

3 Adjusting intensity and its allocation: from concept to practice

The biodiversity/intensity relationship, land sparing/sharing allocations, and the targeting of policy measures are connected. Together, they provide a conceptual framework for the reconciliation of production and biodiversity objectives in farmlands. How should one apply this conceptual framework to real cases?

3.1 Defining the land sparing and land sharing allocations

In real cases, scale, ecosystem type, and species influence the definitions of land sparing and land sharing intensity allocations.

Land sharing corresponds to a variability of land uses at a finer spatial scale (or grain) than in land sparing (Fischer *et al.*, 2008). Indeed, several land sharing practices favor landscape heterogeneity: crop diversity, field margins, tree edges and clumps (Phalan *et al.*, 2011a). How does one determine the level at which heterogeneity is considered land sparing? For instance, a field margin could be considered land sparing on a field scale, and either a grassland field or a tree clump could be considered land sparing on a farm scale. Phalan *et al.* (2011a) argue that both land sparing and land sharing should not be considered the same at different scales. The authors suggest that spared habitat should be sufficiently large to support viable populations. The land sparing definition, therefore, depends on species.

In tropical ecosystems, most of the endemic biodiversity occurs in the pristine forest (Brooks *et al.*, 2002), an unexploited land cover which intensity can thereby be considered zero. Recent and brutal transition from forest to land uses exploited with moderate intensity, led to the loss of most species. In Europe, high biodiversity levels are found in several unexploited land areas (*e.g.*, mountains, forests, wetlands, littoral zones). In contrast to tropical ecosystems, land use exploited with moderate intensity can also show very high biodiversity levels (*e.g.*, permanent grasslands, Bignal & McCracken 1996). These two contrasted examples show that the type of ecosystem can influence what should be considered reserve habitat in a land sparing strategy. In Europe, most unexploited habitats already belong to reserves. Agricultural habitats represent a central conservation issue: they cover more than half of the non-urban area (CLC, 2006) and their farmland specialist species are at high risk from intensification (Section 1.1). Farmland species can not live in the unexploited part of the intensity gradient. The definition of a spared habitat is thus unclear: grasslands could be considered land sharing because they combine production and biodiversity objectives, or, alternatively, as land sparing because they also host unique biodiversity that should be preserved.

The land sparing and land sharing definitions are justified by the details (scale, species, ecosystem) of each case study. Adopting a scale relevant for both intensity allocation and policy targeting allows one to discuss the implications of results with regard to the above elements. The biodiversity/intensity relationship is the other component of the land sparing/sharing model that could vary according to each case study.

3.2 Computing the biodiversity/intensity relationship

What intensity measure?

Agricultural intensity can be defined as increased utilization or productivity of land (Netting, 1993), therefore, either output-oriented (production) or input-oriented (utilization) measures can be used to describe it (Turner & Doolittle, 1978; Dietrich *et al.*, 2012). In the Green *et al.* (2005) model, yield is used to compute the biodiversity/intensity relationship. Yield provides direct insight into the trade-off between food production and biodiversity, yet management intensity is more likely to impact biodiversity.

Several studies have used yield as an indirect proxy of farming intensity because it reflects industrialization, specialization, and/or input use (Donald *et al.*, 2001; Herzog *et al.*, 2006a). Either the concave or convex negative density-yield functions of Green *et al.* (2005) represent either tolerant or less tolerant species to farming intensity. Although yield correlates with management intensity, it also depends on pedo-climatic conditions. Most studies, therefore, address the effect of farming intensity on biodiversity in ways that directly focus on management practices, in order to reveal their impact and understand the underlying mechanisms. Management practices can be intensive on two main input components: the chemical (or more generally matter) inputs and the work inputs. Chemical input intensity concerns the higher use of fertilizers, pesticides, irrigation or seed at the field and farm scale (Giller, 1997). Management practices related to chemical inputs are interesting because they have a strong impact on biodiversity, but also on other environmental issues. In Europe, work inputs mainly relate to mechanization, which largely explains the important landscape simplifications associated with intensity (Björklund, 1999). With large sets of practices and landscape properties, a wide range of indicators have been used to address the effects of intensity on biodiversity. We summarize some of these indicators, along with their mechanisms of impact on bird species (Table S.s1 in Appendix).

Indicator categories focusing on particular practices or landscape properties (Table S.s1 in Appendix) are ecologically relevant because they involve underlying mechanisms of impact on biodiversity. They address, however, single mechanisms, and their narrow definition of intensity make them less relevant from an agricultural viewpoint. In particular, they are less related to yield, which is a disadvantage when studying the trade-off between food production and biodiversity. Some studies have tried to build indicators that combine several intensity components. Herzog *et al.* (2006a) normalized nitrogen input, livestock density, and pesticide input into one indicator, and Pointereau *et al.* (2010) computed a score that accounted for management, crop diversity, and landscape components. The main difficulty for composite indicators is determining how to combine the different components. Every method has disadvantages: The min/max normalization method produces relative values only; and a scored value requires arbitrary computational choices. The strength of such indicators, however, is that they simultaneously account for several ecologically relevant components and provide a more complete vision of intensity that is likely more closely related to yield.

What biodiversity measure?

Birds have been widely used in studies addressing the effects of agricultural intensity on biodiversity. Both the temporal trends and the spatial distributions of bird populations strongly react to agricultural intensity (Fuller *et al.*, 1995; Donald *et al.*, 2001; Gregory *et al.*, 2004). The sizes of bird habitats and the durations of their life cycles are relevant to the temporal and spatial scales of changes in agricultural activities. Because of their high position in trophic networks, birds integrate variation from lower levels. Among all bird species, farmland birds are particularly affected by intensification (Gregory *et al.*, 2005; Wretenberg *et al.*, 2007; Jiguet *et al.*, 2011). In Europe, farmland birds are a rich pool of species specialized in the open agricultural habitat, thereby making them very sensitive to modifications of this habitat.

Among bird taxa, several species traits influence their response to agricultural intensity. Large intensity gradients can correlate with land use gradients (*e.g.*, transition from natural forest, to pasture, and then to croplands). In such cases, the main habitat of a species, within the land use gradient, will evidently influence the species response to intensity. Within farmland bird species, agricultural intensity can have different influences on grassland and arable species (Atkinson *et al.*, 2002; Batáry *et al.*, 2007a; Fischer *et al.*, 2011a). The degree of habitat specialization also influences species responses to intensity. Specialist species are often more sensitive to agricultural intensity (Devictor *et al.* 2008; Doxa *et al.* 2010, see Fig. I.1b). One explanation is that specialists are generally more sensitive to habitat disturbance because their adaptation abilities are lower than those of generalist species (McKinney & Lockwood, 1999). Specialists, however, can partly benefit from intensity when it favors the homogeneity of their habitat (Chiron *et al.*, 2010; Filippi-Codaccioni *et al.*, 2010). Finally, species trophic level can also influence their response to intensity because intensity may not have the same effect on the availability of all food resources (Atkinson *et al.*, 2005). Accounting for species traits, when computing the relationship between bird communities and agricultural intensity, is important because it can reveal mechanisms underlying the intensity effects (McGill *et al.*, 2006).

4 Research question

The introduction above shows a rich theoretical background on agricultural intensity allocation solutions that reconcile production and biodiversity. Few studies either provide empirical evidence for biodiversity/intensity relationships, n=or test theoretical allocation solutions in real contexts. Literature also reveals important elements of the debate on intensity allocations. Agricultural intensity integrates several properties and mechanisms of impact on biodiversity. Not only should the effects of intensity levels and their relative importance be considered, but also their spatial arrangement. The effect of intensity is likely to vary across species, according to their traits. Linking the debate on intensity allocation to spatial targeting of policy measures could benefit both the effectiveness of policy and its transition to sustainable allocation. The general research question of this thesis is:

Is the spatial allocation of agricultural intensity an effective lever to promote the reconciliation between production and biodiversity objectives in farmlands?

Four steps answer the above general research question (see also Fig. I.4):

- (**Q1**) *What is the spatial distribution of agricultural intensity at the national scale?* We created an intensity indicator that integrated several components. It had to be relevant to all the main types of agricultural production in order to display a broad intensity gradient and be computable for most French agricultural areas. We developed a method to estimate the value of this indicator at higher resolution than what is available through existing agricultural databases. We tested the hypothesis that agricultural intensity is spatially structured at country scale.

- (**Q2**) *What is the effect of land use and its heterogeneity on farmland birds?* We computed the response of a farmland bird community to (1) a gradient of land uses, from grassland to arable land; and (2) heterogeneity between these two land uses. We tested the hypothesis that heterogeneity negatively impacts specialist species and positively impacts generalist species.

- (**Q3**) *What is the effect of agricultural intensity and its spatial aggregation on farmland birds?* We computed the biodiversity/intensity relationship of different trait-based groups that composed a farmland bird community. We tested if this relationship varied between groups and if it was influenced by spatial aggregation of intensity.

- (**Q4**) *What allocations of agricultural intensity favor reconciliation between production and farmland birds?* We modeled the consequences of changes of the French intensity allocation, given the trade-offs between intensity, and production, economic, and biodiversity performances. Relationships between these three criteria and intensity were calibrated from real data. We used an optimization procedure to reveal those allocations that maximize the benefits of one criterion, while minimizing the cost on the others. Finally, we describe the intensity changes needed to reach the optimal allocation from the current allocation.

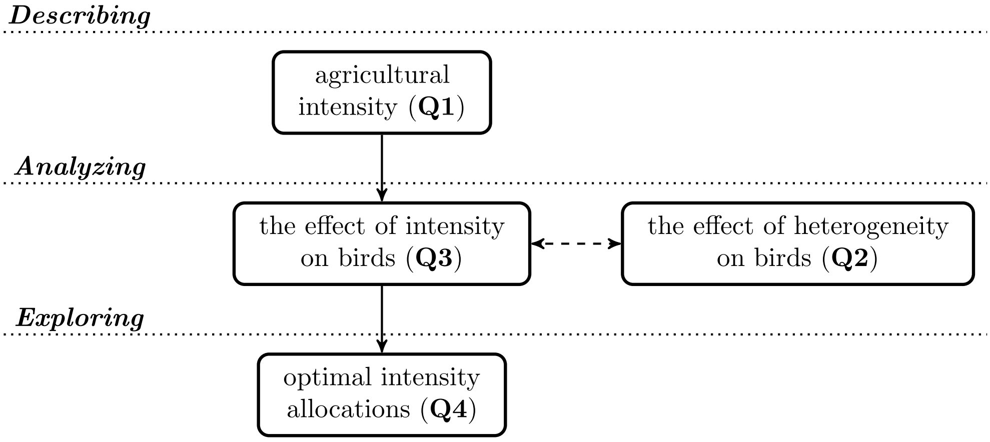


Figure I.4: The four sub-questions of this thesis. Single-headed (solid) arrows indicate that the output of one question is used as the input to answer the next question. The double-headed (dashed) arrow indicates that the outputs of the two questions are compared to give additional insight. All questions are addressed in this General Presentation (Part A). For further details, they correspond to the articles in Chapters V to VIII, respectively.

Chapter II

General Approach

1 Case study

Our case study, to address the research question, had four key features:

- The scale involved the whole country of France.
- Intensity and its allocation were described at the resolution of Small Agricultural Regions.
- We accounted for crop, cattle livestock, and mixed (crop-cattle livestock) agricultural productions.
- We examined biodiversity through a community of 22 farmland bird species.

Agricultural intensity and its allocation were thoroughly described on a nationwide scale by accounting for the five dominant types of agricultural production in France: industrial crops, cereal crops, dairy cattle, beef cattle, and mixed crop-cattle livestock. Sixty-seven percent of French farms belong to these production types, and together they cover almost 80% of agricultural lands (Fig. II.1). These five production types, to the advantage of this study, displayed comparable variation in intensity levels (Section 2.1).

We define "resolution" as the minimal spatial unit at which intensity is described. The resolution of our study is the Small Agricultural Region (SAR). SAR spatial divisions were designed to define homogeneous units in terms of agricultural systems and pedo-climatic conditions (Klatzmann, 1955). The mean width (± standard deviation) of a French SAR is 22.4 ± 13km (mean area = 669.6 km^2). Most agricultural data are available at coarser distributions, most often as either NUTS 2 or NUTS 3. In France, NUTS 2 corresponds to administrative regions, and their mean width is 160 km; NUTS 3 corresponds to departments, and their mean width is 75 km. Finer resolutions than SARs include municipalities (mean width = 4 km), landscapes, and farms. Regarding data availability and accuracy, a trade-off exists between scale and resolution. We managed to reach satisfying data accuracy on a large scale (all of France) and with intermediate resolution (the SAR) therefore, "allocation" of intensity was defined as intensity levels among SARs across all of France.

We did not address all types of agricultural production; therefore, we only analyzed SARs that had farms belonging to our five agricultural types covering more than two-thirds of their total agricultural area. In total, they represented 590 SARs out of 708. France and SAR resolution were also used to describe a land use gradient, from grassland to arable land, and its spatial heterogeneity (Section 2.3).

Our biodiversity focus was on common farmland birds. This focus on common, rather than patrimonial, species ensured that bird distribution range was wide enough to match the national scale addressed in this study. The French Breeding Bird Survey (Section 3.1) provided a sample of monitored sites sufficiently large to cover the national scale (332 sites in farmlands, between 2006 and 2008, Fig. II.1). Our studied bird community consisted of 22 species of common farmland birds (Section 3.1).

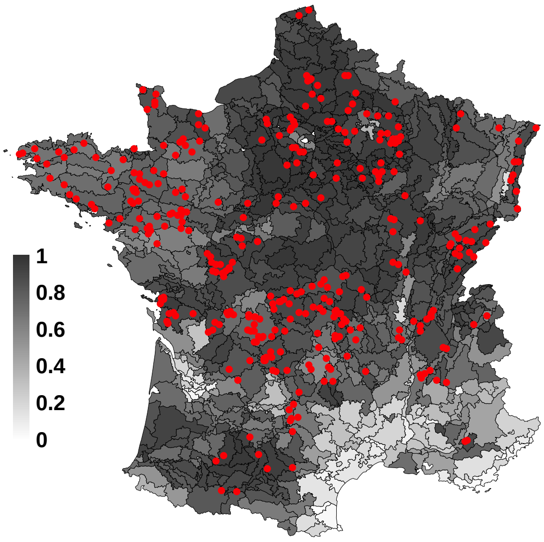


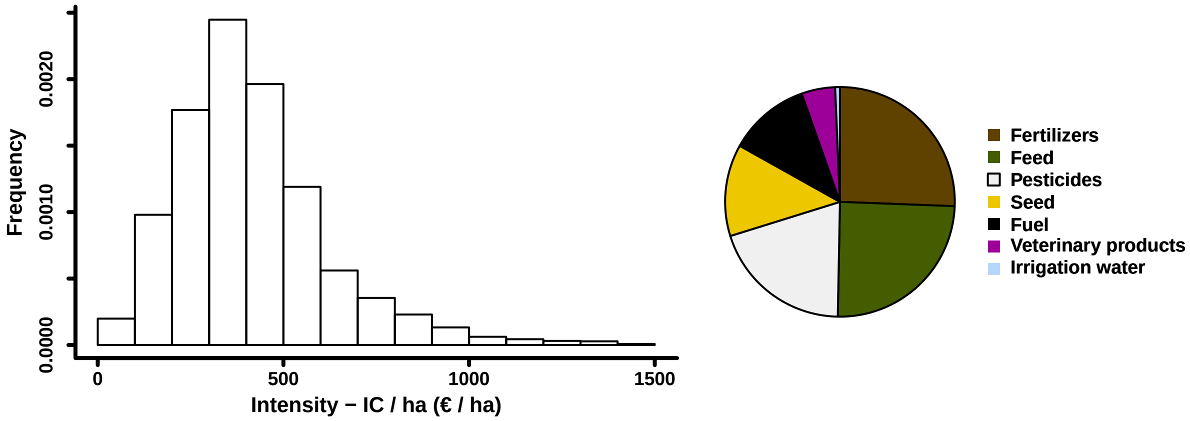
Figure II.1: Proportions of the five production types (gray scale, see legend) in each French Small Agricultural Region (borders in black); and FBBS bird sample sites included in the analyses (red points).

2 *Describing* agriculture

2.1 The *Input Cost/ha* intensity indicator

We developed an *Input Cost/ha* ("IC/ha") intensity indicator. It was defined as the ratio between the sum of different categories of input costs and the total Utilized Agricultural Area (UAA) of the farm. The IC/ha was expressed in €/ha, *per* year. Input categories included fertilizers, feedstuff, pesticides, seeds, fuel, veterinary products, and irrigation water.

Using cost enabled us to include several input categories. The intensity indicator could be computed for both crop and cattle livestock productions. Other types of agricultural production were excluded from the IC/ha computation because they had either very low UAAs (vegetables),



(a) (b)

Figure II.2: Input expenses of French farms, belonging to the five production types. (II.2a) Distribution of the *Input Cost/ha* (IC/ha) intensity indicator values for French farms. (II.2b) Mean relative importance of the different input categories of the IC/ha (2006 values). Source: French Farm Accountancy Data Network (FADN) farms, representing all French farms on a national scale (see Box II.1). n = 4172 FADN farms representing 202383 French farms.

very high input levels (wine and orchards), or low UAA and high input (poultry and pigs), leading to extreme IC/ha values. Some input categories (*e.g.*, pesticides, fertilizers) have direct negative effects on biodiversity (Stoate *et al.*, 2009). Others (*e.g.*, feedstuff, seeds) have indirect effects that collectively put global pressure on habitats, such as intensive livestock farms with high feed costs that produce high rates of nitrogen dissipation (Bleken *et al.*, 2005). To overcome year-to-year variation in price and stock, the IC/ha corresponded to a 3-year averaged value (*i.e.*, the 2006 value is an average of 2004, 2005, and 2006).

The average IC/ha of French farms of all five production types was 459.5 €/ha (Fig. II.2a). Among all five production types, the dominant input category was fertilizers (Fig. II.2b). Together with feed and pesticides, they represented more than 2/3s of the total IC/ha.

The IC/ha indicator was first developed and tested (*i.e.*, using correlation tests with other intensity-related variables) on the French Farm Accountancy Data Network (FADN) dataset. The IC/ha indicator was not available at the SAR resolution with existing datasets; therefore, we developed a method to estimate it accurately at that resolution (Box II.1).

Box II.1: Combining multiple databases to predict intensity with SAR resolution

We combined two groups of databases to predict the IC/ha intensity indicator, on a national scale and with Small Agricultural Region (SAR) resolution. All data were from the year 2006 and were provided by the INRA (French National Institute for Agricultural Research) service unit that manages the French Observatory of Rural Development (ODR, 2011).

The first database group was the FADN (French Accountancy Data Network) survey. It surveys a limited number of farms on a yearly basis (n = 7361 farms in 2006, including 2% of French professional farms). For each farm in the sample, the FADN provides a very broad set of variables related to intensity, production, economy, and land use. The FADN sample is designed to be representative for NUTS 2 and the French country resolution, and for all the types of agricultural production of this study. We, therefore, used the FADN farms to study the distribution of the surveyed variables, and the correlation existing between them, all at the NUTS 2 and French country scale.

The second database group contained five datasets, at SAR resolution, that provided values from a limited set of variables in common with the FADN. These datasets (and the type of variables they provided) were:

- CORINE Land Cover (CLC) data — provided variables on agricultural (*e.g.*, grasslands, croplands) and other (*e.g.*, forest, urban) land uses.
- The farmers' declaration to common agricultural policy — provided detailed variables on agricultural land use and several subsidies received by farmers.
- The National Bovine Identification Database — provided stocking rates of cattle.
- A dataset of the Agricultural Social Security — provided socioeconomic variables.
- "Météo France" (French Meteorological Institute) data — provided topo-climatic data.

We calibrated a multinomial regression on the FADN farms. The IC/ha value of a FADN farm f (X_f^{FADN}) was estimated with a linear combination of p predictors (P):

$$\mathrm{X_f^{FADN}} = \alpha + \beta_1 \mathrm{P_{1f}^{FADN}} + ... + \beta_\mathrm{p} \mathrm{P_{pf}^{FADN}} + \epsilon_\mathrm{f} \tag{II.1}$$

The common variables between the FADN and the second dataset group were the predictors. They were selected with a backward stepwise procedure based on AIC criteria. The regression model was then used to estimate the IC/ha value for every SAR i ($\hat{X}_i^{SAR}$), where the value of the predictors was known, through the second group of datasets, as:

$$\mathrm{\hat{X}_i^{SAR}} = \alpha + \beta_1 \mathrm{P_{1i}^{SAR}} + ... + \beta_\mathrm{p} \mathrm{P_{pi}^{SAR}} \tag{II.2}$$

Leave-one-out cross validation was used to test the predictive abilities of the models and to validate the estimation method (refer to Chapter V for a detailed description of datasets, variables, and estimation methods).

2.2 Studying the aggregation of intensity among small agricultural regions

We studied spatial aggregation of intensity among SARs. Spatial aggregation of intensity was defined as a similarity between the IC/ha value of contiguous neighboring SARs. We adopted a binomial view of aggregation by discriminating aggregated SARs from non-aggregated SARs: Aggregated SARs had an IC/ha value similar to those of contiguous neighbor SARs, while non-aggregated SARs had an IC/ha value in contrast to contiguous neighbor SARs. The indices used to measure aggregation, and to discriminate these two types of SARs, are detailed in Box II.2.

Box II.2: Measuring the spatial aggregation of agricultural intensity

Two different measures were used for the aggregation of the agricultural intensity of any individual SAR i.

First, we used the local Moran index in to compute the spatial aggregation of intensity and its significance (Chapter V). The local Moran of a SAR i (LI_i) is computed as follows:

$$\mathrm{LI_i} = \frac{\mathrm{X_i} - \bar{\mathrm{X}}}{\mathrm{Var(X)}} \sum_{\mathrm{j}} \mathrm{w_{ij}} \frac{\mathrm{X_j} - \bar{\mathrm{X}}}{\mathrm{Var(X)}} \tag{II.3}$$

where X_i = the IC/ha value of SAR; $\bar{X}$ = the mean IC/ha of all SARs; $Var(X)$ = the standard deviation of all the SAR's IC/ha; and w = the connectivity matrix of all SARs, where either $w_{ij} = 1$, when SARs i and j were connected (*i.e.*, contiguous neighbors), or $w_{ij} = 0$ in all other cases. We converted the continuous aggregation index into a binomial index to distinguish aggregated from non-aggregated SARs. Aggregated SARs had LI values significantly higher than the national average LI. Significance was assessed through a bootstrap procedure, with 1000 sample permutations (*lisa* function, *ncf* package of R statistical software, R Development Core Team 2007; procedure adapted from Anselin 1995). The local Moran has already been used to study the spatial aggregation of economic (Getis, 2007) and agricultural (Su *et al.*, 2011) activities.

We also tested for an interacting effect between intensity and its spatial aggregation on the bird community. The measure of aggregation described above was strongly correlated with intensity; therefore, we computed a second aggregation index that was independent from intensity: the absolute difference between the SAR IC/ha and the mean IC/ha of its contiguous neighbors. This aggregation index, AI_i, was computed for any SAR i as:

$$\mathrm{AI_i} = \left| \mathrm{X_i} - \frac{1}{\sum_{\mathrm{j}} \mathrm{w_{i.}}} \sum_{\mathrm{j}} \mathrm{w_{ij}X_j} \right| \tag{II.4}$$

where terms are defined the same as in Eq. II.3. Spatial aggregation is indicated by low values of the AI. Aggregated SARs had aggregation values (AI) strictly (but not necessarily significantly) lower than the average value, which led to balanced samples between aggregated and non-aggregated SARs.

2.3 The grassland/arable land gradient and heterogeneity within small agricultural regions

We studied a gradient of land use from grassland to arable land (the two categories of agricultural land use that we considered). Within each SAR, we described the compositional and configurational heterogeneity of these two land uses (Duelli, 1997). Compositional heterogeneity is low when one land use dominates the SAR and high when the two land uses occupy similar areas. Compositional heterogeneity was computed as a ratio between the arable land area and the grassland area ("arable/grassland ratio"). Configurational heterogeneity occurs when the two land uses are arranged in a complex spatial pattern. It was computed as a probability of adjacency. The two heterogeneity measures are detailed in Box II.3.

Box II.3: Measuring the compositional and configurational heterogeneity of grassland and arable land

The CORINE land cover (CLC, CLC 2006) database was used to compute the compositional and configurational heterogeneity of grassland and arable land, within each SAR. In the CLC database, the distribution of these two land uses was available at the French country scale, with a geo-referenced raster of 25*25m pixels. We used 2006 CLC data.

The compositional heterogeneity was assessed with the arable/grassland ratio, $S_a/(S_a + S_g)$, where S_a was hectares of arable land, and S_g was hectares of grassland. Maximal composition heterogeneity occurred when the arable/grassland ratio was close to 0.5.

The probability of adjacency ($q_{a,g}$) between arable land and grassland was computed, as an indicator of configuration heterogeneity (Turner *et al.*, 2001), with the following:

$$\mathrm{q_{a,g}} = \frac{\mathrm{n_{a,g}}}{\mathrm{n}} \tag{II.5}$$

where $n_{a,g}$ = the number of instances when arable land and grassland land uses were adjacent, and n = the total number of edges between grid cells. Grid cells = the $25 * 25$m pixels of the CLC raster. We considered a “rook” adjacency as one that occurred between one cell and the four neighboring cells that shared its border.

3 The farmland bird community

3.1 Data from the French Breeding Bird Survey

The French Breeding Bird Survey (FBBS) is a standardized monitoring program that is implemented at a national scale (Jiguet *et al.*, 2011). It is managed by the Center of Research in Biology and Populations of Birds (CRBPO) lab at the French Natural History Museum. More than 2000 sites have been surveyed at least one year since the beginning of the program in 1989. The survey relies on skilled volunteer ornithologists to identify and count 175 species of breeding birds during spring.

On $2 * 2$km survey sites, observers conduct 10 evenly-distributed point counts and record every individual bird, either heard or seen, during a 5-min count. Surveys are conducted twice each spring. The habitat at each point count is also recorded.

We calculated the yearly relative abundance of each bird species at each sample site as follows. Since we focused our study on farmland birds, we only included sites with at least five point counts located in the farmland habitat. When sites had more than five farmland point counts, five of them were randomly selected. At each point count, we chose the maximal number of birds *per* species, between the two counts that were made during the same spring. Within each site, we summed the abundances of the five points.

We used 2006 intensity and heterogeneity values. We used yearly relative abundances from 2006 to 2008 to account for potential delayed effects of agricultural intensity on bird abundance. The number of surveyed years varied between squares; therefore, we averaged the local relative abundances, in squares surveyed more than one year, across years. The final sample of FBBS sites consisted of 332 sites located in 152 different SARs (Fig. II.1).

3.2 The farmland bird community and its descriptors

We focused on a community of 22 species of common breeding birds (Table II.1). All species were classified as farmland birds by the European Bird Census Council (Vorisek *et al.*, 2010). We used species richness to describe community size, the Shannon Index to describe community diversity, and several other variables as trait-based descriptors of community composition. They are described in the following paragraphs and their computational detail is presented in Box II.4.

The Community Trophic Index (CTI) provides a functional description of the community composition. It reflects the mean trophic level of the community, for which a high CTI indicates that invertebrate-eating species are dominant in the community and a low value indicates that granivore species are dominant. The CTI was adapted from the Trophic Marine Index (Pauly, 1998). Trophic level has been shown to influence the effect of agricultural intensity on arthropods (Haddad *et al.*, 2000; Attwood *et al.*, 2008). Only a few studies have adapted the CTI to bird communities (see Mouysset *et al.* 2012).

The Community Specialization Index (CSI) measures the habitat specialization of the community. It considers large classes of habitat (*e.g.*, farmland, forest, wetland). A high CSI indicates that habitat specialist species are dominant in the community, and a low value indicates that generalists are dominant. The CSI has already been widely used because it can measure community biotic homogenization, which is an important threat to biodiversity (Julliard *et al.*, 2003). The CSI is also a good indicator of habitat disturbance (Devictor *et al.*, 2008) and it has been shown to be impacted by agricultural intensity (Doxa *et al.*, 2010; Filippi-Codaccioni *et al.*, 2010).

As we focused on farmland birds, we further computed a Community Specialization Index for grassland (CSIg), in order to distinguish between farmland species that were either specialists of grassland or specialists of arable land. A high CSIg indicated that grassland species were dominant in the community and a low value indicated that arable land species were dominant. Agricultural intensity can have contrasting effects on grassland versus arable land species (Batáry *et al.*, 2007a; Fischer *et al.*, 2011a). We provide the first study to develop the CSIg as a continuous and quantitative descriptor of specialization for two different sub-habitats within farmland.

The Species Specialization Index for grassland (SSIg; see Box II.4) was also used to categorize the 22 species as grassland specialists, arable specialists, or mixed arable/grassland habitat (generalist) species. We obtained expert opinion on our SSIg values and found that the eight species with highest SSIg values ($SSIg > 2.2$) could be classified as grassland specialists, whereas the eight species with lowest SSIg values ($SSIg < 1.8$) could be classified as arable specialists (Table II.1). Remaining species were classified as mixed habitat birds. The percentage of grassland, arable, and mixed habitat species within the community were used as the community descriptors. These relative abundances provided complementary information to the CSIg. A medium CSIg value did not discriminate a community were mixed habitat birds are dominant, from a community where grassland and arable specialists are equally abundant.

Species	Specialization index	Trophic index	Grassland specialization index	Main habitat
Perdix perdix	1.31	1.1	1.25	Arable
Motacilla flava	1.19	2	1.33	Arable
Emberiza calandra	1.08	1.28	1.56	Arable
Vanellus vanellus	1.55	1.9	1.56	Arable
Carduelis chloris	0.86	1.05	1.58	Arable
Coturnix coturnix	1.21	1.22	1.59	Arable
Alauda arvensis	1.13	1.25	1.6	Arable
Carduelis carduelis	0.67	1.05	1.66	Arable
Alectoris rufa	0.69	1.1	1.84	Mixed
Carduelis cannabina	0.62	1.05	1.85	Mixed
Corvus frugilegus	0.92	1.63	1.94	Mixed
Anthus pratensis	1.33	1.75	2	Mixed
Sylvia communis	0.63	1.6	2.04	Mixed
Falco tinnunculus	0.48	2.85	2.12	Mixed
Emberiza citrinella	0.54	1.3	2.26	Grassland
Saxicola torquatus	0.66	2	2.29	Grassland
Emberiza cirlus	0.39	1.3	2.37	Grassland
Buteo buteo	0.39	2.9	2.42	Grassland
Saxicola rubetra	1.23	2	2.44	Grassland
Upupa epops	0.29	2	2.53	Grassland
Lanius collurio	0.87	2.15	2.58	Grassland
Lullula arborea	0.58	1.5	2.61	Grassland

Table II.1: The farmland bird community of 22 species, and their corresponding trophic index, habitat specialization index, and grassland specialization index. The grassland specialization index was used to determine the main habitat of each species.

Box II.4: Computing trait-based descriptors of the bird community composition
The CTI was computed as follows:

$$\mathrm{CTI} = \sum_{\mathrm{i=1}}^{\mathrm{n}} \frac{\mathrm{N_i}}{\mathrm{N_{tot}}} * \mathrm{STI_i} \tag{II.6}$$

where STI_i was the trophic index of each species i (see Table II.1), weighted by its abundance, N_i, and divided by the summed abundances of all 22 species, N_{tot}. The STI is computed as the proportion of seeds/plants, invertebrates, and vertebrates in the species diet, each of which is weighted by 1∗, 2∗, and 3∗, respectively (Jiguet *et al.*, 2011). The proportions of these three elements in the diet were previously recorded in the BWPI (2006).

The CSI was computed as follows:

$$\mathrm{CSI} = \sum_{\mathrm{i=1}}^{\mathrm{n}} \frac{\mathrm{N_i}}{\mathrm{N_{tot}}} * \mathrm{SSI_i} \tag{II.7}$$

where SSI_i was the Species Specialization Index of each species i (see Table II.1). The SSI was computed as the coefficient of variation of the species abundances between seven habitat classes, following Julliard *et al.* (2006) methodology. The coefficient of variation was the *standard deviation/average* ratio, which was statistically independent of the average species abundance. The seven habitat classes were: forest, heath/scrub, marshland, farmland, urban settlement, wetland/aquatic, and rocks (recorded at each point count by FBBS observers). We computed SSIs for all FBBS sites, 2006 to 2008.

The CSIg was computed as follows:

$$\mathrm{CSIg} = \sum_{\mathrm{i}} \frac{\mathrm{N_i}}{\mathrm{N_{tot}}} * \mathrm{SSIg_i} \tag{II.8}$$

where $SSIg_i$ was the Species Specialization Index for grassland index of each species i (see Table II.1). The SSIg was computed as a weighted mean of species abundance among the following four sub-habitats of the farmland habitat: unimproved grasslands, improved grasslands, mixed grasslands/arable lands, and arable lands (recorded at each point count by FBBS observers). Weighting coefficients were 4∗, 3∗, 2∗, and 1∗, respectively. All farmland FBBS sites surveyed between 2006 and 2008 were included in this computation.

4 *Analyzing* the effect of agriculture on the bird community

4.1 The correlative approach

We tested for correlation of spatial variations in agricultural intensity and heterogeneity to spatial variations in the bird community. This approach relies on statistical models of habitat use (Norris, 2004), which is the most common approach in studies addressing the effects of either heterogeneity (Batáry *et al.*, 2007b; Filippi-Codaccioni *et al.*, 2010; Chiron *et al.*, 2010) or intensity (Kleijn *et al.*, 2009; Ekroos *et al.*, 2010; Phalan *et al.*, 2011a) on biodiversity.

The results of habitat use models can lead to mistaken conclusions in two main cases. For one, the “buffer effect” can lead to an increased use of poor quality habitats when the population size grows (Green, 1995; Norris, 2004). The population sizes of the species included in our community, however, tended to decline rather than increase (see Fig. I.1b, where the farmland bird index is based on a community sharing 20 species with ours). Secondly, delayed effects of habitat cannot be considered if the habitat changes over time. We compared 2006 values of intensity and heterogeneity to descriptors of the bird community averaged between 2006 and 2008 in order to account for potential delayed effects. Moreover, the value of intensity at a regional scale was rather stable between 2002 and 2008 (Fig. II.3): it only varied within a 6.1% range at the national scale, within a range below 5%, for more than half of the regions, and within a 25.1% range for the region with the biggest variation (Auvergne).

Models of habitat use can be applied to predict the effect of habitat changes on biodiversity (*e.g.*, Steck *et al.* 2007; Fonderflick *et al.* 2010). They rely on correlation, without explicitly addressing the underlying mechanisms; therefore, their predictions are mainly valid for interpolation (*i.e.*, within the same range of explanatory variables rather than the one used for calibration).

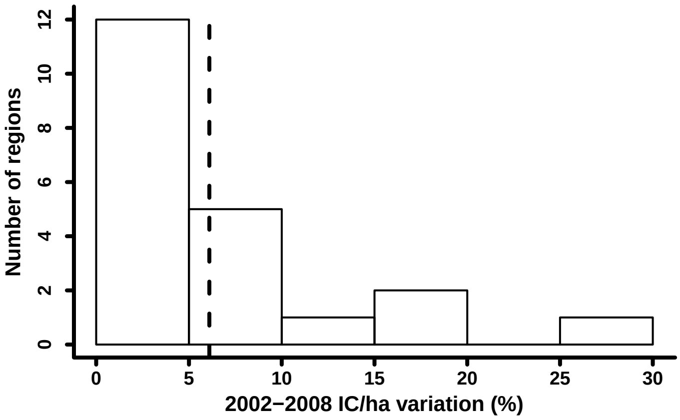


Figure II.3: Distribution of the variation of the *Input Cost/ha* (IC/ha) intensity indicator, between the years 2002 and 2008, for the different French regions. The mean national IC/ha variation for this period is shown as a dotted line.

4.2 Statistical methods

We used generalized linear models (GLMs) and generalized additive models (GAMs) to reveal the effects of intensity and heterogeneity on the bird community. The different community descriptors (Section 3.2) were tested as response variables in separate models. GAMs allowed us to test for complex patterns of response to intensity (Guisan *et al.*, 2002). The biodiversity/intensity relationship is not always linear (Kleijn *et al.*, 2009; Ekroos *et al.*, 2010; Phalan *et al.*, 2011a) and the shape of its non-linearity has important management implications (Section 2 in Chapter I). When a nonlinear effect of intensity was tested, it was included in the GAMs as a spline function. In all the models, explanatory variables also included a set of continuous variables related to climate and land use. These variables could have had an effect on the large geographical gradient of our sample point distribution. Climate variables included mean temperature and annual precipitation (data from Météo France, French Meteorological Institute, available through the ODR), and land use variables included the relative amount of forests and urban land uses (CLC database). As intensity partially correlated to a land use gradient from grassland to arable land, the arable land/grassland ratio (arable area / (arable area + grassland area)) was also included as land use explanatory variable in the models testing for the effect of intensity. Explanatory and response variables were linked at the SAR level: the explanatory variable values available for a given SAR were compared with the bird response variables values of the FBBS sample sites located in that SAR. For all response variables, normal distribution and homoscedasticity of residuals were tested.

When we tested for an interaction effect between intensity and its aggregation, we divided the sample into aggregated and non-aggregated SARs. Because of this sample division and the degrees of freedom added by the interaction, we used GLMs rather than GAMs to avoid overfitting. The same variables from the GAMs were included in the GLMs. In addition, either the aggregation or the non-aggregation of each SAR was added as a factor parameter, as well as each of its interactions with the IC/ha intensity indicator.

4.3 *Exploring* the effect of intensity allocation modifications

Relationships between the CSIg and intensity, and its aggregation, were integrated into a model aimed at predicting the effects of intensity allocation modifications on the production/biodiversity trade-off (Fig. II.4). We also used GAMs to compute the relationships between production and intensity. Production was defined as volume of product/ha, normalized (min/max normalization) within each production type. These relationships were calibrated to the FADN dataset, separately for each production type.

The only decision variable of the model was the agricultural intensity X. The intensity allocation was defined, at the national scale, as the intensity values of all n SARs:

$$\mathrm{X} = (\mathrm{X}_1, \mathrm{X}_2, ..., \mathrm{X}_\mathrm{n}) \tag{II.9}$$

We simulated random intensity allocation modifications from the initial state, within three scenarios. Intensification corresponded to an intensity increase, extensification corresponded to an intensity decrease, and reallocation corresponded to a coupled increase and decrease in separate SARs, without a change in national average intensity.

For each scenario, an optimization procedure was then used to find the optimal intensity allocations, drawing the efficiency frontier between production and biodiversity. This multi-objective optimization problem was written as:

$$\max \mathrm{F(X)} = \Big(\mathrm{F_{Prod}(X)}, \mathrm{F_{Biodiv}(X)}\Big) \tag{II.10}$$

where $F_{prod}(X)$ and $F_{Biodiv}(X)$ were the performance criteria, expressed within one function of intensity and simultaneously maximized. $F_{prod}(X)$ was the national production performance, which was defined as the production volume averaged across all SARs. $F_{Biodiv}(X)$ was the bird community diversity performance, which was defined as the coefficient of variation of the CSIg between SARs. We, therefore, sought optimization that maximized production, and reached a high diversity in the bird community, with regard to their CSIg, between SARs.

We performed multi-objective optimization with an NSGA-II (Non-dominated Sorting Genetic Algorithm-II; detailed description in Deb *et al.* 2002). In Chapter VIII, we also considered a third criterion, the economic performance, which is not presented in this General Presentation (Part A).

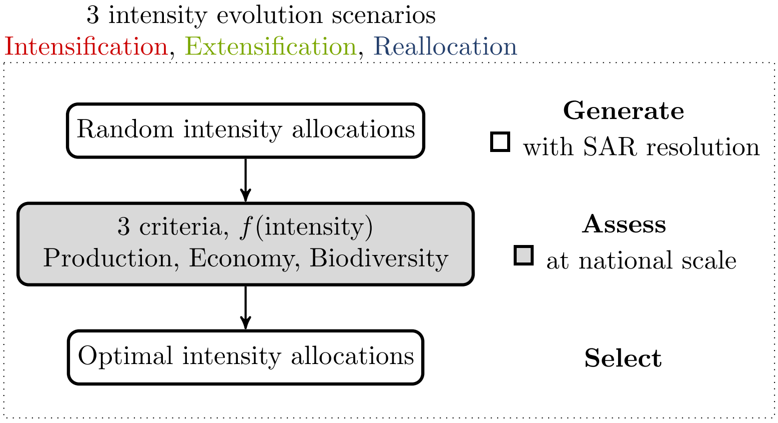


Figure II.4: Conceptual model of the simulation and optimization of intensity allocations. Within each scenario, three steps were conducted: generate random intensity allocations on the scale of France with the resolution of Small Agricultural Regions, assess the national performance of these allocations on three criteria (expressed as functions of intensity), and select optimal allocations.

Chapter III

Summary of the results

1 *Describing* the spatial distribution of intensity at the French country scale, with SAR resolution

In a nutshell:

- Data availability is a limiting factor when addressing the spatial distribution of intensity; it explains why previous studies described intensity coarsely
- We developed a method to estimate the value of a continuous intensity indicator on France scale and with a resolution adequate for fine policy targeting
- We show that intensity was spatially structured, with similar intensity levels aggregated together; but we also reveal areas displaying more heterogeneity
- The nationwide intensity gradient was only moderately correlated to a gradient of land uses

1.1 The distribution of intensity shows spatial structure

We developed a method to estimate the value of intensity at the French country scale, and with intermediate (SAR) resolution. SARs define homogeneous units in terms of agricultural systems and pedo-climatic conditions and they could thereby be an adequate resolution for the targeting of conservation policies and for studying the effect of intensity on biodiversity. We used the IC/ha indicator which provided a continuous intensity value, and was relevant for all the main types of agricultural production in France (both crop and livestock). The estimation method was tested for predictive reliability (see Section 3.2 in Chapter V).

Mapping showed that intensity was structured between regions (NUTS 2) (Fig. III.1). It also revealed intra-regional heterogeneity of intensity values. The spatial distribution of intensity was not consistent at regional borders. The region is the resolution where intensity values originate from existing FADN data; therefore, estimation at SAR resolution provided supplementary information.

Low input systems (IC/ha lower than 300€/ha, *i.e.* in the 20% lower quantile of all SARs) were mainly concentrated in a large area that spread across several regions of the center and eastern parts of France. High input systems were concentrated in the western and northern regions of France. The estimation method also efficiently discriminated SARs with contrasting intensities between neighbors (*e.g.*, the few extensive SARs along the western coastline that corresponded to marshlands).

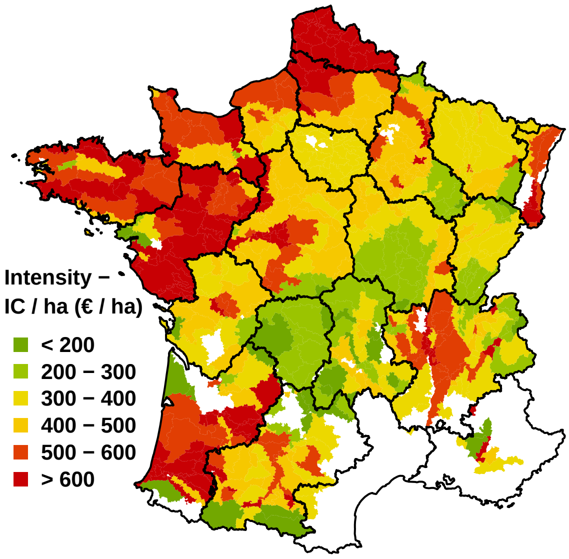


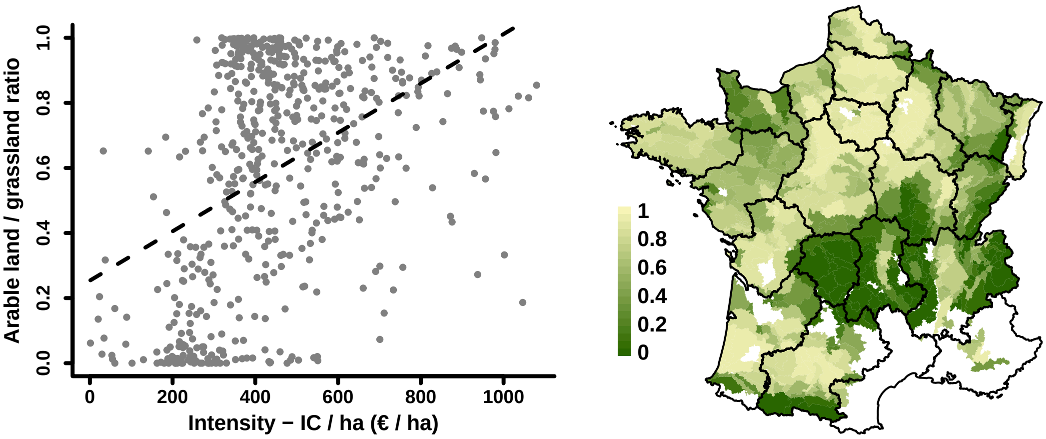
Figure III.1: Intensity (*Input Cost/ha*, IC/ha) of French Small Agricultural Regions (SARs) dominated by crop, livestock, or mixed production (more than two-thirds of the SAR agricultural area). SARs dominated by other production types (often wine production) appear in white. Continuous IC/ha values are represented in six classes, from lowest (green) to highest (red) levels. Administrative region (NUTS 2) borders are in black. This figure corresponds to Fig. V.2 in Part B.

1.2 Moderate correlation between the intensity gradient and the land use gradient

On the national scale, different types of agricultural production (crop, livestock, and mixed) involve different types of agricultural land uses. On such a large gradient, intensity can also be linked to land use: grassland is often a more extensive land use than arable land. In order to disentangle the effects of intensity from the effect of land use, we tested the correlation between these two gradients on France scale (Fig. III.2). The arable/grassland ratio was used to characterized the land use gradient. They are the two main land uses associated with the production types that we considered (crop and livestock).

We found a significant correlation (p-value < 0.001) between the intensity gradient and the land use gradient on the French country scale (Fig. III.2a). The correlation was significant, but its strength was moderate: there was a strong variation around the mean regression curve.

Intensity value only explained 19% of the arable/grassland ratio variance. Comparison between the intensity map (Fig. III.1) and the land use map (Fig. III.2b) shows that most extensive SARs were grassland dominated; however, SARs with large grassland areas could also be moderately extensive (*e.g.*, in eastern parts of France) or even intensive (*e.g.*, in northwestern France). SARs with high arable/grassland ratios could be either moderately intensive (*e.g.*, between the center and northern France) or very intensive (*e.g.*, in northern France).



(a)

(b)

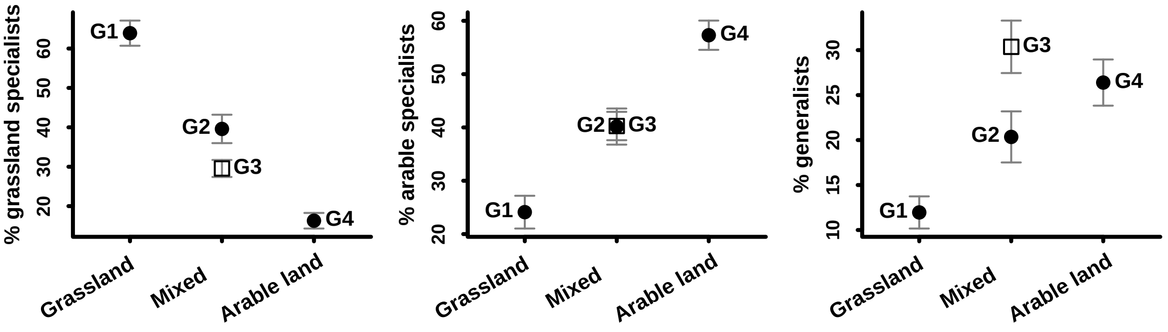
Figure III.2: Correlations between the land use gradient and the intensity gradient (compare to Fig. III.1). (III.2a) Correlation between the arable/grassland ratio and the intensity value (*Input Cost/ha*) at the Small Agricultural Region level. (III.2b) Map of the arable/grassland ratio. The value of the ratio is represented with a color scale from green (low ratio, SARs dominated by grassland) to yellow (high ratio, SARs dominated by arable land) (see legend). This figure was adapted from Fig. VI.1 in Part B.

2 *Analyzing* the response of the bird community to agricultural intensity

In a nutshell:

- Knowing the biodiversity/intensity relationship is important for effective conservation but empirical evidence is lacking, especially in Europe
- We first explore the effect of land uses and their heterogeneity and show that homogeneity benefited habitat specialists while heterogeneity benefited generalists
- Along the intensity gradient, the size of the farmland bird community remained constant but intensity winner species replaced loser species
- The relationship between both winner and loser species, and intensity were non linear and sharper within the lower intensity range

2.1 Homogeneity benefits specialists, heterogeneity benefits generalists



(a) (b) (c)

Figure III.3: Effect of compositional and configurational heterogeneity on habitat specialists and generalists. Abundance of grassland specialists (III.3a), arable specialists (III.3b), and generalists (III.3c), within four heterogeneous groups of Small Agricultural Regions (SARs). Three groups (full circles) have homogeneous land use configuration (*i.e.*, probability of adjacency lower than the median), and they differ in their land use composition: G1 = grassland dominated (arable/grassland ratio < 0.2), G4 = arable dominated (arable/grassland ratio > 0.8), G2 = mixed. The last group, G3 (empty square), has a mixed land use composition, but with a heterogeneous configuration. This figure corresponds to Fig. VI.2 in Part B.

Before computing the relationship between the bird community and intensity, we first focused on the effect of the land use gradient – from grassland to arable land – and its heterogeneity. We compared the mean heterogeneity within SARs to descriptors of the bird community within the same SARs. We differentiated between compositional heterogeneity (the arable/grassland ratio) and configurational heterogeneity (their probability of adjacency). We tested the following hypotheses: (H1) heterogeneity has a negative effect on specialist species (arable specialists and grassland specialists), but (H2) a positive effect on generalist (mixed arable/grassland habitat) species.

The two groups of habitat specialist birds showed opposite responses to the arable land/grassland ratio (Fig. III.3b and III.3a). Expectedly, a higher arable/grassland ratio was beneficial to arable birds and detrimental to grassland birds. This effect was quite linear: for both species groups, the difference in abundance was the same between grassland-dominated SARs and mixed SARs, and between mixed SARs and arable dominated SARs. All these differences in abundance were significant (p-value < 0.001). Configurational heterogeneity in the spatial arrangement of grassland and arable land had a significantly negative effect on grassland specialists. It also had a lower magnitude than that from the effect of composition.

For generalist species, the effects of compositional and configurational heterogeneity were both significant, and they had similar magnitudes (Fig. III.3c). Like arable specialists, generalist species benefited from higher arable/grassland ratios; however, they also significantly benefited from configurational heterogeneity. Their abundances were similar in SARs dominated by arable land and in SARs with mixed land uses arranged with high configurational heterogeneity.

These results validated the H1 and H2 hypothesis. Specialist species benefited from large extents of their habitat and were negatively impacted by composition heterogeneity when it involved habitat loss. For grassland specialists, configuration heterogeneity worsened the negative effect of habitat loss. Generalist species benefited from compositional heterogeneity but only when configurational heterogeneity was also high. Therefore, no unique solution existed to maintain the three groups of farmland birds.

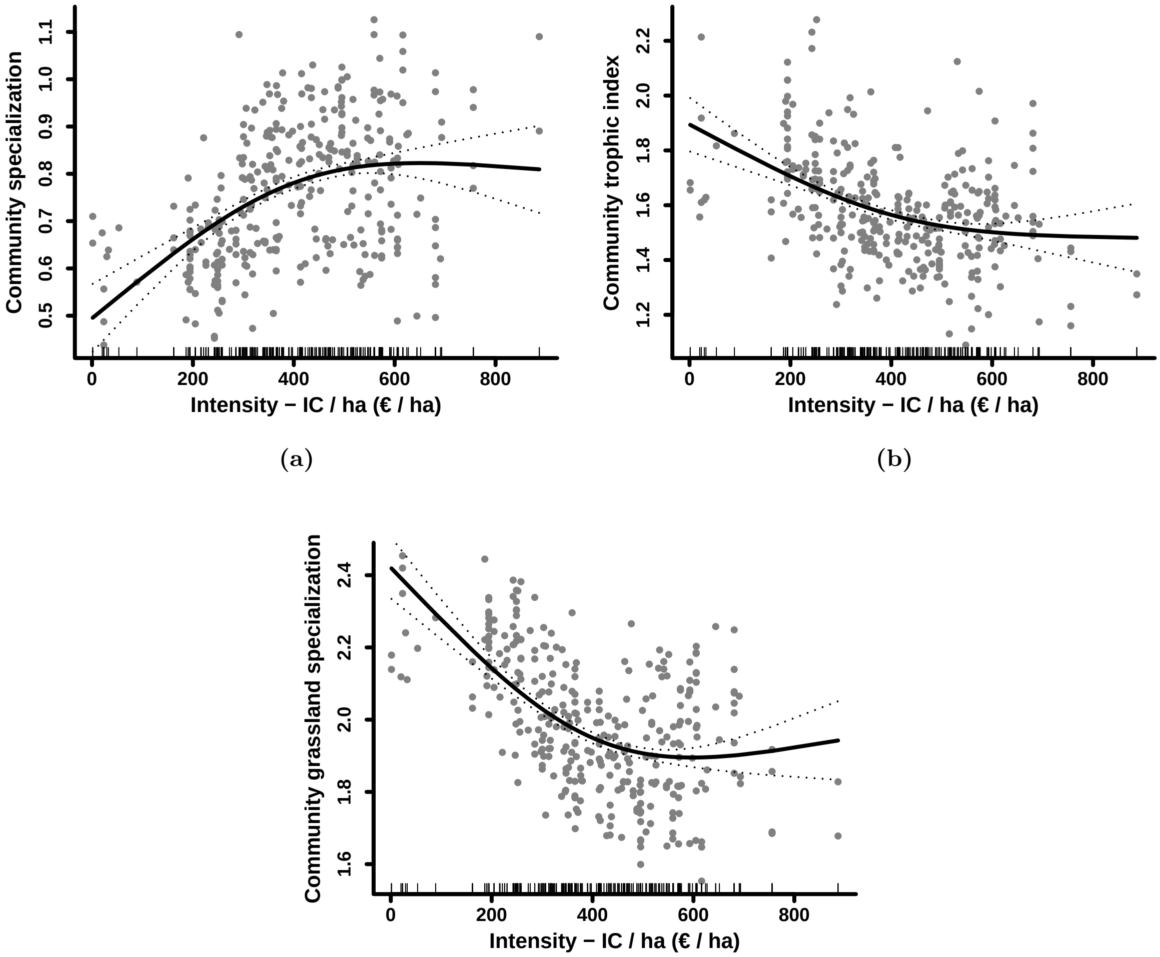
2.2 The response of birds to intensity: sharper in the extensive range, winner and loser species

We further computed the relationship between the bird community and agricultural intensity. Like in the previous Section (2.1), we studied this effect at the intra-SAR level. We aimed to reveal the shape of this relationship and determine if it varied among trait-based groups of species.

The French intensity (IC/ha) gradient neither affected community size nor its diversity (Fig. III.4). Intensity, however, had a significant effect on the three descriptors of the community composition: its specialization for farmland (CSI, Fig. III.4a), its trophic level (CTI, Fig. III.4b) and its specialization for grassland (CSIg, Fig. III.4c). The effect of intensity on community composition while its size remain constant involve that “winner” species replaced “loser” species on the intensity gradient.

CSI (Fig. III.4a) responded positively to intensity, while CTI (Fig. III.4b) and CSIg (Fig. III.4c) responded negatively. All the responses indicated that winner bird species were rather granivore and highly specialized to farmland, with arable land as their main habitat. Loser bird species were rather insectivorous and less specialized to farmland, with grassland as their main habitat.

For all the community descriptors that showed a significant relationship with intensity, this relationship was nonlinear and sharper at low intensities. The shift in community composition thus occurred quickly, when intensity started increasing. Loser species had a convex (negative) response to intensity and winner species had a concave (positive) response.



(a)

(b)

(c)

Non-significant effect: species richness, shannon index, mixed arable/grassland species
Loser species: invertebrate-eating species, moderate farmland specialists, grassland species
Winner species: seed-eating species, high farmland specialists, arable species

Figure III.4: Relationships between the bird community descriptors and agricultural intensity: (III.4a) community specialization index (CSI), (III.4b) community trophic index (CTI), and (III.4c) community specialization for grassland index (CSIg). The relationships fitted by the GAMs (black lines), 95% confidence intervals (dotted lines), and partial residuals (grey points) are shown. We summarize the meaning of these responses, in terms of intensity winner and loser species, and we indicate which descriptors show non-significant responses to intensity. This figure is adapted from Fig. VII.2 in Part B.

3 The spatial aggregation of intensity influences the bird community/intensity relationship

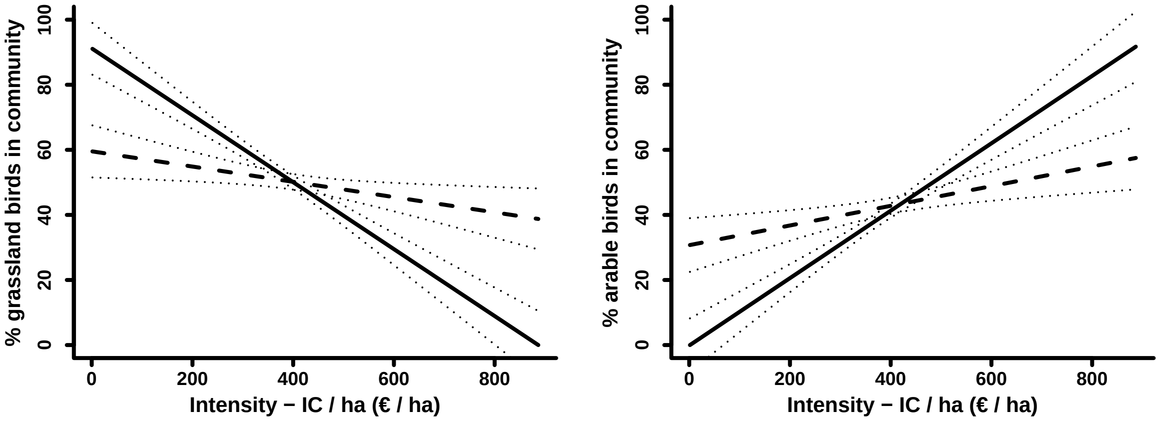
In a nutshell:

- Although the effect of the spatial arrangement of intensity on biodiversity has been evidenced, no study tested its influence on the biodiversity/intensity relationship
- We show that the effect of intensity on biodiversity was reinforced by the spatial aggregation of intensity
- Intensity aggregation have a positive effect in the intensity range favorable to species and a negative effect outside of it

We showed that the allocation of agricultural intensity among SARs in France is not random, but displays spatial structure (Fig. III.1). To a certain extent, this allocation already looks like land sparing, with clusters of aggregated low, medium, and high intensity SARs. Other areas display more intensity heterogeneity between SARs. We tested whether this intensity aggregation influenced the bird community/intensity relationships revealed in Fig. III.4.

For both grassland and arable birds, the response to agricultural intensity was sharper when intensity was spatially aggregated (*i.e.*, in SARs with contiguous neighbors of similar intensity) (Fig. III.5). Responses to intensity in aggregated versus non-aggregated SARs were significantly different for both their intercepts and slopes (Table VII.2 in Part B). The interacting effect of intensity and its aggregation had a lower magnitude than the effect of intensity itself. Grassland birds were more abundant in extensive SARs that were aggregated and intensive SARs that were non-aggregated (Fig. III.5a). Arable birds were more abundant in extensive SARs that were non-aggregated and intensive SARs that were aggregated (Fig. III.5b). The interacting effect of intensity and its spatial aggregation had the same consequences for grassland and arable birds: aggregation had a positive effect, within the favorable range of intensity, and a negative effect outside of it.

This interacting effect of intensity and its spatial aggregation was also significant for the CSIg (Fig. VIII.s2d in Part B). It was not significant for the other community descriptors.



(a) (b)

Figure III.5: Influence of intensity (*Input Cost/ha*, IC/ha) aggregation on the relationship between either grassland (III.5a) or arable (III.5b) birds, and intensity. The two curves represent the relationships in SARs that are either aggregated (aggregation index *AI* is higher than the median, solid line) or non-aggregated (*AI* is lower than the median, dashed line), with neighbors of similar intensity. Dotted lines = 95% confidence intervals. This figure corresponds to Fig. VII.3 in Part B.

4 *Exploring* optimal intensity allocations to overcome the production/biodiversity trade-off

In a nutshell:

- Adjusting the allocation of agricultural intensity on large scale could be a key lever to reconcile production and biodiversity objectives
- We developed a model that relied on relationships between production, biodiversity and intensity to find optimal intensity allocations at France scale
- Optimal allocations were more efficient (*i.e.*, benefits on one criteria achieved at lower cost on the other criteria) and even revealed win-no-lose solutions

4.1 Calibrations: intensity links biodiversity and production

The Sections 2.2 and 3 demonstrated the effect of intensity and its spatial aggregation on the bird community. In order to explore the effect of intensity allocation modifications on the production/biodiversity trade off, we used the relationships between the CSIg, intensity and its aggregation, and we also calibrated the relationships between production and intensity (Fig. III.4c).

Relationships between production and intensity were calibrated separately for each type of agricultural production. Production was a production volume *per* hectare, standardized within each production type in order to have a common scale between liters of milk, kilograms of crops, *etc.*

For all production types, we found a significant, positive correlation between production and intensity. The percentage of variance explained by IC/ha ranged from 18% (crops) to 52% (dairy cattle). The relationships were quite similar among production types. Except for beef cattle, the positive influence of intensity on production was slightly attenuated at high intensities.

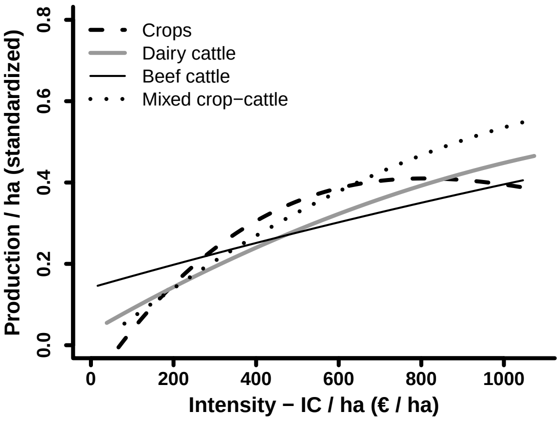


Figure III.6: Calibrated relationships between production and agricultural intensity (*Input Cost/ha* indicator, IC/ha), for each production type (see legend). Productivity is a volume of product/ha, standardized (min/max) within each production type. Calibration was done on 2006 data from the Farm Accountancy Data Network Survey. This figure corresponds to from Fig. VIII.s2a in Part B.

4.2 Intensity allocations draw the trade-off between production and biodiversity, and reveal win-no-lose solutions

The relationships between the CSIg, production and intensity were integrated in a model assessing and optimizing intensity allocations on both production and bird community diversity criteria. The model first generated random allocation for three scenarios: intensification, extensification, and reallocation. The production criterion was the national mean production. The bird community diversity criterion was the national-level coefficient of variation of the CSIg among SARs. A high value for this criterion ensured balanced abundances between loser and winner species at the national scale. Starting from the random allocation, the model performed an optimization procedure to select the optimal intensity allocation that drew the efficiency frontier between the two performance criteria.

Intensity allocations revealed the trade-off between production and biodiversity performances at the national scale (Fig. III.7). Random allocations of extensification and intensification scenarios produced an average trade-off that had the shape of a negative sigmoid function. Optimal allocations of the extensifications improved the cost-effectiveness of that scenario. For a given production loss, higher benefits occurred with bird community diversity. Optimal allocations of the intensifications and reallocations overcame the production/community diversity trade-off. They revealed win-no-lose allocation solutions where one criterion increased as the other did not decrease. Optimal allocations of the intensifications improved production performance, while annulling community diversity losses; however, community diversity level was already low at its initial state. Optimal reallocations improved community diversity at very low production losses, yet, benefits were lower than those from the extensification scenario.

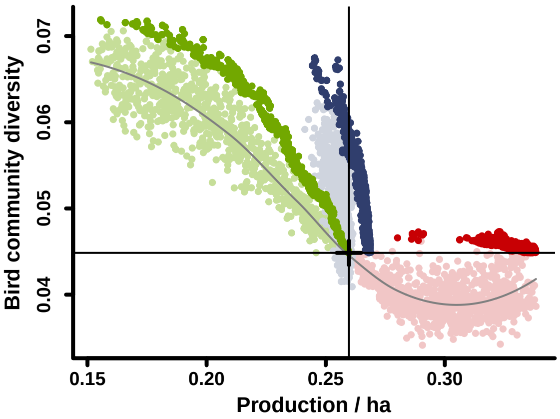


Figure III.7: Prediction of the performances of simulated intensity allocations on production and bird community diversity criteria. The production criterion was the national mean (over all Small Agricultural Regions, SARs) production volume/ha. The bird community diversity criterion was the national coefficient of variation (among all SARs) of the Community Specialization Index for grassland (CSIg). Red = intensification, green = extensification, blue = reallocation. Pale colors = random allocations, bright colors = optimal allocations, the cross = the initial allocation. This figure corresponds to Fig. VIII.2a in Part B.

5 Targeting intensity changes

In a nutshell:

- The spatial targeting of conservation policies could improve their effectiveness, however, large scale data are lacking to achieve it
- We showed that intensity was already spatially structured in France, with clusters of homogeneous intensities within the two intensity extremes; they raise the question of how policies should modify such existing spatial structure
- The optimal intensity allocations revealed by the model (Section 4) corresponded to targeted intensity changes
- Opposite targeting was necessary in the extensification (promote large, homogeneous clusters of extensive SARs) *vs* in the intensification (concentrate intensification in certain SARs and promote heterogeneity) scenario

5.1 The spatial structure of intensity: several clusters with significant aggregation

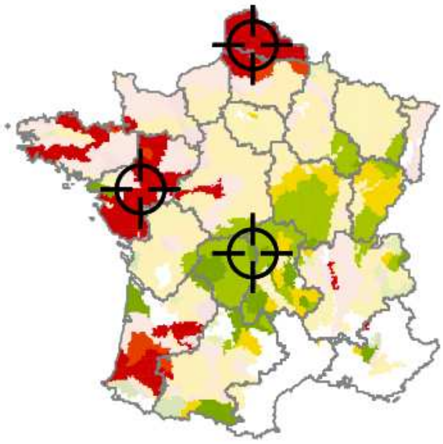


Figure III.8: Intensity (*Input Cost/ha*) of the French Small Agricultural Regions (SARs) and clusters of SARs with significant intensity aggregation. The green to red color indicates the intensity (see legend in Fig. III.1) and bright colors indicate significant aggregation. Significance of the local Moran index (spatial auto-correlation with the intensity of contiguous neighbor SARs) assessed with a bootstrap procedure. Conservation measures could be targeted at these clusters (examples of targeted areas are drawn). This figure is adapted from Fig. V.3b in Part B.

We tested whether the current spatial structure of intensity (Fig. III.1) was statistically significant. We used the local Moran Index of spatial auto-correlation and a bootstrap procedure to determine which SARs had a local Moran significantly higher than the national average.

We revealed several clusters where intensity was spatially aggregated (*i.e.*, where contiguous SARs had similar intensities) (Fig. III.8). Clusters of both low intensity and high intensity SARs existed. The large area of low input SARs observed in the Fig. III.1 consisted mostly of significantly aggregated SARs. This large cluster of extensive SARs spread across the center and eastern parts of France. Some high input SARs were also significantly aggregated and distributed within three main clusters in the southwestern, western, and northern parts of France.

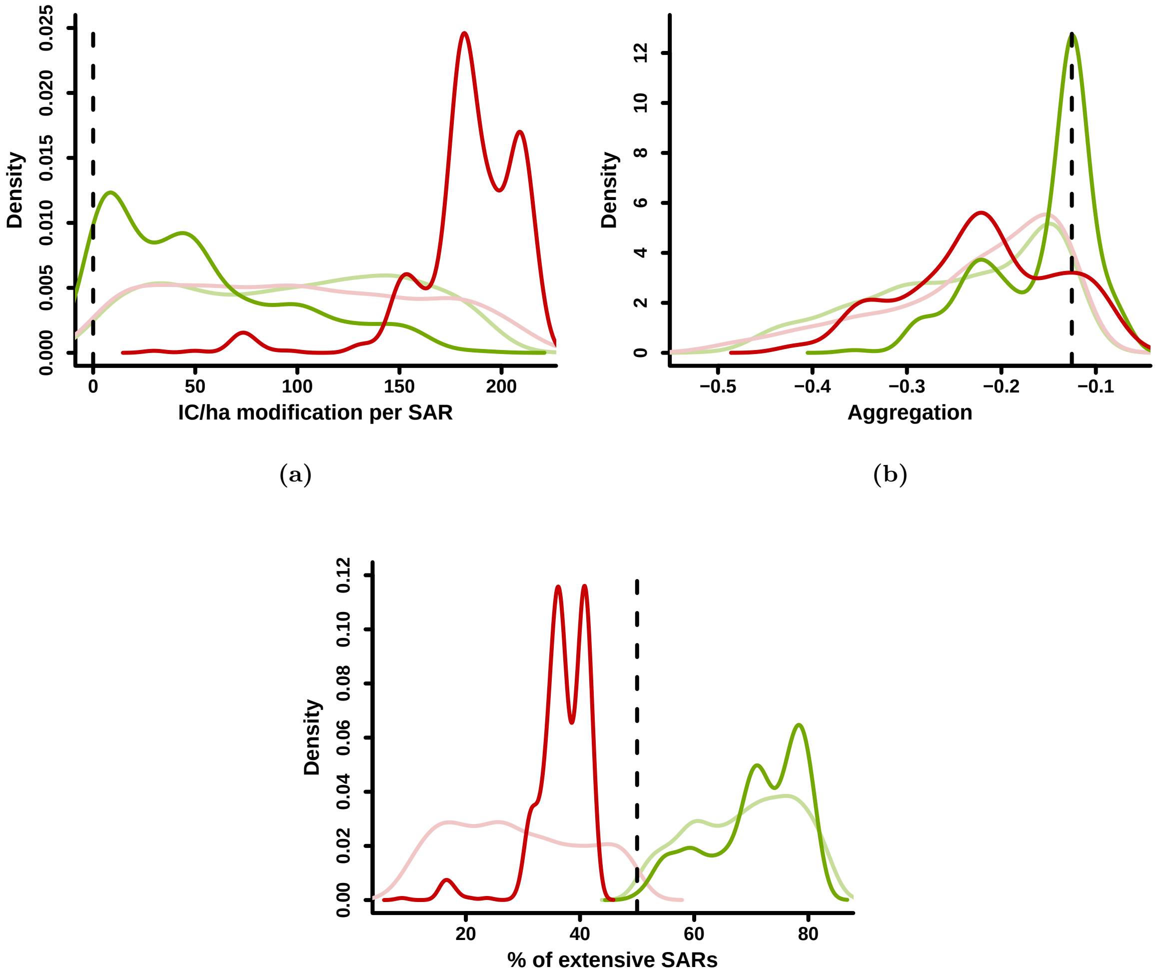
Therefore, agricultural intensity on the France scale was *de facto* spatially structured, *i.e.* significantly segregation between low and high intensities. The existing allocation of intensity at the country scale resembled land sparing theoretical allocation. The SARs clusters could provide targets for policy measures that are specifically adapted to homogeneous intensity contexts. The existing spatial structure of intensity raises the question of how policy measure should modify it.

5.2 Reaching optimal allocations: targeted intensity changes, opposite for extensification and intensification

The model exploring the effect of intensity allocation on the production/biodiversity trade-off (Section 4) further revealed where intensity changes should be targeted for optimal allocations.

Compared to the random allocations, the optimal allocations within the three scenarios (Fig. III.7) corresponded to targeted intensity changes. Interestingly, the opposite targeting of intensity changes optimized extensification and intensification. Fig. III.9 compares three properties of intensity changes between extensification and intensification scenarios (random and optimal allocations). Optimal extensification involved smaller intensity modifications on a higher number of SARs (Fig. III.9a) that promoted intensity aggregation (Fig. III.9b) and targeted more extensive SARs (Fig. III.9c). It enlarged the cluster of aggregated, extensive SARs in central/eastern France. Optimal intensification involved larger intensity modifications concentrated on a lower number of SARs. These modifications promoted heterogeneity and targeted intensive and medium intensity SARs rather than extensive ones (extensive SARs tended to be more preserved than random).

The optimal solutions of the reallocation scenarios combined the optimal intensification and extensification allocations: (i) keep a rather high number of extensive SARs, (ii) intensify by concentrating intensity modifications and promoting spatial heterogeneity of intensity in intensive areas, and (iii) extensify a high number of SARs and by promoting spatial aggregation of intensity in extensive areas.



(a)

(b)

(c)

Figure III.9: Properties of intensity (*Input Cost/ha*, IC/ha) allocations between random and optimal allocations of intensification and extensification scenarios. The densities (smoothed distributions) of the allocations are shown for three properties: (III.9a) mean intensity modification *per* Small Agricultural Region (SAR); (III.9b) mean national aggregation (with aggregated SARs = 1 and non-aggregated SARs = −1); and (III.9c) % of extensive SARs (with intensity value lower than the mean intensity at the initial state). Red = intensification scenario, green = extensification scenario, pale colors = random allocations, bright colors = optimal allocations; dotted line = value at the reference state.

Chapter IV

Discussion

1 Ph.D. contributions: generalization potentials and restrictions

1.1 Describing and mapping agricultural intensity

We mapped agricultural intensity at the French country scale using the IC/ha indicator. The IC/ha has three main advantages: (1) it combines several input categories, (2) it provides a continuous intensity value, (3) it can be computed for both crop and livestock production. These advantages are novel compared to previous studies, but also have some limitations:

1. The majority of studies describing the input intensity focus on a single category (most often nitrogen, Billeter *et al.* 2008; Kleijn *et al.* 2009). The difficulty, when incorporating several input categories, is finding a common unit. For the IC/ha, this common unit is cost. The use of cost results in an absolute intensity value, unlike the separate normalization of different categories that leads to a relative value (Herzog *et al.*, 2006a) and the use of a score that leads to a relative value incorporating arbitrary computational choices (Pointereau *et al.*, 2010). The use of costs also carries limitations. The proportionality between costs and amounts can be biased by fluctuations in either prices or stocks. We averaged the 2006 IC/ha value over the 3 previous years to overcome this limitation. We did not consider certain input molecules that can be more expensive but efficient at lower amounts and less environmentally harmful. This limitation, however, may be more important on a small scale (*i.e.*, when comparing farms) than on a national gradient where intensity is averaged at the SAR level.

Among the input categories included in the IC/ha, some have direct effects on biodiversity and its habitat (*e.g.*, fertilizers and pesticides, Stoate 2001; Vickery *et al.* 2001), while others have indirect effects (*e.g.*, higher feed costs are associated with higher livestock densities and nitrogen dissipation (Dalgaard *et al.*, 1998; Bleken *et al.*, 2005). A 50€/ha IC/ha reduction will probably not have the same effect on biodiversity if it involves a reduction of 50€/ha in pesticides, feeds, or a spread across all categories. Studies that focus on a single input category are complementary to our approach, as they can identify the categories that have the most important adverse effects on biodiversity.

Our IC/ha indicator did not include a measure of the work input. The fuel input category partially reflects the intensity of farming activities; yet, it does no allow to account for differences in practices that can have important implications for biodiversity (*e.g.*, type of ploughing; conventional *vs* delayed hay cutting, Green *et al.* 1997). The IC/ha neither included a measure of the landscape component of agricultural intensity. At the landscape level, higher intensities are often associated with decreased landscape heterogeneity (Roschewitz *et al.*, 2005a; Persson *et al.*, 2010). The landscape component of agricultural intensity has an important effect on biodiversity, which can even interact with the input effect (Tscharntke *et al.*, 2005; Concepción *et al.*, 2008; Batáry *et al.*, 2011a). In Europe, policymakers understand the importance of landscape and conservation measures now promote both lower input use and higher landscape heterogeneity. Although we analyzed the effect of heterogeneity, we focused on two land uses, and our results cannot generalize the effect of specific heterogeneity measures (*e.g.*, hedgerows, grassy margins). The HNV score developed by Pointereau *et al.* (2010) provides a less accurate description of input intensity than the IC/ha: it is based on the relative amount of land use that is predefined as extensive. Its advantage is that it integrates a landscape heterogeneity component. Combining the IC/ha with the landscape component of the HNV could test an interacting effect of these two components on biodiversity, at the French country scale.

2. Data availability is an important limiting factor for studies addressing the spatial distribution of agricultural intensity. It may explain the dichotomous view of intensity, prevailing in such studies, that focuses either on the distribution of organic versus conventional farming (Gabriel *et al.* 2009 and Ilbery & Maye 2011, in the UK; Frederiksen & Langer 2004, in Denmark; Rundlöf & Smith 2006, in Sweden) or on high nature value (HNV) areas (Baldock *et al.*, 1993; Beaufoy *et al.*, 1994; Andersen *et al.*, 2003).

Other methods besides ours have mapped agricultural intensity with higher resolution than that in agricultural surveys such as the FADN. Neumann *et al.* (2009) and Temme & Verburg (2011) developed a method based on multinomial logistic regression to predict intensity from biophysical and socioeconomical variables at a $1*1$km resolution. This $1*1$km grid is much finer than SAR resolution (mean width = 22.4 km). We, however, describe intensity with the IC/ha indicator, which is continuous and incorporates several input categories, while these authors only estimated three intensity classes of an indicator and only based on nitrogen inputs – we showed that some systems could have similar nitrogen input levels but twofold differences in the IC/ha value (Chapter V). A trade-off exists between the accuracy and the resolution of the intensity predictions and methods.

3. Temme & Verburg (2011) estimated separate intensity classes for livestock and crop production. Studies describing agricultural intensity and its impact on biodiversity often focus on one type of production: livestock (review in Vickery *et al.* 2001) or crops (review in Stoate 2001). By including several input categories, the IC/ha indicator can describe the intensity of both livestock and crops. Interestingly, we showed that these two production types alternated along the intensity gradient: the IC/ha revealed differences in intensity both between and within production types. Scenarios of strong intensity modifications may involve changes in types of agricultural production, which, however, were not considered in our study.

1.2 The farmland bird community focus

We focused on the response of common farmland birds to agricultural intensity at the community level. Because farmland birds are closely linked to agricultural habitat and sensitive to its intensity, they are at the center of the production/biodiversity reconciliation issue. Certain countries, such as the UK, recognize common farmland birds as priorities for conservation actions (Gregory *et al.*, 2002).

For the intensity gradient that we studied, intensity did not have an effect on either the absolute size or diversity of the farmland bird community. Intensity strongly influenced the community composition: winner species replaced loser species along the increasing intensity gradient. Recent studies have shown agricultural intensity (or, more generally, habitat disturbance) influences the composition of bird communities, rather than their size (Devictor *et al.*, 2008; Doxa *et al.*, 2010), as well as the existence of intensity winner and loser species (Phalan *et al.*, 2011b). The presence of both loser and winner species, and the absence of an effect on community size, is a result that cannot be used to advocate unequivocal intensity objectives that maximize all species at the same time. Mouysset *et al.* (2012) modeled the effect of public policies on French bird communities and also found that no scenario could maximize all species. The effect of intensity on several community descriptors should be used to inform policymakers, who can further decide on intensity allocation objectives according to conservation priorities. When we optimized intensity allocations, we maximized the coefficient of variation of the CSIg for the bird community. The objectives were to maximize the diversity of the bird communities among French SARs and to have balanced abundances between winner and loser species. Our model and optimization procedure could be further used on other community descriptors (*e.g.*, specialization, trophic level, non-farmland birds).

An increasing number of studies address the effect of agricultural intensity at the community level rather than at the level of a single species (Doxa *et al.*, 2010; Ekroos *et al.*, 2010; Filippi-Codaccioni *et al.*, 2010). Addressing trait-based groups within the community is a good way to understand underlying mechanisms of impact (McGill *et al.*, 2006; Violle *et al.*, 2007). When comparing farmland specialists to generalist species, the previous studies showed agricultural intensity caused biotic homogenization, *i.e.* to favor a few generalist species, while being disadvantageous to many specialists. Within our community of farmland specialists, the species with highest specialization degrees were seed eating species, arable specialists, and intensity winners. Other community descriptors (*e.g.*, trophic index, main sub-habitat), besides specialization, are important for understanding mechanisms of the intensity impact.

Although birds can be used as biodiversity indicators, the response of our community to intensity should not be generalized. Within our community, the responses varied between groups because different mechanisms were involved. The effect of both intensity and heterogeneity has already been shown to vary between taxa (Perfecto *et al.*, 2005; Sjödin *et al.*, 2008; Nabe-Nielsen *et al.*, 2010). Several of our community results, however, are novel and should be tested on other ecosystems and taxa. Several studies that addressed the community level only measured either its size or its diversity (Holzschuh *et al.*, 2006; Kohler *et al.*, 2007). No response on these components could hide important effects on community composition. Nonlinear responses to agricultural intensity should also be tested. Finally, we showed that spatial aggregation can influence the relationship between biodiversity and intensity. This effect should be carefully addressed in future studies because agricultural intensity is *de facto* aggregated in several European countries (Rundlöf & Smith, 2006; Gabriel *et al.*, 2009). Such *de facto* aggregation could influence biodiversity/intensity relationships, and their subsequent conclusions regarding better intensity allocation strategies.

1.3 The scale studied

We studied the influence of spatial aggregation of agricultural intensity, by considering aggregation between surrounding SARs (mean SAR width = 22.4km), on the bird community. Other studies have addressed the interacting impact of intensity with properties of the surrounding area. Most of these studies took place at smaller scales, in which intensity was described at either the field or the farm level, while the surrounding area was a small landscape, within a 100 m (*e.g.* Rundlöf *et al.* 2008) to 5000 m (*e.g.* Roschewitz *et al.* 2005b) radius. For instance, the effects of local management (*e.g.*, an agri-environmental scheme: Concepción *et al.* 2008; organic farming: Roschewitz *et al.* 2005a; Holzschuh *et al.* 2006; Rundlöf & Smith 2006), between simple and complex landscapes, have been compared. These previous studies found significant interactions. Local management improvement yielded higher biodiversity benefits when the surrounding landscapes were simple (intensive).

At our larger scale, we found that intensity changes had stronger effects in extensive SARs that were aggregated with other extensive surrounding neighbors. Studies also found AESs to produce higher biodiversity benefits in more extensive countries (Kohler *et al.*, 2007; Batáry *et al.*, 2010) and in small regions ($10 * 10$km) with already high AES concentrations (Gabriel *et al.*, 2010). Results on the effects of interaction between local intensity and intensity of surrounding areas, therefore, differ between landscape scales and larger scales (*e.g.*, small regions, countries). Such results should not be generalized across scales. One explanation is that different scales involve different mechanisms of the effect of intensity spatial arrangement, on biodiversity (Section 2.2 in Chapter I).

According to the scale that they adopt, studies on the interacting effects of local and surrounding intensity have different strengths and weaknesses for revealing where policy efforts would be more effective. The landscape scale is relevant because it matches the scale of passerine bird habitat ranges (Soderstrom & Part, 2000) and the scale of several mechanisms explaining the impact of intensity and its allocation on birds (Table S.s1 in Appendix, and Section 2.2 in Chapter V). Studies that focus at the landscape level are able to respond to local conservation issues (Drechsler *et al.*, 2007; Polasky *et al.*, 2010; Wilson *et al.*, 2010). The landscape resolution is, however, too fine to target policies and to achieve conservation objectives at the country scale, which is also crucial. To address the country scale thoroughly, one challenge is to find a resolution with adequate data, and which is relevant to ecology and policy. The SAR resolution is a good trade-off between these requirements. It reveals intra-regional heterogeneity and could, thus, be adequate for fine tuning conservation policy. Clusters of contiguous SARs may be large enough to provide significant biodiversity benefits at the national scale. SAR resolution also has weaknesses because unlike the landscape, it is too large to address the direct mechanisms of impact of intensity, and its allocation on biodiversity. Instead, modifications of the intensity allocation at SAR resolution (*e.g.*, intensification, extensification, reallocation) gather a set of local mechanisms that finely impact bird metapopulation dynamics. SAR clusters match the scale used by such dynamics (Devictor & Jiguet, 2007) and other studies have used similar resolution to describe agriculture and discuss consequences for policy targeting on a national scale. Gabriel *et al.* (2009; 2010) used a $10*10$km raster covering all the UK and discuss where organic conversion should be further encouraged; Merckx *et al.* (2009) used $10*20$km small regions to optimize the effects of AESs, with spatial targeting.

1.4 European perspectives

Our case study, data, and methodology make our approach relevant to other European countries. The IC/ha intensity indicator is computed with FADN data, which are collected in the whole EU. The FADN has already been used to describe intensity across several European countries (Neumann *et al.*, 2009); however, the authors were limited to NUTS 2 resolution. Our methods to estimate the IC/ha intensity indicator at higher resolution relies on both the FADN and other agricultural datasets available in other European countries. The method could, thus, be generalized in Europe. Land use proportions and their heterogeneity were computed from the CORINE land cover database, which is available for 38 European countries.

One great advantage of the bird taxa and farmland species in particular, is that several large-scale monitoring programs exist in Europe. The European Bird Census Council brings together the national monitoring programs of several European countries, including the FBBS that we used. The EU officially recognizes a “Farmland Bird Index” (FBI) as an indicator of structural biodiversity (Butler *et al.*, 2010). Our study was based on intensity values computed for a single year; therefore, we could not use the FBI, which is an index of temporal evolution. The responses of the same farmland bird community descriptors to heterogeneity, intensity, and its aggregation, however, could be computed in other European countries.

There is a growing interest for scenario approaches to predict biodiversity impacts (Pereira *et al.*, 2010). Such scenarios can predict impacts, but also reveal mitigation opportunities. In Europe, existing scenarios of impact on biodiversity involve land use (Butler *et al.*, 2010; Barbet-Massin *et al.*, 2012; Mouysset *et al.*, 2011; Scholefield *et al.*, 2011) and climate (Devictor *et al.*, 2012). In addition to these variables, agricultural intensity is also important to biodiversity. Integrating scenarios of intensity evolution could complement the previous approaches.

Several elements of our approach are related to general ecological mechanisms (*e.g.*, the importance of spatial arrangement, the response to intensity at the community level) and could be tested in other global regions. Other elements (*e.g.*, the farmland bird focus, the intensity gradient that excludes unexploited land uses) are more specific to Europe (or temperate regions), which restrains their application to other global regions.

2 The land sparing/sharing framework applied in our case study: the importance of mixed strategies

2.1 The biodiversity/intensity relationship in the European context

Relationships between biodiversity and agricultural intensity that are calibrated from real data are rare. Phalan *et al.* (2011b) provide valuable information on these relationships for bird and tree species. Their study took place in India and Ghana: similar tropical regions, although distant on the globe. Godfray (2011) highlighted an urgent need for similar studies in other habitats. We provide one of the first studies on temperate agroecosystems in Europe.

In tropical regions, the agricultural conversion of pristine forest habitats is one of the land use intensification pathways most threatening to biodiversity. Agricultural land uses are often too recent to now host specifically adapted species. Conversely in Europe, farmland habitats are old and they cover a very large part of nonurban areas. Unexploited land use have long been managed through a reserve strategy stable over time, and their conversion to agriculture no longer occurs (CLC, 2006). They represent conservation issue separate from that of farmlands (intensity allocation scheme in Fig. IV.1b). Intensification of existing agricultural land, however, is the land use intensification pathway most threatening to biodiversity. Among taxa, farmland species have been the most severely impacted. We focused on this conservation issue and, unlike (Phalan *et al.*, 2011b), we did not include unexploited land uses in our intensity gradient (x-axis of the Fig. IV.1a *vs* IV.1b).

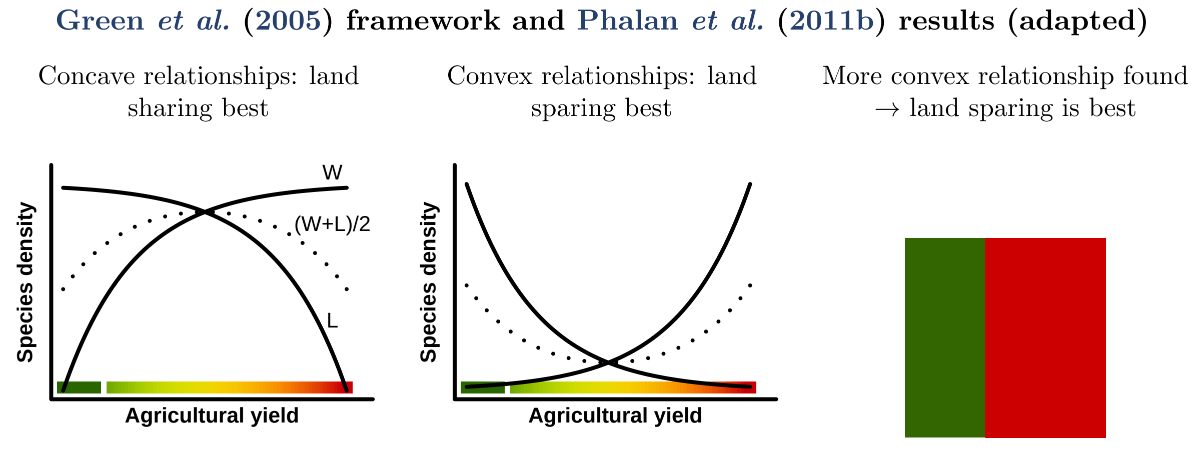
The relationship between loser species and agricultural intensity was convex. The convex shape suggests that even small intensification of the most extensive habitats has very adverse effects on these species. This result confirms the crucial biodiversity value of habitats that are maintained through extensive agricultural management (Bignal & McCracken, 2000; Atkinson *et al.*, 2002; Laiolo, 2005; Doxa *et al.*, 2010). These habitats can be considered land sharing because they are exploited for agricultural production purposes; however, because they have a very high conservation value and host a unique biodiversity, they must be preserved, even within the land sparing strategy (Gabriel *et al.*, 2009).

2.2 The community level reveals how winners substitute losers

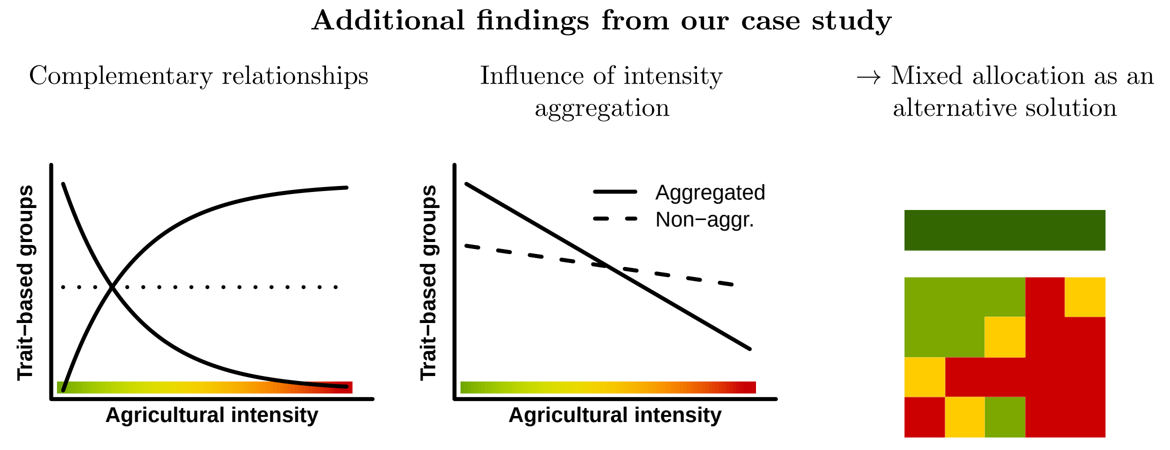
The Green *et al.* (2005) model links the shape of the biodiversity/intensity relationship to the best intensity allocation strategy between land sparing and sharing. Convex negative relationships suggest land sparing is best, while concave negative relationships suggest land sharing to be best. Phalan *et al.* (2011b) also found positive relationships with the presence of intensity winner species. In Green *et al.* (2005) and Phalan *et al.* (2011b), convex positive relationships involve land sparing, and concave positive relationships involve land sharing (Fig. IV.1a).

Phalan *et al.* (2011b) computed their biodiversity/intensity relationships at the level of single species. Overall, they found more species displayed convex negative relationships, and they concluded that land sparing would be the best strategy (Fig. IV.1a). By computing biodiversity/intensity relationships at the community level, on trait-based species groups rather than single species, we showed that community composition could change while its total size remained constant. Winner species substituted loser species on the gradient of agricultural intensity, and their relationships to intensity had complementary shapes (*i.e.*, their sum was constant): loser species had a convex response to intensity and winner species had a concave response (Fig. IV.1b). Loser and winner species having complementary responses means that the best strategy (sparing or sharing) is not the same for the two groups.

Other studies have found intensity to impact the community composition rather than its size (Doxa *et al.*, 2010; Ekroos *et al.*, 2010; Filippi-Codaccioni *et al.*, 2010). Such complementary relationships between loser and winner species could, therefore, be frequent. In these cases, alternatives to land sparing/sharing intensity allocations should be optimal to reconcile production, winner species, and loser species. One could choose to maintain loser species in priority order to avoid biotic homogenization (McKinney & Lockwood, 1999); however, both loser and winner species in our study are farmland specialists that have high conservation value.



(a)



(b)

Figure IV.1: The new elements that our study brings to the land sparing and sharing framework, as originally formalized by Green *et al.* (2005) and further used by Phalan *et al.* (2011b). (IV.1a) Phalan *et al.* (2011b) results, based on Ghana and India data. The agricultural intensity gradient includes unexploited land uses (dark green). Authors state that concave responses for both loser (L, negative response) and winner (W, positive response) species involve land sharing to be best. Convex responses show land sparing to be best. This implies that, within one strategy, the sum between loser and winner [(W+L)/2, dotted lines] is not constant along the intensity gradient. Since the authors find more convex negative responses, they suggest land sparing is the best strategy. (IV.1b) Our findings, based on the nationwide French intensity gradient. Unexploited land uses are excluded from this intensity gradient. We show complementary responses between loser and winners: convex and concave, respectively. Their summed abundance is, therefore, constant along the intensity gradient. We also show that the spatial aggregation of intensity strengthens its effect. We suggest that a mixed strategy that includes the following would be the best: (1) separate consideration of unexploited land use because it has conservation issues that differ from farmland in Europe; (2) promotion of large clusters of homogeneous, extensive areas; and (3) of intensive areas that display more heterogeneity.

2.3 Accounting for spatial arrangement: land sparing can influence the biodiversity/intensity relationship

The land sparing strategy corresponds to an allocation where intensity is aggregated. Agricultural intensity is segregated between the two (low and high) extremes, and aggregated within these extremes. The Green *et al.* (2005) model shows how the biodiversity/intensity relationship shape can help determine the best intensity allocation strategy (*i.e.*, the best aggregation level). Several authors suggest consideration of spatial allocation of intensity can improve models that rely on simple biodiversity/intensity relationships (Vandermeer & Perfecto, 2005; Perfecto *et al.*, 2009; Phalan *et al.*, 2011a). Our results confirm the importance of this improvement because we showed, with the linear component of the biodiversity/intensity relationship, that intensity aggregation reinforced the effect of intensity on biodiversity. Our data were insufficient to compute the interaction between aggregation and the nonlinear effect of intensity. Further studies should test the influence of intensity aggregation on convex and concave relationships.

An implication of the interacting effect of aggregation is that, besides intensity itself, the spatial arrangement of intensity can be used as a lever to enhance biodiversity. For example, the Fig. IV.1b reveals that loser species in intensive areas can be enhanced by either decreasing intensity or promoting spatial heterogeneity of intensity.

2.4 The importance of mixed allocation strategies

The three findings above (Sections 2.1, 2.2 and 2.3) point to the same conclusion that mixed intensity allocation strategies between land sparing and land sharing are important to consider, as highlighted below:

- In Europe, habitats with low, but not null, intensity are crucial to biodiversity, which is also supported by the shape of our biodiversity/intensity relationships. Even the land sparing strategy should include land sharing habitats.
- Studying the community level shows the response of loser and winner species to have complementary shapes, with one group substituting the other along the intensity gradient. Complementary shapes involve that the same strategy (land sparing or sharing) is not optimal for the two groups.
- Even within one group, mixed strategies can take advantage of the significant effect of intensity aggregation. For example, loser species had a convex response to intensity, which would indicate land sparing as the best strategy; however, promoting heterogeneity in an intensive area could also enhance those species.

Those supporting land sparing agree that some land sharing practices could form part of the land sparing strategy (Phalan *et al.*, 2011a). They are concerned that land sharing practices are mostly detrimental to yields and that opportunities to integrate them with land sparing would be rare. Land sharing practices could, however, be a way to enhance biodiversity and the ecosystem services benefiting agricultural production. We show that, by not only planning the relative area of intensity levels, but also their spatial allocation, one could enhance biodiversity with low yield penalties. We do not argue for marginal integration of one strategy into the other, but for a true mixed allocation strategy on a large scale (Fig. IV.1b). In the European context, natural habitat reserves are a distinct conservation issue from what is at stake on farmlands. Within farmlands, loser species need clusters of aggregated, low intensity areas. A complementary way to balance the abundances of loser and winner species will be to promote intensity heterogeneity in more intensive areas.

Interestingly, our findings regarding the effect of land use heterogeneity on the farmland bird community also lead to conclude that no unique solution can benefit all bird groups; mixed homogeneity/heterogeneity strategies will be necessary to maintain them all. Accounting for ecological complexities (*e.g.*, the importance of spatial arrangement, differences between trait based groups) leads to consider alternative, mixed solution for the production/biodiversity reconciliation.

Limitations of our contribution

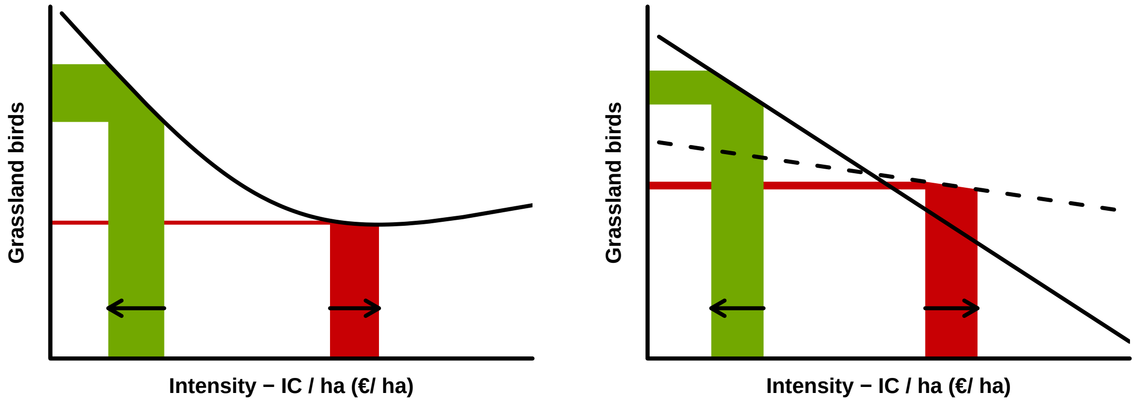
Unlike Phalan *et al.* (2011b), we did not compute density-yield functions, but relationships between trait-based species groups and an intensity indicator that integrated several input categories. Grouping species according to different traits revealed patterns of responses to intensity and provided insight into the underlying mechanisms. Our input intensity measure was more relevant for computing impacts on biodiversity than yield (see section 3.2 in Chapter I). It correlated with yield, but not perfectly; therefore it is less relevant for studying the production/biodiversity trade-off.

We focused on farmland birds and, therefore, excluded unexploited land uses from our intensity gradient. Our assumption was that natural and extensively managed semi-natural habitats have similar conservation value, but do not host the same biodiversity. We, therefore, suggest separate management of natural habitats and focus on farmland species, when deciding on intensity allocation strategies in agricultural regions. The response of non-farmland species to a gradient, including unexploited habitat, should be computed in order to validate this assumption and to determine the best strategy between land sparing and land sharing, for all species.

3 Targeting conservation policies to improve their effectiveness

3.1 Current distribution of the conservation policies

The biodiversity benefits of conservation policies are still under debate (Kleijn *et al.*, 2001; 2006). Some suggest spatial targeting of policy measures will improve their effectiveness (van der



(a) (b)

Figure IV.2: Consequences of intensification modifications on loser species (grassland birds), according to targeted intensity range (IV.2a) and aggregation (IV.2b, where solid line = aggregated areas, dashed line = non aggregated non areas). We propose that extensification should target extensive areas and promote aggregation in order to maximize benefits for loser species (left arrows). Conversely, intensification should target intensive areas and promote heterogeneity in order to minimize harm to loser species (right arrows).

Horst, 2007; Matzdorf *et al.*, 2008). Uthes *et al.* (2010) define targeting as applying conservation measures on the most vulnerable and/or suitable areas, where environmental effects are provided at lower costs than if conducted elsewhere. Kleijn & Sutherland (2003); Kleijn *et al.* (2009) argue that the shape of the biodiversity/intensity relationship can help determine the suitable area that should be targeted by conservation efforts. Exponentially declining relationships suggest that conservation measures that promote more extensive practices are more effective in the lower intensity range. As in the previous hypothesis, we found the relationship between all descriptors of the bird community, and agricultural intensity, to be sharper within the lower intensity range. Conservation measures should thus have a more effective impact on the community within this range. Several believe policy measures would be more effective in extensive areas where biodiversity levels are already high, and where the habitat provides more resources for multiple species requirements (Kleijn & Sutherland, 2003; Feehan *et al.*, 2005; Whittingham, 2007).

Current AESs are mostly *horizontal* (*i.e.*, non-targeted and implemented at the national scale). Some are *zonal* and target specific areas. Given that AES uptake is based on voluntary compliance, the spatial distribution of horizontal schemes is expected to be random and homogeneous; however, studies show unequal spatial adoption. Higher uptake rates occur in extensive areas, where the cost of adaptation to a specific measure is lower, and where farmers are more economically dependent on subsidies because they produce fewer goods (Kleijn & Sutherland, 2003; Latacz-Lohmann & Hodge, 2003; Osterburg *et al.*, 2001). Our results confirm these findings when we compare our map of intensity to the horizontal schemes uptake map (European Commission, 2008), which shows that higher uptakes are encountered in extensive areas. The main zonal schemes currently implemented target less favored areas. The objective of these schemes is to maintain agricultural activities where there is a high risk of land abandonment because of low economic profitability (European Commission, 2008). The large, low intensity cluster in Fig. III.8 (Chapter III) is almost entirely located in the less favored areas of France. Our intensity mapping reveals that zonal AESs, and heterogeneously distributed horizontal AESs, already tend to focus on extensive areas. According to the response of our bird community to intensity (Fig. IV.2a), focus on extensive areas will be more effective. AES benefits to biodiversity, however, are still questionable (Princé *et al.*, 2012). Our results on the significant effect of intensity aggregation can partly elucidate this paradox.

3.2 What kind of targeting will lead to future improvements?

The effect of agricultural intensity among SARs was weaker where intensity levels were heterogeneous. This result could explain why the extensifications promoted by AESs are less effective either when their uptake rate is spatially diffuse (Kleijn & Sutherland, 2003; Gabriel *et al.*, 2010) or in countries that are more intensive overall (Kohler *et al.*, 2007; Batáry *et al.*, 2010). In our case, promoting extensification in one SAR was less effective if neighbor SARs were not also extensive (Fig. IV.2b). The responses of the bird community to intensity and its aggregation suggests that measures promoting extensifications would be more effective if they targeted clusters of aggregated, extensive SARs (Fig. IV.2). In our model, the optimization procedure achieved the targeting of intensity modifications: starting from random allocation of intensity modifications, it sought the allocations that improved the trade-off, and optimal extensifications resulted in favoring clusters of aggregated, extensive SARs.

At the landscape scale, policy measures can have a positive influence in more intensive areas (Tscharntke *et al.*, 2005). They are also critically needed to maintain those species that are more adapted to intensive habitats than permanent grasslands, yet threatened by excessive intensity levels (Verhulst *et al.*, 2007; Wilson *et al.*, 2007).

Primdahl *et al.* (2003) suggested that two different types of measures could target low and high intensities: protection measures could strengthen environmental value of extensive areas, and prevent them from either intensification or abandonment, and improvement measures could reverse the detrimental impact of intensive areas on biodiversity. Compared to this framework, the optimal allocations of revealed by our model show that improving biodiversity is more effective when targeting extensive areas and that promoting heterogeneity in intensive areas can prevent biodiversity from further loss when intensifying.

4 Perspectives

4.1 Down-scaling: the intensity changes at the farm level

We revealed modifications of the intensity allocation that lead to win-no-lose solutions between production and biodiversity performances. In order to modify the intensity allocation at the SAR level, it will have to be modified at the farm level. The farm level is the first level where intensity is determined. At this level, one will need to find ways to adjust intensity. An initial question is how to distribute the IC/ha modification among input categories. Not all input categories are equally essential to production. The use of feed concentrates on intensive dairy farms is strongly correlated with milk productivity, yet pesticides on crop farms are partly used for preventive purpose, to secure harvest. Decreasing pesticide levels, without threatening either production or economic performance may be possible (Pimentel *et al.*, 1991).

Another important way to modify intensity would be to change efficiency. More efficient input use could decrease intensity without losing production (Fig. S.s2a in Appendix). Efficiency could contribute to win-no-lose solutions at the farm level, by enhancing biodiversity at zero production loss.

Improving the efficiency of input use has been suggested as an option for mitigating negative environmental impacts, mainly for components other than biodiversity (*e.g.*, greenhouse gas emissions, nitrogen pollution, Godfray *et al.* 2010; Steinfeld & Gerber 2010). Various opportunities to improve efficiency exist. Better efficiency in livestock uptake of feed inputs could reduce greenhouse gas emissions and nitrogen run-off (Garnett, 2009; Chadwick *et al.*, 2011). Whether such efficiency improvement options that mitigate impact on other environmental components would also benefit biodiversity is unclear. Global mitigation of water pollution and climate change should also have positive biodiversity effects. Some argue that higher efficiency would release pressure on land conversion and spare land for nature conservation (Borlaug, 2007; Godfray *et al.*, 2010). Using technological solutions to mitigate environmental impacts and to spare lands with intensification is part of the sustainable intensification reconciliation vision. Whether intensification actually spares land is subject to debate (Perfecto & Vandermeer, 2008; Ewers *et al.*, 2009; Rudel *et al.*, 2009). Seeking efficiency should not deflect attention from extensive systems, which our results, and many other studies, show to be crucial.

Efficiency can also be viewed as a redesign of the farming system, which is closer to the agroecology reconciliation vision. In France, the sustainable agriculture network (Réseau Agriculture Durable, RAD) provides an interesting case study and database that could be used to integrate the efficiency variable in our model (Rohellec & Mouchet, 2008). The RAD promotes a careful and efficient input use, and its focus is on input costs, like IC/ha. Its efficiency objective is to decrease intensity while maintaining production performances, and improving economic performance by saving input costs (Fig S.s2b in Appendix). The RAD involves a redesign of the system by promoting grassland-based feeding. Grassland adds biodiversity value and makes it possible to decrease forage crops, which require more input (pesticides in particular) for their cultivation. A possible hypothesis is that efficient and redesigned farms, like the RAD, are win-no-lose solutions to the production/biodiversity trade-off, and even win-win solutions to the economy/biodiversity trade-off. Such win-win solutions can promote further synergies between agriculture and conservation (*e.g.*, biodiversity valued with ecosystem services). The RAD database could be used to calibrate a scenario, with our model, that tests this hypothesis and reveals the potential of efficiency in overcoming the trade-offs among performance criteria.

4.2 Up-scaling: policy options to target intensity changes

Our results provide several options to improve the effectiveness of conservation by targeting specific intensity range, and by reaching specific (aggregated or not) allocations. Today, policy instruments that target measures and modify the allocation of intensity at the national scale are lacking. Intensity allocations drew a trade-off between production and biodiversity performance. Some studies have formalized similar trade-offs between production and the environment as trade-offs between private and public benefits (Parra-López *et al.*, 2009; Groot & Rossing, 2011). This formalization matches the policy design framework proposed by Pannell (2008) for determining the policy mechanism that reaches a given target for the private/public benefit space. Applied to our trade-off, this framework suggests that the win-no-lose intensity allocation could be reached with an *extension* policy mechanism. Authors define it as education, communication, and support for a community network. At the scale of our study, communication and networking should be implemented at SAR clusters in order to coordinate the intensity changes between SARs.

Implementing measures at the level of SAR clusters corresponds to local governance of conservation policies. Current European AESs are mainly designed at either EU or national levels. Examples where biodiversity-related measures were successfully elaborated at the local level (Fairbrass & Jordan, 2001; Weber & Christophensen, 2002) also exist. Successful elaboration is dependent on two key elements. Higher levels of governance (*e.g.*, country, EU) have to create opportunities for participation by local stakeholders. The subtle balance between individual and collective interests is also a challenge. Such bottom-up policy design, however, is the only way to promote positive changes (*e.g.*, extensification, reallocations), while current top-down design mainly manage to avoid changes for the worse (Léger *et al.*, 2004). Our model could include a policy component that tests for the most effective policy mechanisms to reach optimal intensity allocations. Mouysset *et al.* (2011) developed a bio-economic model where public policy scenarios influence the land use allocation decisions of farmers, which are then evaluated for their economic and biodiversity performances. This component could be complementary to our model, which already contains a description of farming intensity and policy targeting.

4.3 From biodiversity to other criteria and ecosystem services

Our study focuses on biodiversity, among other environmental components. Agricultural intensity can also have major impacts on many other environmental components, such as greenhouse gas emissions, land use changes, perturbations of the nutrient cycle, and water pollution (Matson, 1997; Foley *et al.*, 2005). Optimal intensity allocations would be valid on these other components if they had the same relationships with both intensity and its aggregation as biodiversity. This is not always the case because synergies and trade-offs exist among the different environmental performance criteria of agriculture. Our results show the importance of extensively managed habitats for several species of the farmland bird community. Extensive systems have lower GHG emission performances, *per* unit of product, and they are associated with grassland feeding, which increases enteric CH_4 production (Eckard *et al.*, 2010; Gerber *et al.*, 2010). We showed that concentrating intensifications in certain SARs makes it possible to increase production, while maintaining the diversity of bird communities at the national scale. Such concentration would likely be very detrimental to other criteria and have a negative impact, not only at the SAR scale, but also at the regional or even global scale (*e.g.*, water pollution, greenhouse gas emission). One way to include other environmental components would be to compute the quantitative relationships between different criteria and intensity.

Another solution would be to focus on ecosystem services in order to get a holistic and utilitarian vision of the different environmental components. Payment for ecosystem services are increasingly common (Farley & Costanza, 2010), and they could add an interesting perspective to AESs (Whittingham, 2011). Today, farmers consider most AESs as constraints. Rewarding ecosystem services, whose value can be concretely quantified, could empower farmers in regard to conservation policies. This would especially be the case in extensive systems where subsidies are an important part of a farmer's income because productivity is too low to guarantee economic viability. Value could be added to these systems by considering the wide range of ecosystem services that they sustain (*e.g.*, carbon sequestration, Soussana *et al.* 2010; pollination, Power & Stout 2011). Evidence for a link between biodiversity and ecosystem services exists but the exact relationship remains unclear (Hooper *et al.*, 2005), and whether measures designed to deliver ecosystem services also benefit biodiversity depends on scale and local context (Anderson *et al.*, 2009). We show that it is crucial to consider complexity: reconciliation solutions differ among species groups and are not generalizable among scales or global regions. Mixed solutions adapted to different contexts, rather than unique solutions, will be needed to valuing ecosystem services and reconciling production, biodiversity and other environmental components.

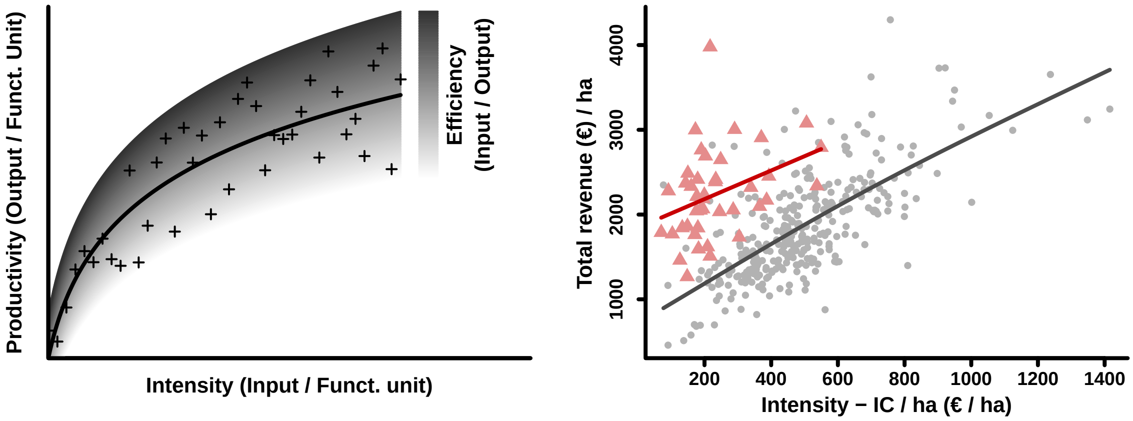
Supplementary material

s1 Agricultural intensity: several measures and effects

Intensity measure	Mechanisms of impacts on birds	Examples of studies
Land use		
Grassland (↓)	Less nesting habitats and rich foraging habitats (especially for the arthropod food resources)	Siriwardena (2001); Olsson *et al.* (2002)
Set-asides (↓)	Less nesting habitats	Poulsen *et al.* (1998); Bracken & Bolger (2006)
Winter stubbles (↓)	Less seed resources for resident birds in winter	Gillings *et al.* (2005); Peach (2001)
Spring sown cereals (↓)	Less short vegetation nesting habitats	Brickle *et al.* (2000)
Particular practice		
Pesticides use (↑)	Direct toxicity, decreased arthropod and (weed) seed food resources	Carson (1962); Boutin & Jobin (1998)
Fertilizer use (↑)	Decreased food resources, vegetation cover less suitable for nesting	Atkinson *et al.* (2005); Durant *et al.* (2008)
Stocking rates (↑)	Direct nest destruction, vegetation cover less suitable for nesting	Beintema & Muskens (1987); Paine *et al.* (1996)
Landscape components		
Semi-natural habitats (↓)	Less nesting habitats	Billeter *et al.* (2008); Batary *et al.* (2010)
Heterogeneity (↓)	Decreased availability of complementary resources (*e.g.*, nesting and foraging habitats) within the species habitat range	Dunning *et al.* (1992); Berg (2008); Brotons *et al.* (2005)

Table S.s1: (Non-comprehensive) list of measures that have been used to describe agricultural intensity, and their effect on birds. The arrow indicates if this measure is positively (up arrow) or negatively (down arrow) associated with intensity. The main mechanisms of effect are detailed. We give example of studies using each measures (several different measures can be used in these studies).

s2 The efficiency lever



(a) (b)

Figure S.s2: Efficiency as a lever for improving production or economic performance without increasing intensity. (S.s2a) Theoretical relationships between the intensity, productivity and efficiency of a set of farms (dots). Black line: average relationship between intensity and productivity. Dark area of the polygon: high efficiency, bright area of the polygon: low efficiency. Funct. unit: functional unit (*e.g.*, ha cultivated, number of cows). (S.s2b) Comparison of the economic efficiency of conventional farms (Farm Accountancy Data Network, FADN, in grey) *vs* farms of the Sustainable Agriculture Network (RAD, in red) promoting careful and efficient input use. 2006 data, n=319 FADN farms, n=41 RAD farms.

Part B

Articles

Chapter V

A novel method for mapping agricultural intensity reveals its spatial aggregation: implications for conservation policies

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Abstract

The objective of this study was to map agricultural intensity on the scale of France with spatial resolution adequate for policy targeting. Using the French Farm Accountancy Data Network (FADN), we computed an intensity indicator based on input costs per ha ("*IC/ha*"). Common variables between the FADN and four other datasets were included in a two steps multinomial regression to estimate the IC/ha value of each Small Agricultural Region ("SAR", units with homogeneous agro-ecological characteristics with mean width = 22.4 km). The local indicator of spatial association was used to reveal clusters where SARs with homogeneous intensities were aggregated. We showed that the IC/ha indicator displayed a broad intensity gradient where production types were fairly evenly distributed. Multinomial regression models provided a reliable estimate of the intensity indicator (mean cross-validation error = 23%, mean $r^2 = 0.7$) with SAR resolution. At the scale of France and within the two intensity extremes (< 300€/ha and > 500€/ha), SARs were significantly aggregated in several clusters. Most low-input SARs were aggregated into a large cluster ranging across several mountainous regions. Less high-input SARs were significantly aggregated. Our results could be used for infra-regional targeting of conservation policies.

1 Introduction

The lack of spatial targeting has been identified as an important cause of the low effectiveness of agri-environmental schemes (AESs) for promoting biodiversity (Feehan *et al.*, 2005; Whittingham, 2007). AESs are policies designed to encourage farmers of the European Union (EU) member states to protect and enhance the environment on their farmland. Horizontal schemes applied across one or several European countries do not always have similar effects on species among regions (Whittingham *et al.*, 2007). Spatial targeting is expected to improve the cost-effectiveness of AESs, as applying conservation measures on the most suitable areas would provide environmental effects at lower costs than if conducted elsewhere (van der Horst, 2007; Piorr *et al.*, 2009; Uthes *et al.*, 2010). Two contrary types of spatially targeted policies have been suggested. On the one hand, policies could target areas with aggregation of extensively managed farmlands, which have been shown to host higher biodiversity levels (Kleijn & Sutherland, 2003) and provide more resources for the multiple species requirements (Whittingham, 2007). Zonal scheme targeting these regions would thereby reinforce the quality of areas with high biodiversity potential, which could be the most effective option (Feehan *et al.*, 2005). On the other hand, policies could target areas with aggregation of intensively managed farmlands in order to reverse biodiversity decline in regions where it is the most severe (Primdahl *et al.*, 2003). In all cases, however, policy options require data on farming intensity for large gradients and scales and at a resolution relevant for fine policy targeting, and these have been lacking up to now.

Many studies tackling the environmental impacts of agricultural intensity focused on a single component, such as nitrogen input (Billeter *et al.*, 2008; Kleijn *et al.*, 2009; Temme & Verburg, 2011) or pesticides (Boutin & Jobin, 1998). Other studies used indirect indicators of agricultural intensity such as yield (Donald *et al.*, 2001) or the relative amount of arable fields (Ekroos *et al.*, 2010). Few studies integrate the various components of agricultural intensity into a more complete indicator. Assessing several complex intensity variables requires a large amount of data. Farm surveys can be conducted (Herzog *et al.*, 2006b) although this would not be feasible on large scales.

Because of the above-mentioned difficulties, a dichotomous view of agricultural intensity prevails in studies addressing intensity distribution on a large spatial scale and at a high resolution. Several studies focus on the distribution of organic *versus* conventional farming (Gabriel *et al.* 2009 and Ilbery & Maye 2011 in the UK, Frederiksen & Langer 2004 in Denmark, Rundlöf & Smith 2006 in Sweden). Even though organic farming seems to have a generally positive effect on species richness and abundance (Bengtsson *et al.*, 2005), it is not the only agricultural management option for promoting biodiversity. Other studies focus on extensively managed farmlands, which are crucial for European biodiversity (Bignal & McCracken, 1996; Benton *et al.*, 2002).

For instance, the indicator of high nature value (HNV) characterizes and maps such low-input agricultural systems with high environmental qualities (Baldock *et al.*, 1993; Beaufoy *et al.*, 1994; Andersen *et al.*, 2003; Pointereau *et al.*, 2007). As for organic farming, it remains a dichotomous view of agriculture (HNV *vs* non-HNV, organic *vs* conventional) regarding its effects on biodiversity.

This dichotomous view of agricultural intensity is insufficient because biodiversity can display continuous response to a large intensity gradient (Kleijn *et al.*, 2009; Ekroos *et al.*, 2010). Studying the distribution of agricultural systems belonging to a large, continuous gradient of intensity is thus important. A few studies have addressed this question and partially overcome the issue of scale and resolution. Reidsma *et al.* (2006) developed an aggregated intensity indicator based on input costs, but due to poor availability of data, it described intensity at a low spatial resolution, unsuitable for the fine-tuning of public policies (*i.e.* NUTS 2). Temme & Verburg (2011) developed a method to estimate and map agricultural intensity with very high resolution (1 km^2 grid) on the scale of Europe. However, their intensity measure was not continuous (two or three intensity classes for livestock and arable farming respectively).

The objective of this study was to map the spatial distribution of agricultural intensity for the whole of France with a spatial resolution that would be adequate for a better targeting and adaptation of conservation policies. Three steps were conducted to fulfill this objective. (i) We produced an intensity indicator relevant for the main agricultural production types in France and studied the distribution of the production types along the intensity gradient. (ii) We developed a method that relied on existing datasets to estimate the value of this indicator at the Small Agricultural Region (SAR) level compatible with the fine-tuning of conservation policies. (iii) We mapped the spatial distribution of our intensity indicator and tested for its spatial aggregation.

2 Methods

2.1 Data

Five datasets from year 2006 were combined to estimate an intensity indicator at the SAR level. All data were provided by the INRA service unit managing the French Observatory of Rural Development (ODR, 2011).

The first dataset was the French FADN (Farm Accountancy Data Network), the FADN follows the same methodology in the 27 countries of EU. It contains a very broad set of variables at the individual farm level. It provides a limited sample of farms surveyed on a yearly basis (n = 7361 farms in 2006, ≈ 2% of French professional farms) and gives statistical representativeness at the NUTS 2 scale for all the main production type. We considered two groups in the variables surveyed. The first group includes intensity-related variables such as the cost of each input

Category	Source	Variable	Unit
Land uses	CAP declarations	Wheat	% of UAA
		Maize	% of UAA
		Protein crops	% of UAA
		Oilseed rape	% of UAA
		Potato	% of UAA
		Beet	% of UAA
		Fallow	% of UAA
		Main fodder area	% of UAA
		Forage maize	% of UAA
		Forage crops	% of UAA
		Permanent grasslands	% of UAA
	BDNI	Stocking rate	Livestock Units/ha
	Corine Land Cover	Forest	% of municipality area
Socio-economic	Agricultural Social Security	Income	€/year
		Salaries	€/year
		Employment	Full-time equivalent
		Farm size	ha
		Number of farmers	Number
		Settlement year	Year
		Production type	Category
Topo-climatic	French Meteorological Institute	Elevation	m
		Mean temperature	° C
		Min temperature	° C
		Max temperature	° C
		Precipitations	mm
		Number of days with precipitations	Number
		Number of frost days	Number
		Mean humidity	%
Subsidies	CAP declarations	Extensive practices	€
		Slaughter	€
		Suckling Cow	€
		Male bovine	€

Table V.1: Source, list and unit of all the variables used as predictors for the IC/ha intensity indicator estimation. Only one source of data is used for each variable category, except when specified. CAP = Common Agricultural Policy, UAA = Utilized Agricultural Area, BDNI = national bovine livestock identification database. All data where provided by the French Observatory of Rural Development (ODR, 2011).

categories. The second group includes a broader set of variables regarding agricultural land uses, socio-economic characteristics, topo-climatic conditions and subsidies.

The above-mentioned variables of the second group were also surveyed in four other datasets (Table V.1). The advantage of these datasets is that they provide the value of variables for an extensive sample at a fine level, unlike the FADN: all individual farms or all municipalities are covered. The dataset from agricultural social security collects socio-economic variables on almost every French farm (n = 306773 farms). As it provides an exhaustive representation of French farms, data can be aggregated to compute variable values at the municipality level. The dataset from Common Agricultural Policy (CAP) declarations provide aggregated information on the agricultural land uses and the subsidies for all French municipalities, except for municipalities that are mostly urban (information on 34609 municipalities out of a total of 36584 municipalities in France). The CAP dataset gathers all European subsidies received by farmers of the EU member states. These subsidies combine direct income payments as well as subsidies for rural development which include agri-environment schemes. For a given municipality, the total area of the different land uses is available, as well as the the sum of the different categories of subsidies received by all of the farms located within the municipality. The dataset from national bovine identification keeps track of every bovine individual. It thus provides the value of the stocking rate in livestock unit per area unit per time unit for every municipality where bovine livestock had been present (n = 27399 municipalities). Finally, topo-climatic data were available for every French municipality through the dataset from the "Météo France" French meteorological institute.

2.2 *Input Cost/ha* intensity indicator computation

We developed the *Input Cost/ha* ("*IC/ha*", expressed in €/ha, and per year) aggregated intensity indicator. It was defined as the ratio between the sum of different categories of input costs and the total Utilized Agricultural Area (UAA) of the farm. Input costs totaled expenses in fertilizers, feed stuff, pesticides, seeds, fuel, veterinary products and irrigation water.

The use of costs rather than amounts made it possible to aggregate diverse categories of input relevant for the different production types. Intensity was computed for five production types (industrial crops, cereals, mixed, bovine dairy, bovine meat) accounting for 67% of French farms and covering almost 80% of French agricultural lands. We excluded production types with low territorial importance (vegetables). We also excluded production types where the value of the IC/ha indicator was too high to be compared with that of the five production types. It was the case for wine and orchard that have very high input levels, as well as poultry and pigs which have both very high input levels and often very low UAA leading to extreme IC/ha values. In order to overcome year-to-year variation in price and stock an averaged value of the IC/ha intensity indicator was computed for years 2004, 2005 and 2006.

A hierarchical clustering analysis was performed on the various cost categories of the IC/ha indicator in order to reveal the intensity gradient and to study the distribution of production types along it. The hierarchical clustering was performed on the FADN farms of our five production types (n = 3928 farms). We used the *hclust* function within the R statistical software (R Development Core Team, 2007). The scaled values of the *per* ha input cost categories were used to compute Euclidean distances between individuals (farms). We used Ward's minimum variance clustering method to define groups such that the within-group sum of squares (*i.e.* the squared error of ANOVA) was minimized. The agglomeration procedure was stopped with seven groups showing contrasting intensities and cost structures.

The FADN provides statistical representativeness at NUTS2 and national scale. To compute the total farm number of each production type and the national cover of the groups obtained from the hierarchical clustering analysis, an extrapolation coefficient was applied to the individual farms (Agreste, 2006).

2.3 Estimation method of the *Input Cost/ha* at SAR resolution

We developed a method for providing a reliable estimated value of the IC/ha intensity indicator at the SAR level and for France as a whole. The SAR level is a zoning that was specifically designed to define units with homogeneous conditions in terms of agricultural systems, soil and climate (Klatzmann, 1955). The mean width (± standard deviation) of a French SAR is 22.4 ± 13km. The SAR level of aggregation provided the best trade-off between accuracy of the estimation and accuracy of the resolution (Section 2.3). Estimated IC/ha values at the SAR level were obtained from aggregated IC/ha values first estimated at the municipality level. In order to estimate the IC/ha at a municipality level, we used variables common between the FADN and the other datasets providing their value for every municipality (Section 2.1). These variables were used as predictors of the IC/ha intensity indicator in a multinomial regression model calibrated on FADN farms. The multinomial regression model was then used to estimate the IC/ha value for every municipality, where the value of the predictors was known through the other datasets (Section 3.2).

Method validation

The quality of the estimation was assessed on several criteria. The goodness of fit of each model was computed through the r^2 and the AIC criterion was used for model selection (see Section 3.2). After their calibration, the models were used for prediction. Because there can be a trade-off between the goodness of fit of a model and its prediction abilities, cross-validation was used to assess the prediction accuracy of the models (Geisser, 1975; Hawkins *et al.*, 2003). As the FADN sample sizes used for calibration were rather small, leave-one-out cross-validation (LOO CV) was used. For each model, we computed the mean cross-validation error, expressed as a percentage of the observed value (Geisser, 1975; Zuur *et al.*, 2007):

$$\mathrm{CV} = \frac{1}{\mathrm{n}} \sum_{\mathrm{i}=1}^{\mathrm{n}} \frac{100 * \left|\mathrm{Y_i} - \hat{\mathrm{f}}^{-\mathrm{i}}(\mathrm{X_i})\right|}{\mathrm{Y_i}} \tag{V.1}$$

The CV indicator is the mean absolute difference (in %) between the real IC/ha value of an FADN farm i (Y_i) and the value estimated by the model from its predictor variables when the farm is excluded from model calibration ($\hat{f}^{-i}(X_i)$).

The r^2 and the LOO CV were used to assess the quality of the estimation. Additionally, the LOO CV was used to determine the level of aggregation that provided the best trade-off between resolution and estimation accuracy. Four aggregation levels were tested: municipality (no aggregation), county, SAR and department (NUTS 3). The respective mean LOO CV values for these aggregation levels were: 56%, 38%, 23% and 18%. The extra 5% in prediction accuracy at NUTS 3 level compared to the SAR level would be achieved at the cost of a too large reduction in spatial resolution. The SAR level of aggregation was thus retained, as it seemed to be the best trade-off between spatial resolution adequate for policy targeting and estimation accuracy.

Estimation method

We performed a multinomial regression on the FADN. The IC/ha intensity indicator value (Y_i^{FADN}) of a farm i was estimated with a linear combination of its p predictors:

$$\mathrm{Y_i^{FADN}} = \alpha + \beta_1 \mathrm{X_{1i}^{FADN}} + ... + \beta_\mathrm{p} \mathrm{X_{pi}^{FADN}} + \epsilon_\mathrm{i} \tag{V.2}$$

The model computed the regression intercept (α) and slopes (β) of the p predictors. Normal distribution of residuals ϵ was assumed. Starting from the maximal model containing predictors as explaining variables, we used a backward stepwise procedure to the minimal adequate model including only the p' predictors with the best explanatory power. The minimal adequate model is the one that produces the least unexplained variation while retaining the minimal number of predictors according to the parsimony principle (Crawley, 2007). The stepwise procedure was carried out automatically using the mixAIC function within MMIX R package (Morfin & Makowski, 2008; 2009). It performs iterative statistical selection procedures based on the Akaike Information Criterion (AIC). As shown by Barbottin *et al.* (2010), AIC-based selection procedure enables keeping in the models explaining variables that are weakly significant (*i.e.* $0.05 < pvalue < 0.1$).

The minimal adequate model was then used to estimate the IC/ha intensity indicator for every municipality ($\hat{Y}_j^M$) (Eq. V.3). This estimation relied on the known values of municipality p' predictors left in the minimal model, as well as the intercept (α) and slopes (β) previously computed.

$$\mathrm{\hat{Y}_j^M} = \alpha + \beta_1 \mathrm{X_{1j}^M} + ... + \beta_\mathrm{p'} \mathrm{X_{p'j}^M} \tag{V.3}$$

The variables used as predictors were expected to have a good explanatory power of intensity only within relatively homogeneous systems. The preceding procedure was thus repeated separately for each production type within each region where it was present (84 combinations). In order to avoid overparametrization, a model was computed only when the FADN sample size was large enough (> 20 farms, n = 58 models). Over these 58 models, the average number of observation used for calibration was 69.9 (standard deviation = 42.5, min = 22, max = 215). For the other combinations of production types and regions ($n = 84 - 56 = 28$), the IC/ha estimation was thus “not applicable”.

Municipality IC/ha values were finally aggregated (weighted average) at the SAR level (see section 2.3). The average IC/ha value did not consider the other production types than the five included types (see section 2.2). Therefore, the IC/ha value at the SAR level was considered “not applicable” when the farms of these five types represented less than 2/3 of the total agricultural area.

2.4 Testing the intensity aggregation

To test for the spatial aggregation of agricultural intensity, we used the local Moran (Anselin, 1995) which is a local version of the Moran's I (Cliff & Ord, 1981). It measures the spatial auto-correlation. Positive values indicate spatial auto correlation, *i.e.* clustering of SARs with close IC/ha whereas negative values indicate more heterogeneity.

The local Moran of a SAR i (LI_i) is computed as follows:

$$\mathrm{LI_i} = \frac{\mathrm{X_i} - \bar{\mathrm{X}}}{\mathrm{Var(X)}} \sum_{\mathrm{j}} \mathrm{w_{ij}} \frac{\mathrm{X_j} - \bar{\mathrm{X}}}{\mathrm{Var(X)}} \tag{V.4}$$

where X_i stands for the IC/ha value of the SAR i, $\bar{X}$ the mean IC/ha of all SARs and $Var(X)$ the standard deviation of all SARs *IC/ha*. The connectivity matrix of the SARs is w where $w_{ij} = 1$ if SARs i and j are connected and $w_{ij} = 0$ otherwise. The connectivity matrix was then row-standardized (*i.e.* $\sum_j w_{.j} = 1$). A correlogram of the total spatial auto-correlation (Moran's I) against distance classes of connectivity was computed. Maximum total auto-correlation was reached for contiguous SARs. The local Moran was thus computed on contiguous SARs, *i.e.* only contiguous SARs were considered connected ($w_{ij} = 1$).

A bootstrap procedure was used to assess the significance of spatial aggregation, *i.e.* of the local Moran (bootstrap procedure adapted from Anselin 1995). Due to the presence of global spatial autocorrelation, inference was based on a conditional permutation approach. For each SAR, we computed a one-sided p-value (significant threshold = 0.1) of the local Moran based on 1000 sample permutations. It indicated if the local Moran was significantly higher than the average local Moran. We used the *lisa* function within the *ncf* R package to compute the local Moran and to run the bootstrap procedure.

We tested for a significant relationship between the SARs IC/ha values and their local Moran using a general additive model with a spline function allowing to fit non-linear relationships. We used the *gam* function within the *mgcv* R package that solves the smoothing parameter estimation problem by using the Generalized Cross Validation criterion.

3 Results

3.1 Agricultural intensity and input categories distribution across production types

The characteristics of the seven groups computed by the cluster analysis of input cost structure are detailed in Table V.2. It shows the distribution of the whole IC/ha intensity gradient across production types. The seven groups were distributed along a broad intensity gradient, group means ranging from 231.5 to 681.6 €/ha. Along this intensity gradient, groups dominated by livestock alternated with groups dominated by arable farming. Groups 1, 3, 5 and 7 were

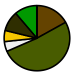
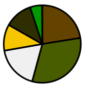
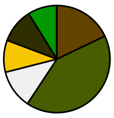
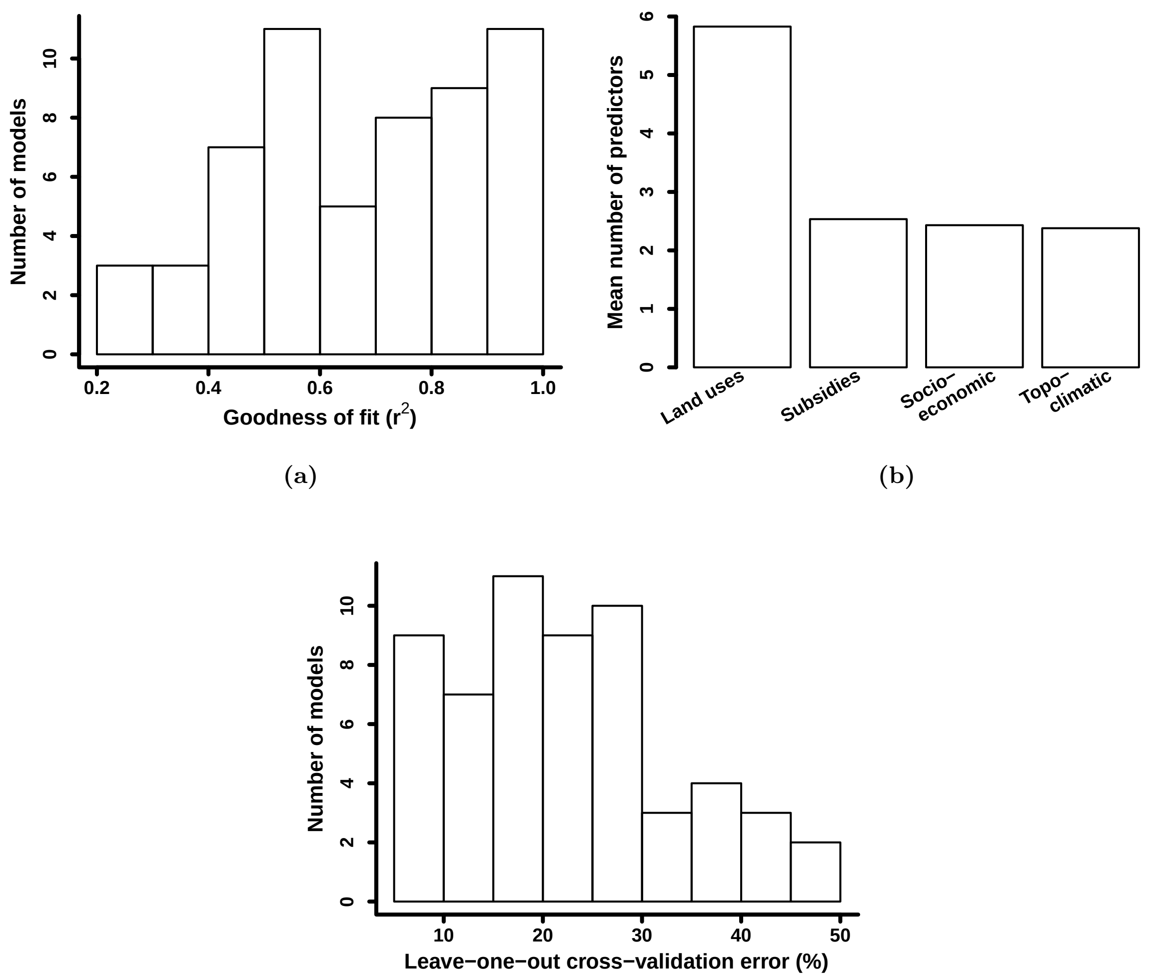
	Groups	1	2	3	4	5	6	7
Number of farms in each production type	Industrial crops	7	129	0	27	25	**300**	5
	Crops	15	**880**	1	**127**	44	202	6
	Mixed	122	161	18	20	**258**	58	82
	Bovine dairy	283	21	**229**	8	167	4	**143**
	Bovine meat	**354**	33	144	5	28	0	22
Total area	In 10^6 ha	4.29	6.46	1.73	0.77	2.50	2.08	0.99
	In % UAA	17.00	26.00	7.00	3.00	10.00	8.00	4.00
Input cost €/ha	Graphical representation							
	🟫 Fertilizers	47.20	124.10	71.10	129.60	108.70	165.60	124.40
	🟩 Feed	90.10	17.70	213.30	31.20	160.70	40.30	279.70
	☐ Pesticides	18.80	107.80	19.40	89.00	82.20	169.10	72.60
	🟨 Seed	19.40	51.10	24.30	81.40	55.10	133.30	67.10
	⬛ Fuel	35.10	39.80	39.90	48.20	56.60	74.30	71.80
	🟩 Veterinary products	20.70	3.60	45.00	6.60	26.00	4.80	65.40
	🟦 Irrigation water	0.10	0.40	0.10	63.00	0.20	1.60	0.60
	IC/ha	231.50	344.30	413.10	449.00	489.60	588.90	681.60

Table V.2: Characteristics of the 7 groups of FADN (Farm Accountancy Data Network) farms based on the clustering analysis. For each group: number of farms belonging to each production type, area extrapolated on the scale of France and level of the different input categories (in €/ha) integrated in the *Input Cost/ha* ("*IC/ha*") intensity indicator. In the graphical representation of the input categories, the size is proportional to the absolute value. Bold values indicate the dominant production type of each group. UAA = Utilized Agricultural Area. FADN data provided by the French Observatory of Rural Development (ODR, 2011).

dominated by livestock and mixed farming; they had contrasting total input costs, cattle feed and fertilizers always being the most important input categories. Conversely, the remaining groups (2, 4 and 6) were dominated by arable farms, where most of the input costs concerned fertilizers, pesticides and seeds. The bovine dairy farm-dominated group 7 showed the highest IC/ha of all groups. Feed was the most important cost category of this group that had lower expenses for pesticides and fertilizers than most arable groups. In comparison, group 6 had a slightly lower total IC/ha but it was dominated by industrial crop farming and had the highest pesticide and fertilizers costs ha among all groups.

We characterized low-input systems as the 20% quantile of IC/ha values, *i.e.* with an IC/ha value lower than 300 €/ha (20% quantile = 303.4536 €/ha). These low-input systems were concentrated in group 1, whose total IC/ha was 231.5 ± 87.9 €/ha, much lower than the total sample mean: 410.3±167.1 €/ha. Livestock farming and some mixed farming were the dominant production types in this low-input group. It covered an important part of French UAA (Utilized Agricultural Area) (17%). In the second lowest IC/ha group, most farms did not belong to the low-input systems (81% of the farms had an IC/ha value higher than 300 €/ha). This group was dominated by arable farms and had a high territorial importance (26% of the French UAA). In total, all the medium IC/ha groups (2 to 5) covered an important part of the French UAA. The most intensive systems (groups 6 and 7) had relatively low territorial importance.

3.2 Intensity estimation with SAR resolution



(a)

(b)

(c)

Figure V.1: Characteristics of the regression models used for the estimation of the *Input Cost/ha* indicator. One model is computed for each agricultural system of each region (n = 58 models in total). (V.1a) Distribution of the r^2 values of these models. (V.1b) Mean number of predictors of each categories left in the models after variable selection (variables of each categories are listed in Table V.1, data source: ODR 2011). (V.1c) Distribution of the relative prediction error (in % of the observed value) when performing leave-one-out cross-validation.

Regression models estimating the IC/ha intensity indicator had good descriptive and predictive performances (Fig. V.1). Among production types and regions, the goodness of fit of the regression models ranged from 0.26 to 0.96 with a mean (± standard deviation) of 0.68 ± 0.22 (Fig. V.1a). Only 23% of the models showed a r^2 value lower than 0.5 while most of the models showed a r^2 value higher than 0.7. On average, 13 predictors were selected to fit the IC/ha value (standard deviation = 2.1, min = 7, max = 16, minimum difference between number of observations and number of predictors = 12, lower than 20 for only 3 models out of 58) (Fig. V.1b). Variables related to land uses were the most used predictors: on average, 6 land use predictors were kept in the minimal adequate models based on the AIC criterion. The other variable types had a similar selection frequency, ≈ 23 variables of each category being kept in the final model. The models had good predictive abilities. The mean leave-one-out cross-validation (LOO CV) relative error was 23% (Fig. V.1c). A large majority (> 60%) of models yielded LOO CV relative errors lower than 25%.

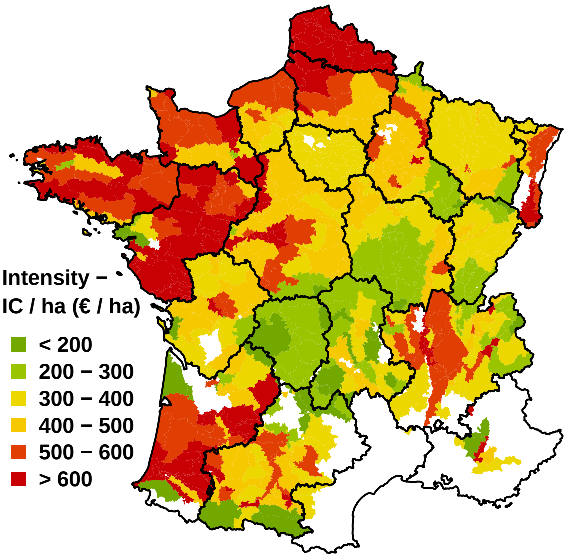
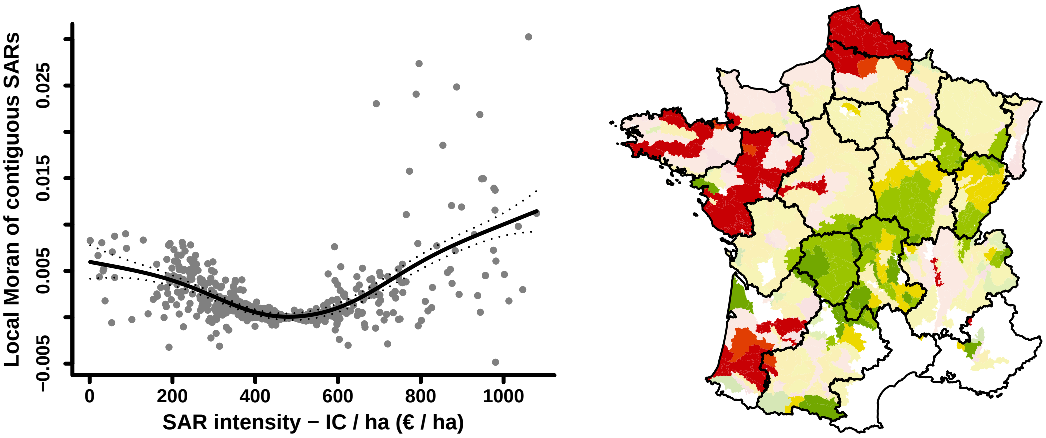


Figure V.2: *Input Cost/ha* (*IC/ha*) value of French Small Agricultural Regions (SARs) dominated by crop, livestock or mixed production (UAA > 2/3 of total UAA). SARs dominated by other production types appear in white. Continuous IC/ha values are represented in 6 classes from lowest (green) to highest (red) level. Administrative region (NUTS 2) borders in black.

The estimation method provided continuous value of the IC/ha intensity indicator at an infra-regional resolution (higher resolution than the NUTS 2 region): the SARs (Fig. V.2). The IC/ha indicator displayed a broad gradient of intensity, SAR values ranging from 37 to 1080 €/ha (mean ± sd = 452 ± 194 €/ha). The map revealed the location of low-input systems, with an IC/ha lower than 300 €/ha and thus mostly resembling the first group of FADN farms described in Table V.2, dominated by grassland-based livestock farming (meat or dairy bovine). They were mainly concentrated in a large area spreading across several administrative regions of the center and eastern parts of France. Several other regions also contained more isolated low-input SARs along with more intensive ones. SARs with high input levels were concentrated in western and northern regions of France. They had an IC/ha value higher than 500 €/ha and were thus close to the last two clustering analysis groups, one being dominated by arable farming systems (industrial crops) and the other by bovine dairy farming systems. SARs with medium IC/ha filled the large remaining part of the territory. The spatial coverage of the map (Fig. V.2) was consistent with the UAA coverage of the groups of farm types (Table V.2).

The map added information on the location of the different agricultural intensities. Along with sharp contrasts between the NUTS 2 intensity (*IC/ha*), the maps also revealed an important infra-regional heterogeneity of agricultural intensity.

3.3 Spatial aggregation of farming intensity



(a) **(b)**

Figure V.3: Spatial aggregation (local Moran) of the intensity of Small Agricultural Regions (SARs). Intensity is expressed by the means of the *Input Cost/ha* indicator ("*IC/ha*"). (V.3a) Each point stands for a SAR. The value of the local Moran of contiguous SARs is plotted against the SAR IC/ha value. Black curve: generalized additive model determining the average relation between the SAR IC/ha and local Morans. Dotted curves: 95% confidence interval. (V.3b) Map of SARs IC/ha values and local Moran significance. The color indicates the IC/ha value of a SAR while the brightness reveals whether the IC/ha value is significantly auto-correlated with the ones of contiguous SARs. Legend is the same than in Fig. V.2, continuous IC/ha values are represented in 6 classes from lowest (green) to highest (red) level. Dark colors: significant auto-correlation with IC/ha of contiguous SARs, pale colors: no significant auto-correlation.

There was a significant relationship between the intensity of the SARs and their tendency to display IC/ha values close to those of their contiguous neighbors (local Moran) (Fig. V.3a, GAM, spin function with 5.835 degrees of freedom, p-value $< 2e^{-16}$, explained variance = 43.1%). The general pattern was that of an aggregation of SARs with low intensity on the one hand and of SARs with high intensity on the other hand. These SARs showed positive local Moran value, reflecting that they tended to have contiguous neighbors with close IC/ha values. Conversely, SARs with IC/ha values close to the sample mean (454.7 ± 215.2 €/ha) showed almost null local Moran.

There was significant aggregation of both low and high IC/ha SARs (Fig. V.3b). A majority of the low-input SARs revealed in Fig. V.2 showed significant value of the local Moran aggregation index. There was thus a large cluster of SARs with low IC/ha values that were significantly auto-correlated between them. This cluster included some SARs with medium IC/ha levels and spread mainly across five regions encompassing mountainous areas. To a lower extent, some SARs with high IC/ha values showed a significant value of the local Moran aggregation index. They were distributed in three main clusters of SARs with high IC/ha values, significantly auto-correlated. The clusters of low and high input SARs did not display consistency with administrative region borders. Apart from these low and high intensity clusters, the remaining territory was filled with SARs mostly of medium and high IC/ha, but without showing significant aggregation.

4 Discussion

This study describes the distribution of farming intensity on the scale of France with spatial resolution relevant for the policy targeting of homogeneous conditions in terms of agricultural systems, soil and climate. The intensity indicator, based on input costs, was relevant for the main production types. We showed strong spatial aggregation of low-input systems and also revealed some aggregation clusters of high-input systems.

4.1 Weakness and strength of the intensity indicator and its estimation

The IC/ha intensity indicator aggregated several categories of inputs. It was relevant for different production types and it strongly correlated with yield. Some input categories like pesticides or fertilizers have direct negative effects on biodiversity (Stoate, 2001) while others, such as feed stuffs and seeds are expected to have indirect effects. For instance, intensive livestock farms with high feed costs are reported to produce higher rates of nitrogen dissipation (Bleken *et al.*, 2005). Among the groups of FADN farms, feed costs were strongly correlated to the other input categories across the different livestock farming systems, which is consistent with Andersen *et al.* (2004). The seeds are also an indirect component of intensity because they are usually treated with crop protection products and are frequently included in a technological package.

The IC/ha estimation had some limitations arising from the FADN variables and the estimation method. Input costs were used rather than amounts because the FADN does not provide any information on absolute amounts of inputs. Price or stock fluctuation can cause a bias in the proportionality between costs and amounts. To overcome this limitation, we averaged input cost value between years. However, we could not account for very recent chemicals, at the cutting edge of the technology, which can be expensive but efficient at low amounts. The input costs were divided by the *utilized agricultural area* (UAA) FADN variable. In mountainous regions, rangelands make a significant contribution to the livestock feeding system but they are not taken into account in the UAA. The estimated *Input Cost/ha* of several SARs located in the French Alps may thus be higher than in reality. The intensity estimation at the SAR level was the intensity of the five production types, in SARs where they covered more than 2/3 of the total agricultural area (intensity was not estimated otherwise). Bias aroused from ignoring a few very intensive farms that were too small to represent more than 1/3 of the SAR agricultural area. This was the case for pig and poultry farms which, due to being very intensive although small in size, put pressure on the environment through manure and slurry spreading. In this case, such pressure was not revealed by our intensity value. Intensity was thus under estimated for the few SAR concentrating intensive pig or poultry farms, mainly in the Brittany region.

Comparison with the high nature value (HNV) score of French municipalities (Pointereau *et al.*, 2010) indicates a good consistency with our intensity indicator as 96% of the SARs we defined as low input (20% most extensive, IC/ha <300€/ha) included HNV municipalities. Compared to the HNV score, one strength of our indicator is that it is not based on a scoring method requiring arbitrary computational choice but one weakness is that it does not integrate other components of agricultural intensity. For instance, the HNV score integrates land cover diversity and landscape complexity components of global agricultural intensity. Mixing our input cost indicator with other intensity components such as compositional or configurational indicators of landscape heterogeneity could be an interesting perspective.

We combined several agricultural data sets to compute the intensity indicator at SAR spatial resolution. These datasets are available for most European countries and over several years. Some variables of the FADN have already been used to describe agricultural intensity by Reidsma *et al.* (2006). These authors focused on livestock farming only and used an aggregated input cost variable gathering costs for fertilizers, crop protection and feed stuffs. They computed the input cost for 12 countries. However, they faced the FADN limitation in terms of representative scale, which cannot be finer than NUTS 2.

A few other authors have developed methods to estimate agricultural intensity at a finer level than directly available through agricultural surveys (*e.g.* $1km^2$ resolution in Neumann *et al.* 2009 and Temme & Verburg 2011). Temme & Verburg (2011) used biophysical and socio-economical variables to estimate a few classes of N-input through a multinomial logistic regression. Neumann *et al.* (2009) compared an expert-based approach (based on allocation rules) to an empirical approach (based on linear regression) for estimating livestock density. Compared to these two studies, our method provides an estimation at coarser spatial resolution. However, it is continuous and aggregates several input categories. Moreover, it is relevant for both arable and livestock systems, unlike that of Neumann *et al.* (2009). Our clustering analysis showed that focusing only on fertilizer, like in Temme & Verburg (2011), would have led us to conclude that some systems had similar intensity (fertilizer costs ≈ 124€/ha for groups 2 and 7 in Table V.2), whereas the other input categories led to a twofold difference in the total IC/ha value (334 and 682€/ha respectively for groups 2 and 7).

As they also used regression, the two preceding studies provide interesting comparison for the intensity estimation method. The goodness of fit between the linear combination of predictors and the actual intensity value seems pretty similar between our models and those of the two previous studies. In Neumann *et al.* (2009) r^2 ranges from 0.4 to 0.5 for the livestock distribution estimation in Germany. In Temme & Verburg (2011), ROC values ("Receiver Operating Characteristics") were used to assess the goodness of fit of logistic models, they ranged from 0.687 to 0.897 (unlike the r^2, the ROC value for no correlation is 0.5). Land use variables were the most frequently selected variables in our minimal adequate models used for intensity prediction. Temme & Verburg (2011) did not use land use predictors and variables left in the minimal model were thus mostly topo-climatic and socio-economic to a lesser extent. In Neumann *et al.* (2009), land use predictors seemed to be selected as frequently as socio-economic and pedo-climatic variables. The reason for these differences in variable selection may be that we used less precise topo-climatic variables (pedological information was not available in our case).

4.2 The spatial aggregation of intensity and its implications for conservation policies

The aggregation clusters of both high-input and low-input SARs did not show consistency with administrative region borders. Therefore, it would not be possible to spot them on the sole basis of regional averages provided by available agricultural statistics such as the FADN. Our intensity indicator and estimation method may be used in other European countries. As a spatial tool, it could prove helpful to design spatially targeted, effective conservation policy. By targeting homogeneous clusters of agricultural intensity, measures could be well adapted to the intensity context. These clusters could provide an opportune target to concentrate policy measures. Such concentration has been shown to improve AES effectiveness (Gabriel *et al.*, 2010). Primdahl *et al.* (2003) suggests that two different types of measures should target low versus high intensity clusters. Measures targeting low intensity clusters can be seen as "protection measures" preventing these areas from intensification or abandonment and strengthening their already high environmental value. Such infra-regional targeting of extensively managed areas could improve the efficiency of agri-environmental schemes (Kleijn & Sutherland, 2003; Feehan *et al.*, 2005). Conversely, measures targeting high intensity clusters can be regarded as "improvement measures" mitigating the detrimental effects that an intensive agricultural management has on biodiversity. Such improvement measures should be implemented in the high intensity clusters revealed in our study in order to achieve efficient spatial targeting.

The spatial segregation of agricultural intensity we highlight reveals that both zonal AESs and heterogeneously distributed horizontal AESs tend to focus on extensive areas. In France, zonal schemes mainly target less favored areas. The objective is to maintain agricultural activities where there is a high risk of land abandonment (European Commission, 2008). The large low-intensity cluster we revealed is almost entirely located in the French less favoured areas that cover around half of the territory. Horizontal schemes are expected to be widely implemented across the country. However the mapping provided by the European Commission (2008) reveals that more horizontal scheme subsidies are received in our extensive clusters compared to the intensive ones. This result is consistent with other studies that have shown that horizontal schemes are very unequally adopted spatially (Osterburg *et al.*, 2001; Kleijn & Sutherland, 2003) and that higher uptake rates are encountered in extensive areas where the cost of adaptation to the measure is lower. Territorial institutional factors also influence the contracting rate at a local scale (Allaire *et al.*, 2009).

In line with Gabriel *et al.* (2009) showing spatial aggregation of organic farming in the UK, our results show a strong spatial aggregation of low-input systems in France. In both cases, spatial aggregation seems to correspond de facto to a segregation of agricultural intensities at a national scale, as proposed in the Green *et al.* (2005) land sparing strategy. The opposite strategy would involve all agricultural lands being farmed with moderate intensity in order to fulfill both conservation and production objectives (wildlife friendly farming strategy, also formalized by Green *et al.* 2005). Gabriel *et al.* (2009) proposes to increase this segregation of objectives by promoting organic conversion (or extensive management in general) in areas where organic farming is already aggregated. Similarly, we suggest that protection measures should target areas with aggregated low-input systems, because they have been shown to be crucial for biodiversity. Spatial segregation of different agricultural intensities and objectives is a consequence of agricultural history and is congruous with local governance. However, the historical process of agricultural intensification has already led to a strong decline in farmland biodiversity. Intensifying the spatial segregation with protection measures targeting the remaining low-input areas might not be sufficient to reverse the trend. In this context, improving the quality of the agricultural matrix in the more intensive farmlands may also be important (Fischer *et al.*, 2008; Perfecto & Vandermeer, 2008).

Targeting areas with homogeneous agricultural intensity clusters rather than according to administrative region borders demands local governance of conservation policies. Currently, European agri-environment policies, AESs in particular, are mainly designed at a national scale. Two studies have revealed evidences of local governance leading to the successful elaboration of biodiversity-related policies (Fairbrass & Jordan, 2001; Weber & Christophensen, 2002). In these two studies, the European Union created opportunities for the participation of local actors, mainly non-governmental organizations. In the case of our results, local conservation policies adapted to homogeneous agricultural intensity clusters should involve stakeholders from agricultural and administrative sectors, as well as non-governmental organizations. However, building local and collective conservation policies can be a challenging task as it requires striking a subtle balance between individual and collective interests (Urbano & Vollet, 2005). As in studies from Fairbrass & Jordan (2001) and from Weber & Christophensen (2002), local governance initiatives would benefit from more support and frameworks designed at the European Union level.

5 Conclusions

Our method combines existing agricultural datasets to accurately estimate the distribution of agricultural intensity at higher resolution than directly available through the FADN data. We only accessed French data but similar datasets are available in other European countries where our method could be used. Moreover, we developed a single, continuous intensity indicator that is appropriate for all the main agricultural production types covering the territory. However, the intensity indicator does not integrate the landscape components of agricultural intensity that also impact biodiversity. It may thus be important to integrate these in an indicator of agricultural intensity. Our results show strong spatial segregation in clusters of homogeneous intensities. These clusters could be targets for adjusted and concentrated conservation policies. More research effort would be needed to provide the framework for efficiently designing conservation policies at an infra-regional scale.

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Chapter VI

Mixed benefits of compositional and configurational heterogeneity on farmland birds according to their habitat specialization

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In revision in *Biological Conservation*

Abstract

Restoring the heterogeneity of agricultural landscapes has been proposed as a key measure to promote farmland biodiversity. Recent studies, however, warn against generalizing the positive effects of heterogeneity on biodiversity because effects can vary across agricultural contexts and species. In this study, we tested the hypothesis that heterogeneity has a negative effect on habitat specialists and a positive effect on generalists, and we investigated underlying mechanisms. We studied three trait-based groups of farmland birds: arable specialists, grassland specialists, and mixed habitat (arable/grassland) "generalist" species. Abundances of these three groups were compared on a nationwide gradient of heterogeneity. We addressed the heterogeneity of the two land uses occupying most farmland habitat of the studied species: arable land and grassland. We measured two heterogeneity components: composition (arable land/grassland ratio) and configuration (probability of adjacency). We showed that both components were not always correlated. Although maximal configurational heterogeneity was found at maximal compositional heterogeneity, several landscapes had high compositional heterogeneity but low configurational heterogeneity. Habitat specialists were negatively impacted by compositional heterogeneity, which suggests that habitat loss is the most important mechanism influencing their population level. For grassland specialists, configurational heterogeneity had a negative impact, suggesting that fragmentation worsened the effects of habitat loss. Generalist species benefited from configurational heterogeneity, which suggests resource supplementation is the mechanism that improves their population level. Depending on targeted species, potentially opposite effects of heterogeneity can occur. No unique conservation policy solution to maintain all groups of farmland birds exists.

1 Introduction

Agricultural intensification has been associated with a loss of heterogeneity at the landscape level (Robinson & Sutherland, 2002; Sutherland, 2004). Enhancing landscape heterogeneity, therefore, may significantly mitigate biodiversity declines caused by intensification (Benton, 2003; Tscharntke *et al.*, 2005). Several findings, however, advise against generalizing the potential biodiversity benefits of measures that promote heterogeneity in agricultural landscapes. In fact, special attention should be paid to heterogeneity effects that differ according to agricultural context and the degree of species habitat specialization.

Heterogeneity effects can vary according to landscape context. Tscharntke *et al.* (2005) proposed that local measures to promote heterogeneity in simple landscapes yield the highest biodiversity gains. Empirical findings also support this hypothesis (Roschewitz *et al.*, 2005a; Concepción *et al.*, 2008). Batáry *et al.* (2011b) argue that heterogeneity can be detrimental to specialist species in homogeneous, grassland-dominated landscapes and found that bird species, specialized to extensive Hungarian grasslands, decline with heterogeneity (Batáry *et al.*, 2007a). Evidence of heterogeneity effects on large gradients, from grassland-dominated to arable land-dominated landscapes is lacking.

Two components of landscape heterogeneity are explicitly recognized: composition and configuration (Duelli, 1997; Fahrig *et al.*, 2011). A landscape will have high compositional heterogeneity if it has a large variety of land uses in approximate equal proportion. Furthermore, spatial arrangement of land uses in a complex pattern leads to high configurational heterogeneity. A wide range of heterogeneity descriptors has been used in the literature, with no consensual measure. Many authors use the percentage of semi-natural habitat as an indicator of compositional heterogeneity (Billeter *et al.*, 2008; Batáry *et al.*, 2010). This emphasis on semi-natural habitat assumes that species mainly find resources (*e.g.*, food, nesting habitat) in either natural or semi-natural patches of habitat. The underlying mechanism of the heterogeneous impact is loss of those habitats, with fragmentation potentially worsening its effect (Steffan-Dewenter, 2002; Fahrig, 2003). It also assumes that the matrix does not offer any resources (Debinski & Holt, 2000). These assumptions are not accurate for several farmland species, for which agricultural landscape is a mosaic of habitats that offer different resources with different qualities (Duelli, 1997; Law & Dickman, 1998). In these cases, the mechanisms of the heterogeneity impact on species distribution are habitat compensation, complementation, and supplementation

(Dunning *et al.*, 1992; Brotons *et al.*, 2005). Compensatory land use provides resources in lower quality than those in ideal land use, while two complementary land uses each contain essential resources. The last mechanism allows species to supplement their resources from nearby patches of alternative land use that has equal quality.

Because species do not have the same resource requirements, the effects of heterogeneity can vary among them. Accounting for species traits is necessary, to understand the mechanisms underlying the landscape heterogeneity effect (Steffan-Dewenter, 2000; McGill *et al.*, 2006). The degree of habitat specialization for a species is particularly important (Andrén *et al.*, 1997). Filippi-Codaccioni *et al.* (2010) showed that the most specialized bird species were negatively affected by landscape heterogeneity. This result is similar to most findings that show specialist species to be more severely impacted by habitat disturbance, which conversely benefits generalist species (Marvier & Kareiva, 2004; Schweiger *et al.*, 2007; Devictor *et al.*, 2008). Two hypotheses suggest how heterogeneity influences the distribution of specialist species (Hypothesis 1, H1) and generalist species (Hypothesis 2, H2). In H1, heterogeneity affects specialists through the mechanisms of habitat loss, fragmentation, and/or detrimental resource compensation (*i.e.*, resource quality is lower in alternative habitat than in ideal habitat). In H2, heterogeneity benefits generalists through the mechanisms of resource complementation, supplementation, and/or pure compensation (*i.e.*, similar resource quality is in both alternative and ideal habitats).

Most studies addressing the effects of heterogeneity on specialists versus generalists have been limited to compositional heterogeneity indicators, such as studies revealing the importance of the proportion of arable lands (Ekroos *et al.*, 2010; Filippi-Codaccioni *et al.*, 2010). Chiron *et al.* (2010) combined several land uses into a Shannon index of landscape diversity. Brotons *et al.* (2005) used a steppe/improved pasture ratio to determine whether land uses provided either compensatory or complementary resources to several bird species. These studies did not account for configurational heterogeneity (*i.e.*, for the spatial arrangement of the land uses). However, configuration determines if the land uses and their resources are available within species habitat ranges, and thus influence species distribution (Dunning *et al.*, 1992).

Here we tested hypotheses that state opposite effects of heterogeneity on habitat specialists *vs* generalists (H1 and H2). We did this on a nationwide gradient of grassland and arable land heterogeneity. We explicitly described compositional and configurational heterogeneity. We studied species of a farmland bird community that we discriminated into three groups: two groups of habitat specialists (grassland specialists and arable specialists) and one group of generalists (mixed arable/grassland habitat species).

2 Methods

2.1 The French Breeding Bird Survey

We used data from the French Breeding Bird Survey (FBBS). The FBBS is a nationwide, standardized, monitoring program for which skilled volunteer ornithologists count breeding birds at randomly selected sites each spring (Jiguet *et al.*, 2011). Surveyed sites are $2 * 2$km squares, where observers carry out 10 evenly-distributed point counts, recording every individual bird either heard or seen during a 5-min survey. Observers record the 10 point counts twice in the spring.

We calculated the relative abundance of each bird species at each sample site as follows. Since we focused our study on farmland birds, we only used sites with at least five points located within farmland. When sites had more than five farmland points, we randomly selected five of them. As each point is surveyed twice a year during the spring, we retained the maximum of both counts. We then summed the abundances of the five points, within the square, to obtain the yearly local, relative abundance per square.

Heterogeneity values were available for 2006. Therefore, we retained bird relative abundances, surveyed from 2006 to 2008 to account for potential delayed effects. The number of surveyed years varied between sites. To avoid certain sites contributing more than others towards the effect of agricultural intensity, we averaged the local relative abundance *per* site in sites surveyed more than 1 year, resulting in a total of 510 sites (average number of sites *per* SAR ± standard deviation = 2.15 ± 2.01).

2.2 Trait-based species groups

We focused on a community of 22 common bird species (Table VI.1), classified as farmland birds by the European Bird Census Council (Vorisek *et al.*, 2010). Within this community, we formed three species groups according to their habitat specialization: grassland specialists, arable specialists, and generalists (mixed arable/grassland habitat species). The main habitat of farmland bird species can influence their response to landscape heterogeneity (Batáry *et al.*, 2007a; Fischer *et al.*, 2011a).

To determine the main habitat of each species within farmland, we first computed a continuous Species Specialization Index for grassland (SSIg) for each species. The SSIg was computed similarly to the Species Specialization Index (SSI), which reflects species specialization in larger habitat classes (*e.g.*, farmland, forest, wetland) (Julliard *et al.*, 2006). FBBS and SSI data have already been used in studies testing for landscape heterogeneity effects on birds (Devictor *et al.*, 2008; Filippi-Codaccioni *et al.*, 2010).

We computed SSIg as a weighted mean of species abundance across four sub-habitats within farmland habitat: unimproved grassland, improved grassland, mixed grassland/arable land, and arable land, all with respective sub-habitat weighting coefficients of 4∗, 3∗, 2∗, and 1∗ (Teillard *et al.* In prep.). FBBS observers recorded these habitat classes, during the bird survey, in a 100-m radius around each surveyed site. These data, therefore, came from a different source on a different scale than data used to compute compositional and configurational heterogeneity (see Section 2.3). All farmland FBBS sites surveyed between 2006 and 2008 were included in this computation.

We obtained expert opinion on the SSIg values and found that the eight species with the highest SSIg values ($SSIg > 2.2$) could be classified as grassland specialists, whereas the eight species with lowest SSIg values ($SSIg < 1.8$) could be classified as arable specialists. Remaining species were classified as generalists (Table VI.1, Teillard *et al.* In prep.). At each FBBS sample site, we described the bird community composition by computing the percentage of individuals of grassland specialists, arable specialists, and generalists within the community.

Grassland specialists		Arable specialists		Generalists	
Species	SSIg	Species	SSIg	Species	SSIg
Emberiza citrinella	2.26	*Perdix perdix*	1.25	*Alectoris rufa*	1.84
Saxicola torquatus	2.29	*Motacilla flava*	1.33	*Carduelis cannabina*	1.85
Emberiza cirlus	2.37	*Vanellus vanellus*	1.56	*Corvus frugilegus*	1.94
Buteo buteo	2.42	*Emberiza calandra*	1.56	*Anthus pratensis*	2
Saxicola rubetra	2.44	*Carduelis chloris*	1.58	*Sylvia communis*	2.04
Upupa epops	2.53	*Coturnix coturnix*	1.59	*Falco tinnunculus*	2.12
Lanius collurio	2.58	*Alauda arvensis*	1.6		
Lullula arborea	2.61	*Carduelis carduelis*	1.66		

Table VI.1: List of studied farmland bird species, all of which fall within one of three habitat specialization groups. SSIg = Species Specialization Index for grassland.

2.3 Land uses and heterogeneity

Within the habitats of the studied bird groups, we consistently focused on grassland and arable land to compute heterogeneity. The relative proportion of these two land uses and their configurational heterogeneity were computed at the Small Agricultural Region (SAR) level, using the Corine Land Cover (CLC) database, for the year 2006 (CLC, 2006). The SAR level defines homogeneous areas in terms of agricultural systems and pedo-climatic conditions (Klatzmann, 1955). The mean width of a French SAR (± standard deviation) is 22.4 ± 13km (mean area = $669.6km^2$). The CLC database is a national geo-referenced raster classifying land uses into 44 different categories. The raster is a grid of $25 * 25$-m pixels that has a minimum unit mapping size of 25 ha. The 44 categories were grouped into four main land use types: arable land, grassland (including pasture and natural grassland), woodland, and artificial land (*e.g.*, urban land, roads). Only arable land and grassland were used to compute heterogeneity.

Compositional and configurational heterogeneity indicators were computed at the SAR level. The arable land/grassland ratio, $S_a/(S_a+S_g)$, where S_a is the surface of arable land and S_g is the surface of grassland (both in ha), was computed as the measure of compositional heterogeneity. Maximal compositional heterogeneity is reached at an approximate equal proportion (*i.e.*, when the arable/grassland ratio ≈ 0.5).

We further used the probability of adjacency ($q_{a,g}$) between arable land and grassland as an indicator of configurational heterogeneity (Turner *et al.*, 2001):

$$\mathrm{q_{a,g}} = \frac{\mathrm{n_{a,g}}}{\mathrm{n}} \tag{VI.1}$$

where $n_{a,g}$ = the number of instances when arable land and grassland land use types were adjacent and n = the total number of edges between grid cells (where one grid cell is a $25 * 25$-m pixel of the CLC raster). We considered a “rook” adjacency as one that occurred between one cell and the four neighboring cells that shared its border.

The probability of adjacency depended on the arable/grassland ratio: $n_{a,g}$ was lower when one land use had a very small area. We computed a theoretical probability of adjacency ($q_{i,j}^{TH}$), corresponding to a checkerboard pattern, that could be compared with the actual probability of adjacency for a given arable/grassland ratio. $q_{i,j}^{TH}$ was the probability of adjacency that was reached when the minority land use ($min(S_a, S_g)$) was arranged in square patches of minimal area (minimum unit mapping size of CLC data = 25 ha).

CLC raster data were analyzed using the *rgdal*, *sp* and *spatstat* packages of R statistical software (R Development Core Team, 2007).

2.4 Statistical analysis

Generalized linear models (GLMs) were used to reveal the effects of compositional and configurational heterogeneity on the three groups of birds. The percentage of grassland specialist, arable specialist, and generalist species were tested as response variables. The descriptors of compositional heterogeneity (arable/grassland ratio) and configurational (probability of adjacency) heterogeneity were integrated into the GLMs as continuous explanatory variables. Explanatory variables also included a set of continuous variables related to climate and land uses, that could have had an effect on the large geographical gradient of our sample point distribution. Climate variables included mean temperature and annual precipitation (data from Météo France, French Meteorological Institute), and their values were averages across 2006-2008). Land use variables included relative amounts of forest and urban land uses (CLC data of 2006). Explanatory and response variables were linked at the SAR level; we compared the explaining variable values, available for a given SAR, to the bird response variable values of the FBBS sample sites in the same SAR. We tested for normal distribution and homoscedasticity of the residuals for all response variables. Performing an *arcsine* transformation was not necessary despite the variables being expressed in percentages.

We also compared the percentages of grassland specialists, arable specialists, and generalists across four groups of SARs that were established according to their compositional and configurational heterogeneity (Table VI.2). Groups G1 and G4 had homogeneous composition and configuration because they were dominated by one land use: grassland or arable land, respectively. Groups G1 and G4, therefore, consisted of SARs with arable/grassland ratios of either < 0.2 or > 0.8, respectively. Groups G2 and G3 encompassed mixed land uses, and were thereby heterogeneous in composition. Configuration differentiated those two groups: homogeneous within the SARs of group G2 (*i.e.*, probability of adjacency was lower than the median) and heterogeneous within group G3 (*i.e.*, probability of adjacency was strictly higher than the median). The mean arable/grassland ratio was close to 0.5, and similar between the two mixed land uses groups (G2 and G3), while it was very uneven within the groups dominated by a single land use (G1 and G4, Table VI.2). The mean probability of adjacency was similar between homogeneous groups (G1, G2, and G4), and much higher in the heterogeneous group (G3).

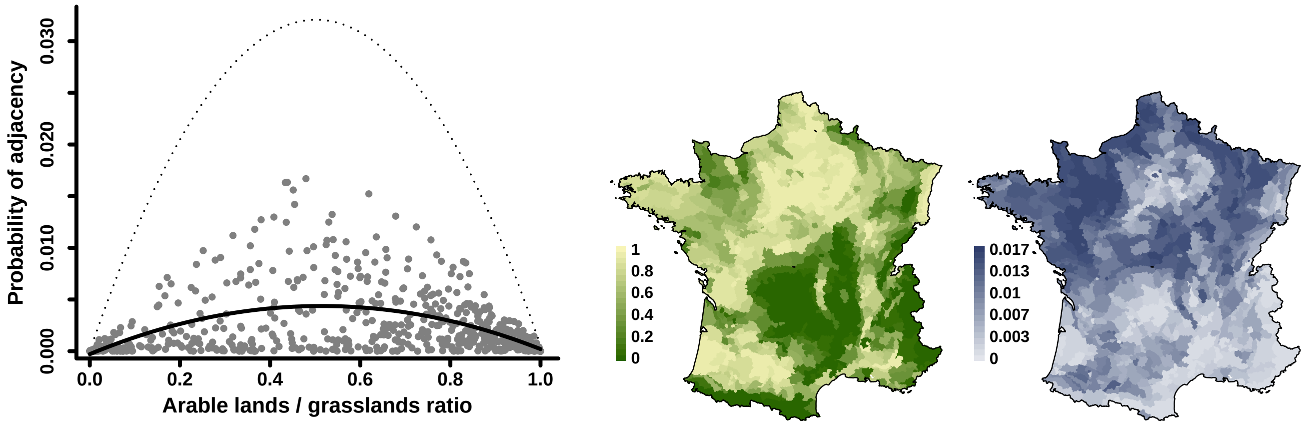
		Land use ratio		Probability of adjacency	
Group	n	mean		mean	
G1	35	0.05	Grassland dominated	$0.91.10^{-3}$	Homogenous
G2	53	0.54	Mixed	$0.93.10^{-3}$	Homogenous
G3	79	0.56	Mixed	$6.79.10^{-3}$	Heterogenous
G4	69	0.93	Arable dominated	$1.1.10^{-3}$	Homogenous

Table VI.2: Characteristics of four groups of Small Agricultural Regions (SARs) that were established according to their compositional and configurational heterogeneity. Only SARs with bird sample sites were considered.

3 Results

3.1 Arable/grassland ratio *vs* heterogeneity

The French SARs followed a relationship that predicts the highest configurational heterogeneity levels are found at approximately equal land use proportions, although important variation occurred around the relationship (Fig. VI.1a). The quadratic regression between configurational heterogeneity and the arable/grassland ratio was very significant (p-value$<$ 0.001 for both quadratic and linear terms). Grassland dominated (G1) and arable land dominated (G4) SARs showed weak heterogeneity values. The greatest probability of adjacency was 0.0017 (with a 0.48 arable/grassland ratio). This value was almost 2 times smaller (0.017 vs 0.0317) than the theoretical probability of adjacency, which had square patches of 25 ha arranged in a checkerboard of grasslands interspersed with arable lands. We also found important variability in the



(a) **(b)** **(c)**

Figure VI.1: Arable/grassland ratio and configurational heterogeneity (probability of adjacency) of French Small Agricultural Regions (SARs). (VI.1a) Relationship between configurational and compositional heterogeneity. Each point = one SAR; full line = the quadratic regression; dotted line = the theoretical probability of adjacency (checkerboard pattern). (VI.1b) Spatial distribution of the arable/grassland ratio, ranging from dark green (low ratio, grassland dominated) to yellow (high ratio, arable land dominated). (VI.1c) Spatial distribution of the probability of adjacency, ranging from pale blue (low configurational heterogeneity) to dark blue (high configurational heterogeneity).

heterogeneity of the SARs, around the mean relationship obtained with the regression: r^2 of the correlation = 0.29. At arable/grassland ratios of approximately 0.5, we found SARs with both very high and very low configurational heterogeneity.

Several areas, mainly in the central and eastern parts of France, had homogeneous landscapes dominated by one of the two land uses (Fig.VI.1b). Configurational and compositional heterogeneity were especially strong in the northwestern and northeastern parts of France (Fig. VI.1c, arable/grassland ratio close to 0.5). Several areas in the eastern and southern parts of France showed approximately equal land use proportions, yet with low configurational heterogeneity.

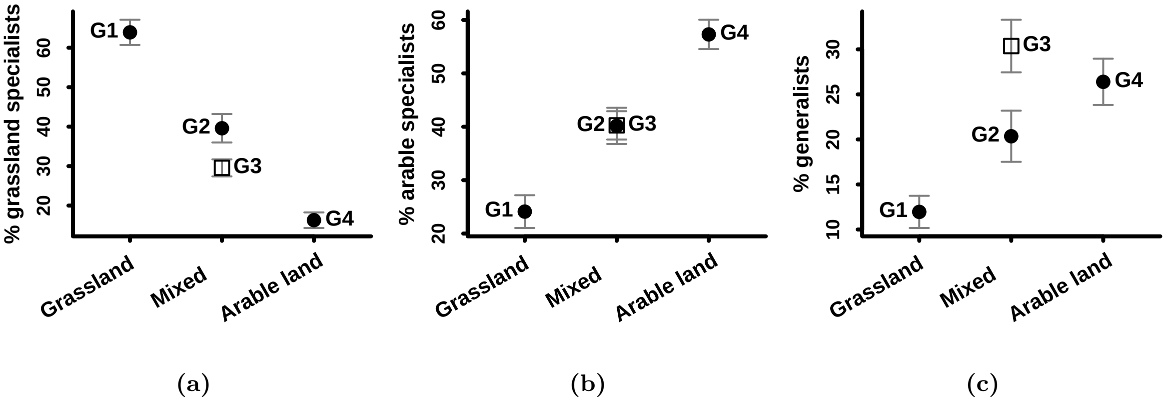
3.2 Effects of compositional and configurational heterogeneity on the bird community

		Land use ratio				Probability of adjacency			
Variable	d.f.	Estimate	*t*	*p-value*	% dev.	Estimate	*t*	*p-value*	% dev.
% grassland specialists	503	-52.21	-17.45	< 0.001***	17	-901.47	-3.8	< 0.001***	2
% arable specialists	503	35.86	10.18	< 0.001***	14	-399.6	-1.43	0.153	0
% generalists	503	17.13	5.32	< 0.001***	5	1336.31	5.23	< 0.001***	5

Table VI.3: Summary of the effect of compositional (arable land/grassland ratio) and configurational (probability of adjacency) heterogeneity on the three groups of farmland birds, as computed by Generalized Linear Models, where % dev = percentage of explained deviance.

According to their habitat specialization, the three groups of farmland bird species had different responses to compositional and configurational heterogeneity (Table VI.3 and Fig. VI.2). The two groups of habitat specialists – arable land and grassland species – showed opposite responses to composition. Arable/grassland ratios had significant impact on both of those groups. It was expectedly beneficial to arable birds and detrimental to grassland birds (Table VI.3). Compositional heterogeneity had a negative effect on both groups of habitat specialists, as their abundance was lower in mixed SARs than in SARs dominated by their main habitat (Fig. VI.2a and VI.2b). The effect of composition was rather linear in homogeneous groups: abundance differences were similar between grassland-dominated and mixed SARs, and between mixed and arable-dominated SARs. The effect of configurational heterogeneity was not significant for arable specialists, but it was significantly negative for grassland specialists. Configurational heterogeneity worsened the effect of composition in mixed SARs.

For generalist species, both composition and configurational heterogeneity had a significant effect. The effect of configurational heterogeneity was positive (Table VI.3 and Fig. VI.2c). Like arable specialists, generalist species benefited from higher arable/grassland ratios. Unlike arable specialists, however, the abundances of generalist species were equivalent in SARs dominated by arable land, and in mixed land use SARs with high configurational heterogeneity.



(a) (b) (c)

Figure VI.2: Relative abundances of the three groups of birds within the four heterogeneity groups of Small Agricultural Regions. (VI.2a) Grassland specialists; (VI.2b) arable specialists; (VI.2c) generalists. Full circles: homogeneous groups (G1, G2 and G4), open square: heterogeneous group (G3) (details of the groups in Table VI.2).

4 Discussion

On a nationwide gradient of observed heterogeneity, our results confirm the importance of accounting for its two components – composition and configuration – to evaluate biodiversity impacts. Although maximal heterogeneity coincided with equal land use proportions (*i.e.*, maximal compositional heterogeneity), many SARs with even land use proportions displayed very weak heterogeneity levels. In real agricultural landscapes, land uses are not randomly distributed in space, which can lead to deviation from the theoretical relationship between compositional and configurational heterogeneity (Andrén, 1994). We argue that more attention should be paid to configuration in studies that address heterogeneity, since previous studies mainly looked at composition by measuring the proportions of several land uses (Filippi-Codaccioni *et al.*, 2010; Ekroos *et al.*, 2010). We did find the effects of composition to be more important than the effects of configuration: configuration was not significant for one of the studied groups of species (the arable specialists), and it had a lower magnitude than the effect of composition. This result is consistent with other studies that have addressed both heterogeneity components and showed composition to be more important (Weibull, 2003; Billeter *et al.*, 2008).

Composition largely drove the relative abundances of the two groups of specialist species (grassland specialists and arable specialists). The highest abundances of the two groups of specialists occurred in homogeneous landscapes dominated by their main habitat. Increasing compositional heterogeneity (*i.e.*, the amount of the minority land use) had a negative effect. Several studies report that habitat specialists benefit from homogeneous, either arable-dominated (Chiron *et al.*, 2010; Filippi-Codaccioni *et al.*, 2010) or grassland-dominated (Batáry *et al.*, 2007a; Silva *et al.*, 2010) landscapes. Here, we showed homogeneity simultaneously benefited grassland specialists and arable specialists on the same gradient of land use composition and heterogeneity. The negative effect of heterogeneity was stronger for composition than for configuration, which suggests that habitat loss is the main mechanism underlying this negative effect on specialist species. Such habitat extent is critical for specialist species, as already highlighted by (Bennett *et al.*, 2006). For grassland specialists, configurational heterogeneity also had a significantly negative effect, although smaller than the compositional effect. This pattern suggests that configurational heterogeneity involves fragmentation, which worsens the negative effect of habitat loss on grassland specialists (Andrén, 1996).

In contrast to specialist species, compositional and configurational heterogeneity effects on generalist species had similar magnitude. These species displayed similar abundances within SARs that had mixed land use and high configurational heterogeneity, and within SARs dominated by arable lands. These observed patterns of response to composition and configurational heterogeneity follow the prediction of the resource supplementation hypothesis (Dunning *et al.*, 1992; Andrén *et al.*, 1997). Generalist species seem to mainly find resources in arable land. They may be able to supplement their resource levels by moving between arable land patches when high configurational heterogeneity lowers the distance between them. A similar contrast between specialist and generalist species regarding their response to heterogeneity has been found in previous studies (Devictor *et al.*, 2008; Filippi-Codaccioni *et al.*, 2010), and (Brotons *et al.*, 2005) provide evidence of a supplementation mechanism. These studies, however, only account for compositional heterogeneity. Consistent with the supplementation hypothesis formulated by Dunning *et al.* (1992), we show that compositional heterogeneity insufficiently supplements resources, and that configurational heterogeneity needs to be high.

Our results validate our two hypotheses formulated in the introduction: the heterogeneity effect is mainly negative for habitat specialists (H1) and positive for habitat generalists (H2). The negative effect of heterogeneity on specialists was mainly driven by habitat loss. For grassland specialists, we demonstrated that fragmentation could slightly worsen this effect. The positive effect of heterogeneity on generalists was likely due to a resource supplementation mechanism. Accounting for species specialization is needed to differentiate effects of landscape heterogeneity, and to understand the underlying mechanisms. We highlight the importance of considering both compositional and configurational heterogeneity because they are not always associated and because configuration can elicit additional significant effects.

We provide one of the first studies to address the effects of both compositional and configurational heterogeneity on a nationwide scale. However, our heterogeneity measures and groups of landscapes were less precise than those in several studies conducted on a smaller scale (*e.g.*, Butet *et al.* 2010; Persson *et al.* 2010). The minimum mapping size unit of CLC data, 25 ha (*e.g.*, $500 * 500$m), made it impossible to account for smaller patches. This CLC unit size is slightly larger than the size of the habitat ranges of most species we studied (Soderstrom & Part, 2000). It could be one explanation for the limited effect of fragmentation that we found. In our study, we focused on two land uses, which were the main habitats of our studied species. We used the probability of adjacency as measure of habitat configuration, a variable reflecting ecotones (Duelli, 1997). Our results cannot be used to assess the effects of other specific heterogeneity measures, such as crop diversity, grassy strips, or tree clumps (composition heterogeneity); and networks of tree edges or the spatial Shannon index (configuration heterogeneity). The minimum mapping size unit of CLC data did not allow us to consider smaller fragments, such as shrubs and trees. Integrating this component could be an interesting perspective because several farmland species nest above ground (Bas *et al.*, 2009).

4.1 Implications for conservation

Negative impacts of landscape simplification on biodiversity have been widely documented (Burel, 1998; Weibull *et al.*, 2000; Lindborg & Eriksson, 2004; Butet *et al.*, 2010). Similar to several recent studies, we found that heterogeneity can elicit ambiguous benefits in accordance to the habitat specialization degree of the species (Chiron *et al.*, 2010; Filippi-Codaccioni *et al.*, 2010; Silva *et al.*, 2010; Pickett & Siriwardena, 2011). Revealing the contrasted effects of heterogeneity between specialist and generalist species is important to provide accurate information that can be applied to conservation policy. Explicit consideration of species specialization and configurational heterogeneity also gives insight into the underlying mechanisms. Báldi & Batáry (2011); Batáry *et al.* (2011b;a) argue that the history of the agricultural landscape must also be considered: heterogeneity should only be promoted if biodiversity loss stems from loss of previous heterogeneity. Authors emphasize the potential negative effect of heterogeneity in homogeneous, extensively managed landscapes. Our findings also support this hypothesis. Grassland specialists were the most abundant in homogeneous, grassland dominated SARs. Comparison of the heterogeneity maps of this study with the intensity mapping of Teillard *et al.* (2012) shows that homogeneous, grassland-dominated SARs were also extensive.

Agri-environmental schemes (AESs) are the main policy instrument currently used to enhance biodiversity in European agricultural landscapes. AESs include a wide range of measures that provide tools needed to promote both landscape heterogeneity and habitat homogeneity. Several measures offer subsidies for the creation and maintenance of linear elements (*e.g.*, shrub edges, tree edges, field margins, and grassy strips), which enhance the landscape heterogeneity. Other measures offer subsidies that compensate for voluntary reduction in management intensity of either pastures or meadows (European Commission, 2005). Such measures typically promote homogeneous landscape similar to the extensive, grassland-dominated SARs that we describe; thus, they could favor grassland specialist species. The effectiveness of AESs at promoting biodiversity is still debated (Kleijn *et al.*, 2006; Princé *et al.*, 2012). One main limitation of these measures is that their application, which is based on voluntary compliance, is often spatially diffuse (Kleijn & Sutherland, 2003). Such spatially diffuse application across farms cannot always produce high quality habitat that is homogeneous at the landscape scale. This may explain the lack of effectiveness of current policy and why habitat homogeneity is necessary. Achieving significant changes on the landscape scale, from measures contracted on the farm scale, is a significant challenge for AESs, in order to improve their effectiveness.

The common agricultural policy of the European Union will be deeply reformed in 2013. To strengthen the biodiversity component of this policy, which still mainly supports production, ecological cross-compliance has been proposed. Farmers would have to meet environmental standards in order to qualify for production subsidies (*i.e.*, area-related direct payments). Ecological cross-compliance is already applied in Switzerland, where farmers have to manage 7% of their area as Ecological Compensation Areas (ECAs) (SFOA, 2007). The Swiss agri-environment program has yielded significantly higher biodiversity benefits than those of other European countries (Aviron *et al.*, 2009), which supports extension of this ECA cross-compliance system to all the EU. The question will be whether to invest 7% of ECAs for either landscape heterogeneity (*e.g.*, edges or field margins) or habitat homogeneity (*e.g.*, extensive grasslands). To make this choice, the specialization of targeted species, and the intensity context of agricultural landscapes, will have to be taken into account.

5 Conclusion

We showed that heterogeneity of agricultural landscapes benefited habitat generalists, whereas specialists needed a large and homogeneous extent of their main habitat. We highlight the importance of considering species specialization and the two components of landscape heterogeneity (composition and configuration), when testing the effects of heterogeneity on biodiversity and identifying their underlying mechanisms. While there has been a recent interest in options to improve the Farmland Bird Index (FBI), we conclude that farmland birds comprehend different groups with contrasted ecological requirements and that no unique solution exists to maintain them all. Managing a diversity of agricultural landscape – both homogeneous and heterogeneous – at the region or country scale is necessary.

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Chapter VII

The spatial aggregation of agricultural intensity influences the variations of farmland bird communities on a nationwide intensity gradient

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Abstract

1. Improving the effectiveness of conservation policies is important to reverse the farmland biodiversity decline related to agriculture intensification. The relationship between biodiversity and agricultural intensity has been proposed as a way to determine the most effective strategy (*e.g.* land sparing *vs* sharing). Although preliminary evidence of this relationship has recently been provided, the influence of the spatial arrangement of intensity on biodiversity remains untested.

2. We conducted a nationwide study linking agricultural intensity and its spatial arrangement to a farmland bird community of 22 species. We used a continuous intensity indicator assembling several categories of input cost which were relevant for both livestock and crop production. It was available on the scale of the whole of France and at the resolution of small agricultural regions (mean width=22.4 km). We used the French Breeding Bird Survey to compute several descriptors of the farmland bird community along the intensity gradient. We tested for the significance of an interaction effect between intensity and its aggregation on these descriptors.

3. We revealed that the community was comprised of both intensity winner and loser species. Intensity impacted the community composition rather than the species richness. The community composition descriptors (mean trophic and specialization level, relative abundance of grassland and arable birds) displayed non-linear relationships to intensity: their slopes were steeper within extensive areas.

4. We showed a significant interaction effect between intensity and its spatial aggregation on the relative abundance of grassland and arable birds. The effect of agricultural intensity was strengthened by its spatial aggregation.

5. *Synthesis and applications.* We suggest that an opportunity to improve the effectiveness of conservation policies exists by targeting measures in areas where intensity is low and aggregated. Our results show that the effect of intensity aggregation on biodiversity should be considered when looking for optimal allocation strategies. In particular, if the land sparing allocation that corresponds to spatial aggregation of the two intensity extremes is adopted, it may influence biodiversity. The role of intensity aggregation should be further tested on other taxa and habitats.

1 Introduction

The decline in farmland biodiversity related to agricultural intensification (Donald *et al.*, 2006) highlights the need to develop public policy aimed at reversing the trend, and more immediately, to improve the effectiveness of existing plans (Kleijn *et al.*, 2006; Princé *et al.*, 2012). To do this, the relationship between biodiversity and agricultural intensity should be quantified, which would help to identify: (1) the range of intensities that could be targeted to obtain the greatest environmental benefits, and (2) the measures or land use strategies needed to accomplish those benefits (Kleijn & Sutherland, 2003; Green *et al.*, 2005). Two main shapes of this relationship have been hypothesized: a convex shape, where biodiversity loss is greatest when intensifying unfarmed and very extensive habitat; and a concave shape, where biodiversity loss is greatest at the highest intensities. Other shapes could exists, *e.g.* positive, threshold, optimum. Some evidence of the shape of the biodiversity/intensity relationship exists (Kleijn *et al.*, 2009; Phalan *et al.*, 2011b), but evidence of the species differences and of the intensity spatial arrangement influence are lacking.

The relationships between biodiversity and agricultural intensity can vary by taxa. Specialist species can be more sensitive to intensity than generalist species (Ekroos *et al.* 2010 for butterflies; Filippi-Codaccioni *et al.* 2010 for birds). Among farmland specialists, differences are also reported between grassland and non-grassland species (Batáry *et al.*, 2007b; Fischer *et al.*, 2011b). This distinction is particularly important in Europe, where grassland agro-ecosystems hold numerous steppic species adapted to open, extensive habitat (Bignal & McCracken, 1996; Benton *et al.*, 2002). Functional traits of species can also influence their responses to intensity, particularly trophic level (Haddad *et al.*, 2000; Attwood *et al.*, 2008). Specific responses of species groups, therefore, need to be included at the community level when computing biodiversity responses to intensity.

The spatial arrangement of agricultural intensity affects biodiversity. The intensity of the agricultural matrix affects species that use patches of either natural or semi-natural habitat (Donald & Evans, 2006; Vandermeer & Perfecto, 2007). Devictor & Jiguet (2007) demonstrated the effects of surrounding land use, which had various intensity levels, for more than two habitats. Surrounding habitats may impact biodiversity when inputs affect non-target organisms outside farming areas (Freemark, 1995), and when the various mechanisms related to metapopulation dynamics (*e.g.*, source-sink dynamics and compensation/complementation between habitats) affect mobile species (Dunning *et al.*, 1992).

In the Green *et al.* (2005) land sparing/sharing framework, the shape of the trade-off curve between biodiversity and yield can help determine the most sustainable pattern of agricultural intensity aggregation. Land sparing corresponds to spatial aggregation within the two intensity extremes: high intensities for food production and low intensities (unfarmed) for conservation. The important role of surrounding habitats suggests that spatial aggregation of intensity could affect biodiversity. Some (Perfecto *et al.*, 2009; Phalan *et al.*, 2011a) propose that the effect of land use configuration should be addressed to improve the simple trade-off model of Green *et al.* (2005). Previous studies that tested biodiversity responses to intensity to improve the effectiveness of conservation policies (*e.g.* Kleijn *et al.* 2009; Phalan *et al.* 2011b) have not included empirical testing of intensity aggregation effects. If research can identify the shape of the biodiversity/intensity relationship along with the interacting effect of the spatial aggregation of agricultural intensity, conservation policies could be proved to be more effective in areas with aggregation of either low (Whittingham, 2007; Gabriel *et al.*, 2009) or high (Tscharntke *et al.*, 2005; Concepción *et al.*, 2008) agricultural intensities.

The objective of this study was to test the two following hypotheses: (1) the relationship between a community of farmland birds, and agricultural intensity, varies according to species traits; and (2) this relationship is influence by the spatial aggregation of agricultural intensity. To do this, we used a continuous intensity indicator (2006 value) that incorporates several input categories and was available across a nationwide gradient. We focused on a community of farmland birds and their response to agricultural intensity. Both the temporal trends and the spatial distributions of bird communities strongly react to agricultural intensity (Fuller *et al.*, 1995; Gregory *et al.*, 2004). Among all the bird species, farmland birds have been particularly affected by agricultural intensification (Gregory *et al.*, 2004; Jiguet *et al.*, 2011). We determined the shape of the relationship between several descriptors of the community and the nationwide intensity gradient. Community composition descriptors included trophic level and degree of specialization, both which have been shown to be good indicators of habitat disturbance (Devictor *et al.*, 2008). We used data from the French Breeding Bird Survey, a nationwide monitoring program, to compute descriptors of the farmland bird community, 2006 to 2008. Finally, we tested for interaction effect between intensity and its aggregation on the bird community descriptors.

2 Methods

2.1 Agricultural intensity and its aggregation

Agricultural intensity is described with the *Input Cost/ha* (IC/ha) intensity indicator, where IC is expressed in Euros (€) (Teillard *et al.*, 2012). In the IC/ha ratio, IC is the sum of different categories of input costs; and hectares includes the total utilized agricultural area of a farm. Input cost categories include fertilizers, feedstuff, pesticides, seeds, fuel, veterinary products, and irrigation water. In 2006, IC/ha was computed at the Small Agricultural Region (SAR) level (Fig. VII.1) from data provided by the French Observatory of Rural Development (ODR[1]), a service unit of the French Institute for Agricultural Research that manages agricultural data for research access. French SAR level defines homogeneous agricultural systems and pedoclimatic conditions (Klatzmann, 1955). The mean width of a French SAR (± standard deviation) is 22.4±13 km (mean area = $669.6km^2$). The values of the IC/ha intensity indicators at SAR levels, and the computation method, are available in Teillard *et al.* (2012), and on the French ODR website (ODR, 2011).

The use of costs enabled us to aggregate several categories of inputs of agricultural intensity for different types of agricultural production. Some input categories (*e.g.*, pesticides and fertilizers) have direct negative effects on birds and their habitat: toxicity, decreased availability of food resources, and nesting sites (Stoate *et al.*, 2009). Others (*e.g.*, feed stuffs and seeds) have indirect effects that collectively put global pressure on habitats. For instance, intensive livestock farms with high feed costs that produce high rates of nitrogen dissipation (Bleken *et al.*, 2005). We computed IC/ha for five production types: industrial crops, cereals, bovine dairy, bovine meat, and mixed (crop/bovine). Together, they account for 67% of French farms and cover 80% of French agricultural lands. Remaining production types excluded from the IC/ha computation included vegetables of low territorial importance, granivore livestock (poultry and pigs), and wine and orchards where input levels display extremely high values.

To measure the spatial aggregation of the agricultural intensity of any SAR i (AI_i), we computed the difference between its IC/ha and the mean IC/ha of its contiguous neighbors:

$$\mathrm{AI_i} = \left| \mathrm{X_i} - \frac{1}{\sum_{\mathrm{j}} \mathrm{w_{i.}}} \sum_{\mathrm{j}} \mathrm{w_{ij} X_j} \right| \tag{VII.1}$$

where X_i is the IC/ha value of the SAR i and w the connectivity matrix of all SARs. $w_{ij} = 1$ if SARs i and j are connected and $w_{ij} = 0$ in all other cases. Spatial aggregation is indicated

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[1] http://esrcarto.supagro.inra.fr

by low values of the AI. To choose the distance class at which SARs should be connected, we used the Moran's I index of spatial auto-correlation (Cliff & Ord, 1981). We computed a spatial correlogram of the Moran's I plotted against the distance connectivity classes. Maximum spatial autocorrelation was reached for contiguous SARs; therefore, only contiguous SARs were considered connected in the connectivity matrix ($w_{ij} = 1$). Aggregated SARs had aggregation values lower than the average value.

2.2 Bird data

Bird data were collected by the French Breeding Bird Survey (FBBS), a standardized monitoring program implemented at the national scale, in which skilled volunteer ornithologists count breeding birds in randomly selected sites each spring (Jiguet *et al.*, 2011). On $2 * 2$ km survey sites, observers conduct ten evenly-distributed point counts. Point counts are unbounded, observers record every individual bird either heard or seen, along with the distance of contact (<25m, 25-100m, >100m), during a 5-min survey. Surveys are conducted twice each spring.

We calculated the relative abundance of each bird species at each sample site as follows. Since we focused our study on farmland birds, we only included farmland sites with at least five farmland point counts. When sites had more than five farmland point counts, we randomly selected five of them. Since each point was surveyed twice *per* year during the spring, we chose the maximum of the two counts for each species (Bibby *et al.*, 1992). We then summed the abundances of the five points within each square to obtain a yearly local relative abundance of a species *per* square.

Intensity values were from 2006; therefore, we used bird relative abundance from 2006 to 2008 to account for potential delayed effects of agricultural intensity on bird abundance. The number of surveyed years varied between squares. To avoid certain squares contributing more than others when testing for the effect of agricultural intensity, we averaged the local relative abundances in squares surveyed more than 1 year, across years.

The final sample of FBBS sites consisted of 332 sites located in 152 SARs. FBBS sites had to be located in SARs where the total area of the five production types was greater than two-thirds of the total agricultural area. Of the 332 sites, 103 were located in aggregated intensive SARs (IC/ha more than the national average); 63 were located in non-aggregated intensive SARs; 121 were located in aggregated extensive SARs (IC/ha less than national average); and 45 were located in non-aggregated extensive SARs (see Section 2.1 for intensity and aggregation indicators).

We computed a matrix of the presence / absence of each species, at each point count in order to compare their detection probability between extensive SARs and intensive SARs (first and last quartiles of IC/ha values, respectively). We used the model M(h) which stipulates that the detection probability can vary between sites (between rows of the matrix), and the associated jackknife estimator, as in Jiguet *et al.* (2006). Detection probabilities were obtained by running the program MARK (White & Burnham, 1999). No important differences were found between the detection probabilities of the species in extensive *vs* intensive SARs (Appendix s4). Moreover, there was no pattern in the detection probabilities of grassland, arable and mixed habitat species (please refer to Section 2.2 for the definition of these species groups).

The studied bird community

Species	Specialization index	Trophic index	Grassland specialization index	Main habitat
Perdix perdix	1.31	1.1	1.25	Arable
Motacilla flava	1.19	2	1.33	Arable
Miliaria calandra	1.08	1.28	1.56	Arable
Vanellus vanellus	1.55	1.9	1.56	Arable
Carduelis chloris	0.86	1.05	1.58	Arable
Coturnix coturnix	1.21	1.22	1.59	Arable
Alauda arvensis	1.13	1.25	1.6	Arable
Carduelis carduelis	0.67	1.05	1.66	Arable
Alectoris rufa	0.69	1.1	1.84	Mixed
Carduelis cannabina	0.62	1.05	1.85	Mixed
Corvus frugilegus	0.92	1.63	1.94	Mixed
Anthus pratensis	1.33	1.75	2	Mixed
Sylvia communis	0.63	1.6	2.04	Mixed
Falco tinnunculus	0.48	2.85	2.12	Mixed
Emberiza citrinella	0.54	1.3	2.26	Grassland
Saxicola torquatus	0.66	2	2.29	Grassland
Emberiza cirlus	0.39	1.3	2.37	Grassland
Buteo buteo	0.39	2.9	2.42	Grassland
Saxicola rubetra	1.23	2	2.44	Grassland
Upupa epops	0.29	2	2.53	Grassland
Lanius collurio	0.87	2.15	2.58	Grassland
Lullula arborea	0.58	1.5	2.61	Grassland

Table VII.1: Farmland bird community: species, habitat specialization index, trophic index, and grassland specialization index. The grassland specialization index is used to determine the species main habitat.

We focused on a community of 22 bird species (Table VII.1) classified as farmland birds by the European Bird Census Council (Vorisek *et al.*, 2010). The community encompassed species nesting on the ground, in either grassland or arable land (*e.g.*, fallows, crops) and in either trees or shrubs that were present in agricultural landscapes. Species found most of their food resources within agricultural lands. Arable species were more dependent on seed resources abundant in arable land. We used six variables to describe the bird community: species richness, community specialization for farmland over other habitats (Community Specialization Index, CSI), mean trophic level in the community (Community Trophic Index, CTI), and percentage of birds having grasslands, arable lands, and mixed lands as their main habitat.

The CSI was computed as:

$$\mathrm{CSI} = \sum_{\mathrm{i=1}}^{\mathrm{n}} \frac{\mathrm{N_i}}{\mathrm{N_{tot}}} * \mathrm{SSI_i} \tag{VII.2}$$

where SSI_i is the specialization index of each species i, weighted by its abundance, N_i, and divided by the summed abundances of all 22 species, N_{tot}. SSI indicated if a species was only associated with farmlands, or if it could be found in other habitats. Similar to Julliard *et al.* (2006), we set SSI equivalent to the species density coefficient of variation ($standard\ deviation/average$, statistically independent of the average species density) for seven habitat classes (forest, heath/scrub, marshland, farmland, urban settlement, wetland/aquatic environment, rocks). These habitat classes were recorded with bird abundances at each FBBS site. We computed SSIs for all FBBS sites, 2006 to 2008. At the community level, CSI is high when the community is dominated by highly specialized farmland species.

The CTI describes a community functional composition. Similar to CSI, it is also computed as a summation of indices (species trophic indices, STI_i) weighted by abundances:

$$\mathrm{CTI} = \sum_{\mathrm{i=1}}^{\mathrm{n}} \frac{\mathrm{N_i}}{\mathrm{N_{tot}}} * \mathrm{STI_i} \tag{VII.3}$$

where STI_i was computed as the proportion of seeds/plants, invertebrates, and vertebrates in the species' diet, each of which is weighted by 1, 2, and 3, respectively (Jiguet *et al.*, 2011). The proportions of these three elements in the diet were previously recorded in the Bird of the Western Paleartic interactive (BWPI, 2006). At the community level, CTI is high when invertebrate-eating species are dominant in the community, and low, when granivore species are dominant in the community.

We further calculated a species specialization index for grasslands (SSIg) to determine if the main habitat of each species was grasslands, arable lands, or mixed grasslands/arable lands. We then computed the percentage of grassland, arable, and mixed habitat birds within the community. The SSIg was computed as weighted mean of species abundance among four sub-habitats of the farmland habitat: unimproved grasslands, improved grasslands, mixed grasslands/arable lands, and arable lands. Weighting coefficients were 4, 3, 2, and 1, respectively. All farmland FBBS sites surveyed between 2006 and 2008 were included in this computation. We obtained expert opinion on our SSIg values and found that the eight species with the highest SSIg values ($SSIg > 2.2$) were classified as grassland birds, whereas the eight species with lowest SSIg values ($SSIg < 1.8$) were classified as arable birds. Remaining species were classified as mixed habitat species. Testing of those classifications showed our results to be insensitive to small perturbations.

2.3 Statistical analysis

We used generalized additive models (GAMs) to test the intensity effect on the size and composition of the community. Responses to agricultural intensity may not always be linear; hence the use of GAMs, which can accommodate more complex patterns (Guisan *et al.*, 2002). We used all six community descriptors (species richness, CSI, CTI, and percentages of grassland, arable, and mixed habitat birds within the community) as response variables. The IC/ha intensity indicator, a continuous explanatory variable with two degrees of freedom, was integrated into the GAMs as a spline function. Additional explanatory variables included a set of continuous variables related to climate and land uses since these variables could impact species on the large geographical gradient of our sample point distribution. They included mean temperature and annual precipitation (data from Meteo-France, the French meteorological institute; available through the ODR), and the relative amount of forest and urban land use (CORINE land cover data). As intensity partially correlated to a land use gradient from grassland to arable land (Appendix s3), the arable land/grassland ratio (arable area / (arable area + grassland area), CORINE land cover data) was also included as explanatory variable. We tested for an interaction between intensity and the arable/grassland ratio in separate Generalized Linear Models (Table s1b in Appendix s1). It was not significant for any response variable; therefore, we did not include it in the final analyses. We used the 2006 value of land use (*i.e.*, only year available in the CORINE land cover database), and we averaged the climate variables from three years (2006 to 2008). We linked explanatory and response variables at the SAR level by comparing explanatory variables for a given SAR to bird response variables of FBBS sample sites located in the same SAR. We tested all response variables for normal distributions and homoscedasticity of residuals, and found no need to perform an *arcsin* transformation of percentage variables (grassland, arable and mixed habitats). GAM models were computed with the *mgcv* package in R Statistical Software.

SARs were divided into aggregated and non-aggregated groups (see Sections 2.1 and 2.2) to test for the interacting effect between intensity and its spatial aggregation. Because of this sample division, the use of non-linear models (GAMs) would have led to over-fitting. We, therefore, used generalized linear models (GLMs) to test for the interacting effect on the six community descriptors. Similar to GAM models, explanatory variables included the IC/ha intensity indicator, the mean temperature and precipitation, and the relative amount of forest and urban land use. In addition, either the aggregation or the non-aggregation of each SAR was added as a factor parameter, as well as its interaction with the IC/ha intensity indicator. GLMs were also tested for normal distributions and homoscedasticity of residuals.

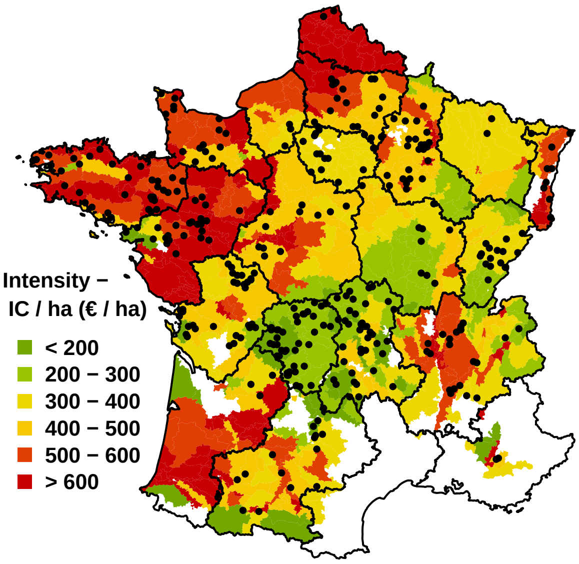


Figure VII.1: Agricultural intensity value (*Input Cost/ha*, IC/ha) of SARs, and sample sites (black dots) of the FBBS that we included in our analysis. Sample sites shown were surveyed between 2006 and 2008, and located in SARs dominated by industrial crops, cereals, bovine dairy, bovine meat, and mixed (crop/bovine) productions. SARs dominated by other production types appear in white. Continuous IC/ha values are represented by six classes, from lowest (green) to highest (red) intensity.

3 Results

3.1 Effects of agricultural intensity on the bird community

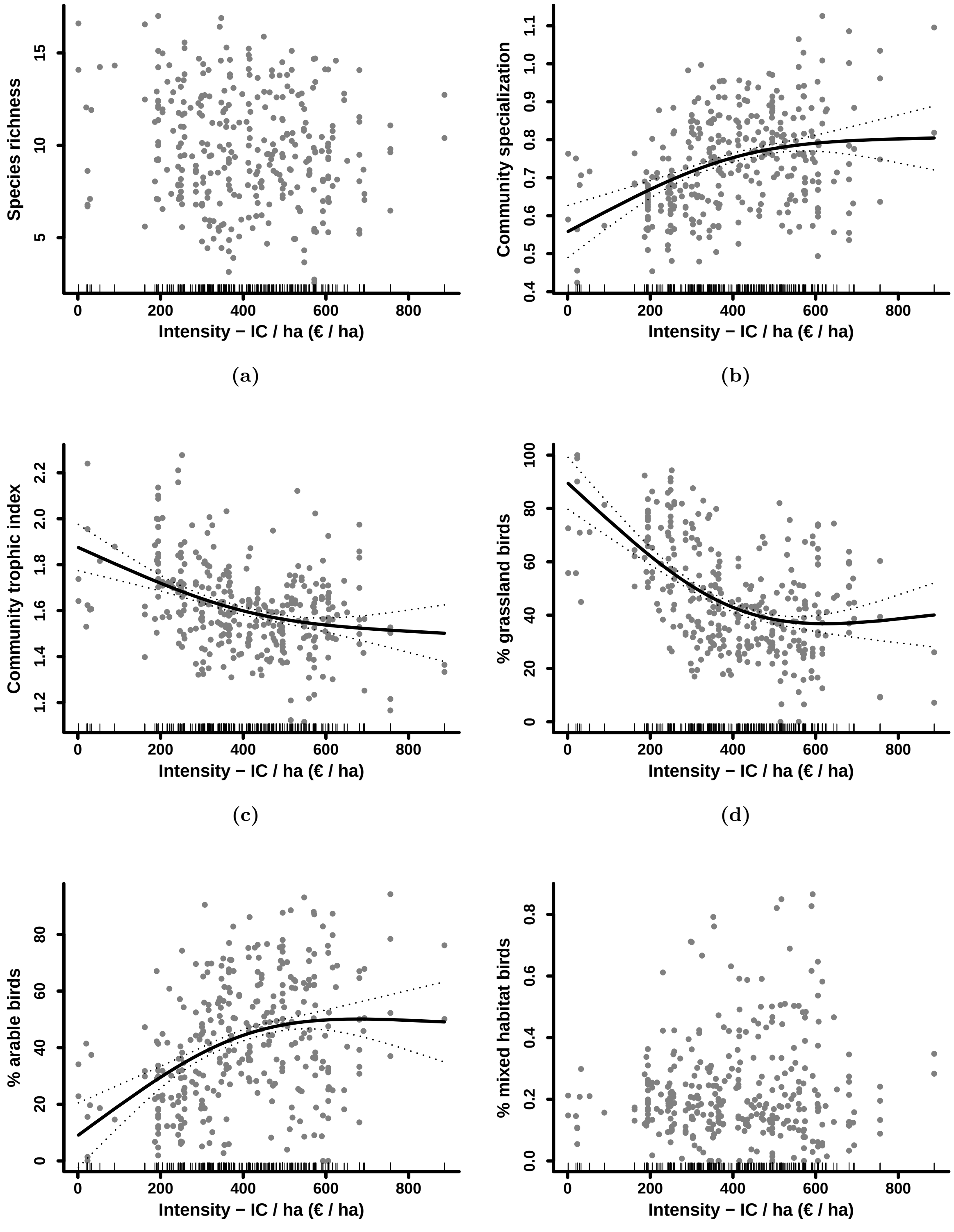
We detail the effects of the agricultural intensity explanatory variable in our results, but the effects of the other explanatory variables are in Table S.1a (Appendix s1).

Agricultural intensity had an effect on community composition, but not on its total size (species richness), and it was sharper at low intensities (Fig. VII.2 and Table VII.2). IC/ha intensity was not significantly related to community species richness ($p - value = 0.055$, Fig. VII.2a), but was significantly related to four of five community composition descriptors. Relationships with bird composition descriptors were both positive and negative, suggesting the community was comprised of both intensity "loser" and "winner" species. When significant, the effect of intensity on all community descriptors was nonlinear (see also Appendix s2) and sharper at low intensities.

Except for percentage of mixed arable birds within the community (Fig. VII.2f), the effect of the IC/ha intensity indicator on all other descriptors of community composition was significant and had similar explanatory powers (explained deviance from 6 to 11 %). Agricultural intensity had a positive effect on both community specialization and percentage of arable birds (Fig. VII.2b and VII.2e). Its effect was negative on both the community trophic level and the percentage of grassland birds (Fig. VII.2c and VII.2d). Therefore, loser species were invertebrate-eating birds (high trophic level), with moderate farmland specialization and preference for grassland habitats, and they dominated the bird communities of extensive SARs. Conversely, winner species were seed-eating birds (low trophic level), with high farmland specialization and preference for arable habitats, and they replaced loser species in more intensive SARs. The shape of the significant relationships between bird community descriptors and agricultural intensity was convex for negative relationships and concave for positive ones. For all these descriptors, the intensity effect was strong at low intensities and attenuated (becoming almost null) at higher intensity levels where IC/ha values > 400 €/ha (approximately the national mean IC/ha value, 405.1 €/ha).

	Intensity (GAMs)				Intensity * Aggregation interaction (GLMs)					
					Intercept		Slope			
Variable	*F*	*p-value*	d.f.	% dev.	*t*	*p-value*	*t*	*p-value*	d.f.	% dev.
Species richness	3.13	0.055	324	2	0.44	0.663	0.11	0.909	323	1
CSI	19.1	< 0.001***	324	6	2.7	0.115	-3.22	0.091	323	2
CTI	19.25	< 0.001***	324	9	-2.61	0.456	2.87	0.328	323	1
% arable birds	20.19	< 0.001***	324	8	3.36	< 0.001***	-3.32	< 0.001***	323	4
% grassland birds	45.67	< 0.001***	324	11	-3.56	< 0.001***	3.93	< 0.001***	323	4
% mixed habitat birds	1.67	0.189	324	1	-0.59	0.557	0.41	0.681	323	0

Table VII.2: Performance summary of the GAM and GLM models on the six community descriptors. GAMs computed the effects of the *Input Cost / ha* (IC/ha) intensity indicator, and GLMs computed the interacting effect of intensity and its spatial aggregation. % dev. is the percent deviance explained by either the IC/ha variable (GAMs) or the IC/ha *aggregation interaction (GLMs). For the GLMs, *t* and *P-values* are given for the differences of intercept and slope of the intensity effect between aggregated and non-aggregated small agricultural regions. CSI: community specialization index, CTI: community trophic index.



(a)

(b)

(c)

(d)

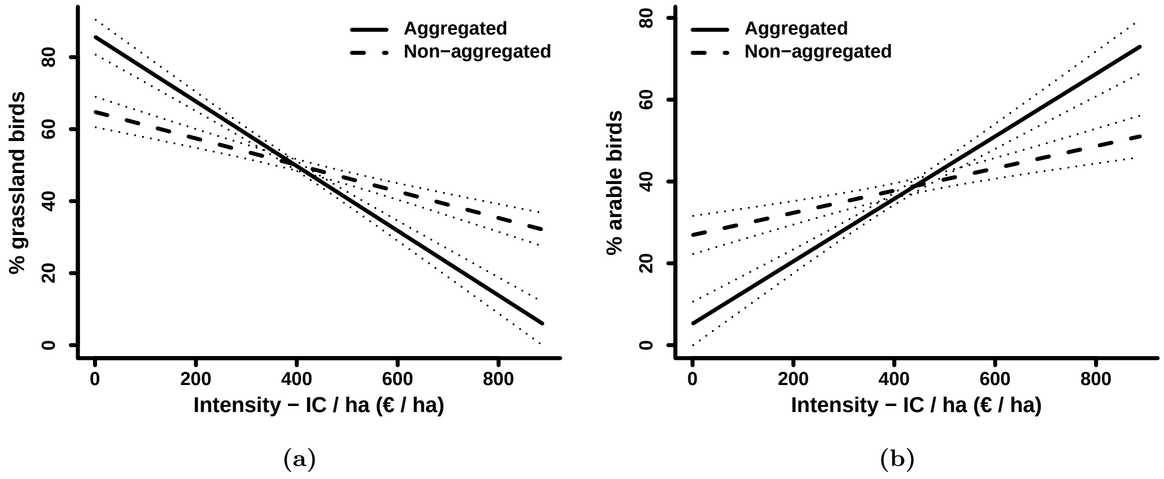
(e)

(f)

Figure VII.2: Effects of the *Input Cost/ha* (IC/ha) intensity indicator on size and composition of the bird community: (VII.2a) species richness, (VII.2b) community specialization index, (VII.2c) community trophic level, (VII.2d) percentage of grassland species, (VII.2e) percentage of arable species, and (VII.2f) percentage of mixed habitat species. Black curves: responses to the IC/ha intensity indicator, as predicted by the GAM, and plotted with 95% confidence intervals (dotted lines) and partial residuals (grey points).

3.2 Interacting effect of intensity and aggregation

For both the percentage of grassland and arable birds within the community, the effect of agricultural intensity was stronger when intensity was spatially aggregated (*i.e.* in SARs with contiguous neighbors of similar intensity; Fig. VII.3 and Table VII.2). The interacting effect, between intensity and its spatial aggregation, was highly significant on grassland and arable birds (significant difference in both intercepts and slopes, Table VII.2). This interaction effect had a lower magnitude than the effect of intensity itself (see the percentages of explained deviance in Table VII.2). The relative abundance of grassland birds was significantly higher in extensive SARs when they were aggregated, but significantly higher in intensive SARs when they were non-aggregated (Fig. VII.3a). Conversely, arable birds were significantly more abundant in extensive SARs when non-aggregated and in intensive SARs when aggregated (Fig. VII.3b). The interacting effect of intensity and its spatial aggregation therefore had the same consequences for both grassland and arable birds: aggregation had a positive effect within the favorable range of intensity and a negative effect outside of it. Significant interacting effects didn't occur for the other community descriptors (Table VII.2).



(a) (b)

Figure VII.3: Interactions between agricultural intensity (*Input Cost/ha*, IC/ha) and intensity aggregation for the percentage of (VII.3a) grassland and (VII.3) arable birds within the community. The two curves represent the effect in small agricultural regions, either aggregated (solid line) or non-aggregated (dashed line), with neighbors of similar intensity. Dotted lines = 95% confidence intervals.

4 Discussion

4.1 Underlying mechanisms of the effect of intensity and its aggregation

Agricultural intensity had a strong effect on bird community composition but not on species richness. Doxa *et al.* (2010) found no significant difference in the taxonomic diversity of a

French bird community in intensive versus extensive areas, but its average specialization index was influenced. These effects on community composition imply "winner" replace "loser" species, as agricultural intensity increases. The presence of such winner and loser species has already been shown in the context of habitat disturbance (Devictor *et al.*, 2008) and agricultural yield (Phalan *et al.*, 2011b). It pleads for use of several community composition indicators when and policy makers address the effects of intensity and determine priority species and actions.

Although intensity was partially correlated to land use (Appendix s3), Teillard *et al.* (2012) showed that crop and livestock systems alternated along the IC/ha gradient. In our study, winner species benefited from more intensive areas, which has also been documented in Europe (Atkinson *et al.*, 2005; Woodhouse *et al.*, 2005). In the most extensive landscapes, the lack of nearby crop fields limits foraging opportunities for seed-eating birds in winter, and influences local breeding densities (Robinson *et al.*, 2001; Gillings *et al.*, 2005). Conversely, more intensive and homogeneous landscapes benefit specialists of open field habitats (Filippi-Codaccioni *et al.*, 2010). The input level effect of the IC/ha may explain why the positive response of winner species was attenuated at high intensities. It reflects the negative effect of high input levels on biodiversity that has been widely documented in the literature (see review in Stoate *et al.* 2009). Phalan *et al.* (2011b) also found more species displayed concave positive responses to yield than convex responses. Here, we averaged intensities at the SAR scale, and could not examine the effects of very high intensities that can be found at lower scales (*e.g.*, one to several farms) and that may be detrimental even to winner species.

Most local studies that compare farmland specialists to habitat generalists show specialists to be the intensity loser species (Ekroos *et al.*, 2010; Filippi-Codaccioni *et al.*, 2010). We found grassland specialists to be loser species, with high sensitivity to intensity (convex negative response); however, their degree of specialization in farmlands was lower than arable specialists that seemed better adapted to higher agricultural intensity. As a result, our community specialization index was higher in intensive areas. Interestingly, the shift in community composition with increasing intensity was the most pronounced in extensive areas. This result highlights the importance for hosting a unique pool of specialized species in extensive European grasslands (Bignal & McCracken, 1996). Even with small levels of intensification, habitat quickly becomes unsuitable for specialized grassland species, and the effects of habitat loss are likely worsened by habitat fragmentation (Herkert, 1994), which may be one explanation for our nonlinear relationship.

The farmland bird community was significantly impacted by intensity aggregation, *i.e.* by the intensity of contiguous SARs. During the breeding season, movements may occur between SARs only for communities sampled close to SAR borders, since territory size of most species is smaller than SAR size (Soderstrom & Part, 2000). The movements of resident birds (16 out of 22 species) are larger to forage food resources during winter. These winter food resources impact the over-winter survival rates and the breeding success during the next season (Siriwardena *et al.*, 2008). More importantly, surrounding SARs are likely to influence the observed community composition through an impact on their longer term, metapopulation dynamics. Evidences of the metapopulation dynamics of birds in the farmland habitat have already been demonstrated (Opdam, 1991; Vandermeer & Perfecto, 2007). Moreover, the scale at which surrounding habitats influence the stability of bird's metacommunies matches the scale that we addressed in our study (Devictor & Jiguet, 2007).

4.2 The significant effect of intensity aggregation: implications for conservation

The Green *et al.* (2005) model relies on the shape of the trade-off between biodiversity and yield to help determine the optimal land use allocation strategy between land sparing and land sharing. Several authors have suggested that including the effect of spatial allocation should be an improvement to this model (Vandermeer & Perfecto, 2007; Perfecto *et al.*, 2009; Phalan *et al.*, 2011a). Our results confirm the importance of this improvement. Indeed, the land sparing strategy corresponds to a high level of intensity aggregation, since the two intensity extremes are spatially segregated, and we show that such aggregation can impact biodiversity. Agricultural intensity is already spatially structured in several countries (*e.g.*, organic farming in the UK, Gabriel *et al.* 2009; high nature value areas, Pointereau *et al.* 2010; intensive versus extensive areas in France, Teillard *et al.* 2012). If the effects of spatial aggregation are not carefully assessed, bias could occur in the sample used to compute the biodiversity/production trade-offs, and thus affect the conclusions drawn from their shapes.

The methodology used in this study has two main differences from those in the Green *et al.* (2005) land sparing/sharing model. First, we did not compute density-yield relationships, but relationships between several descriptors of the bird community, and input intensity. Both output-oriented measures (*e.g.* yield) and input-oriented measures can be used to describe agricultural intensity (Shriar, 2000). Yield is the best measure for understanding the production/biodiversity trade-off. However, biodiversity is rather impacted by the intensity of management practices such as the input use. Yield correlates with management intensity but also depends on pedoclimatic conditions. In the land sparing strategy, more intensity and aggregation are needed to compensate for lost farmed area. Therefore, it is important for the land sparing/sharing debate to understand how these affect biodiversity. Ideally, the effect of both yield and intensity should be assessed because over-intensification can result in both biodiversity and yield losses. Phalan *et al.* (2011a) encourage the use of straightforward biodiversity measures such as species' abundances or densities. Our bird community descriptors were derived from species relative abundances, with the same method used to monitor bird populations in several European countries (Butler *et al.*, 2010). We grouped species by traits in order to reveal patterns of response to intensity, and to give insight into the underlying mechanisms. The presence of both loser and winner species does not permit unequivocal conclusions about optimal allocation strategies; however, these descriptors are informative to policymakers who have to make decisions on land allocation strategies in response to conservation priorities. Secondly, we focused our study on farmland birds. Among all bird species in Europe, farmland birds have been particularly affected by intensification, and therefore represent a central conservation issue (Gregory *et al.*, 2004; Jiguet *et al.*, 2011). Due to our farmland bird focus, we excluded zero-yield land uses from our sample. Natural habitats and other species, however, should be considered when determining the best strategy between land sparing and land sharing.

For grassland specialists, the exponentially declining response to intensity supports the hypothesis that policies promoting extensive practices will elicit higher benefits in extensively farmed than in intensively farmed areas (Kleijn & Sutherland, 2003; Whittingham, 2007). In Europe, current agri-environmental schemes (AESs) already tend to focus on extensive areas (*e.g.*, "less-favored areas" measures), where according to our results, they are expected to be the most effective. AES effectiveness, however, is currently questionable (Kleijn *et al.*, 2006; Princé *et al.*, 2012). We found that the effect of agricultural intensity on biodiversity was stronger in areas where intensity was spatially aggregated. This result partially explains low effectiveness of AESs that occurs when uptake rate is spatially diffuse (Kleijn & Sutherland, 2003; Gabriel *et al.*, 2010). Conversely, targeting and concentrating policies in areas with spatial aggregation of intensity could be an opportunity for improving their effectiveness (Merckx *et al.*, 2009; Uthes *et al.*, 2010). Our results support the general argument that policy measures that target areas where extensive farmlands are aggregated will yield the greatest environmental benefit (Kleijn & Sutherland, 2003; Whittingham, 2007). However, policy measures should not be excluded from intensive areas where their positive influence has been emphasized at the landscape scale (Tscharntke *et al.*, 2005) and on endangered species (Verhulst *et al.*, 2007; Wilson *et al.*, 2007).

Improving the effectiveness of conservation policy on the scale of countries or all of Europe is crucial for reversing biodiversity loss. On such large scales, our results suggest that targeting conservation efforts in areas of aggregated, extensive agriculture could be a way to achieve this improvement. The exponential decline of loser species with increasing intensity supports the important role of extensively managed habitats for biodiversity in Europe (as already highlighted by Bignal & McCracken 1996; Bakker & Berendse 1999). The value of natural habitats should be further assessed to conclude what habitats gain priority. Both extensive and natural habitats may be necessary. Although the land sparing/sharing model relies on direct measures of biodiversity and yield (Green *et al.*, 2005), the level of intensity spatial aggregation varies between allocation strategies. We show that this aggregation can influence biodiversity. Consideration of the effect of spatial arrangement of intensity will be an important improvement to the land sparing/sharing model.

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Supplementary material

s1 Effect of the other explanatory variables than intensity

Effects of all other explanatory variables from agricultural intensity in the GAM models that predict the six community descriptors.

	Estimate	t-value	p-value
Species richness			
Arable/grassland ratio	1.8271	1.4677	0.1432
Urban	-1.4749	-0.6669	0.5053
Forest	-3.1138	-1.8324	0.0678
Temperature	-0.5039	-4.7825	< 0.001
Precipitations	-0.0099	-7.1707	< 0.001
Community specialization			
Arable/grassland ratio	0.3833	7.7933	< 0.001
Urban	0.2633	3.0192	0.0027
Forest	-0.0238	-0.3531	0.7242
Temperature	-0.0197	-4.7085	< 0.001
Precipitations	-4e-04	-6.5799	< 0.001
Community trophic index			
Arable/grassland ratio	-0.2316	-3.1691	0.0017
Urban	-0.058	-0.4469	0.6553
Forest	-0.2814	-2.8224	0.0051
Temperature	0.0026	0.4098	0.6822
Precipitations	2e-04	2.7573	0.0062
% arable birds			
Arable/grassland ratio	37.7018	4.5259	< 0.001
Urban	18.9776	1.2893	0.1982
Forest	16.0139	1.416	0.1578
Temperature	-1.1711	-1.6549	0.0989
Precipitations	-0.032	-3.3559	< 0.001
% grassland birds			
Arable/grassland ratio	-41.4795	-6.0093	< 0.001
Urban	-55.7707	-4.5826	< 0.001
Forest	1.1685	0.1244	0.9011
Temperature	1.2982	2.2056	0.0281
Precipitations	0.0575	7.264	< 0.001
% mixed habitat birds			
Arable/grassland ratio	0.0726	1.0674	0.2866
Urban	0.3527	2.9289	0.0036
Forest	-0.1929	-2.0864	0.0377
Temperature	-0.0044	-0.7593	0.4482
Precipitations	-2e-04	-3.0681	0.0023

Table VII.s1a: Summary of the GAM models used to compute the effect of agricultural intensity (*Input cost / ha, "IC / ha"*) on the six descriptors of the bird community. The estimate, t-value and p-value of all explanatory variables are given, except for the intensity which is integrated in the GAMs with a splin function (refer to Table 2 in main manuscript for the effect of intensity).

	Estimate	t-value	p-value
Species richness	6e-04	0.0771	0.9386
Community specialization	0	0.0414	0.967
Community trophic index	0	-0.0682	0.9456
% arable birds	-0.0556	-1.1528	0.2498
% grassland birds	0.0424	1.0401	0.2991
% mixed habitat birds	2e-04	0.5212	0.6026

Table VII.s1b: Effect of the interaction between intensity and the arable/grassland ratio as computed in separate GLMs. The estimate, t-value and p-value are given.

s2 Linear *vs* non-linear models for the bird community/intensity relationship

Performance comparisons of linear versus nonlinear models of the relationships between community descriptors and intensity.

	GAM, 1 d.f. (linear)		GAM, 2 d.f. (non-linear)	
Variable	% Deviance	AIC	% Deviance	AIC
Species richness	0	1689.78	2	1666.82
Community specialization	3	-431.65	6	-487.2
Community trophic index	8	-173.55	9	-204.1
% arable birds	4	2958.77	8	2819.25
% grassland birds	6	2869.34	11	2713.82
% mixed habitat birds	0	-216.54	1	-245.5

Table VII.s2: Performance comparison of models computing the effect of intensity (*Input Cost/ha, "IC/ha"*) on the bird community through linear (1 degree of freedom) *vs* non-linear (2 degrees of freedom) relationships. Performances are the Akaike Information Criterion (AIC) and the percentage of deviance explained by the IC/ha variable.

s3 Correlation between intensity and land uses

Correlation between the agricultural intensity gradient and the land use gradient.

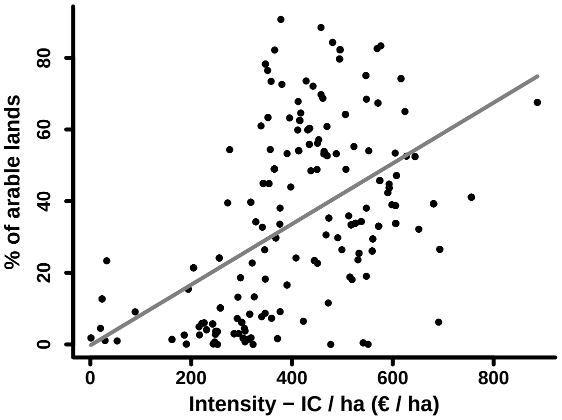
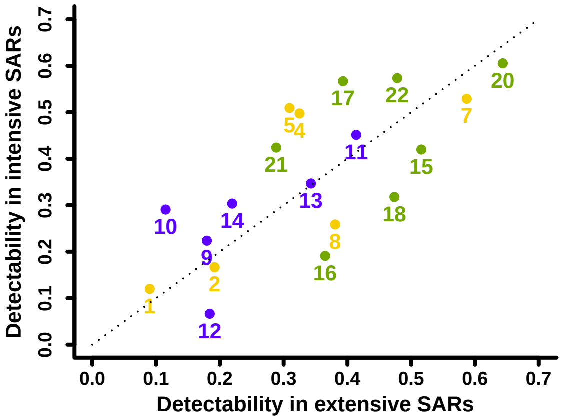


Figure VII.s3: Correlation between the gradient of agricultural intensity (*Input Cost/ha, "IC/ha"* intensity indicator) and a land use gradient (% of arable lands). The regression curve is shown in black.

There was a significant correlation between the intensity of the small agricultural regions and (*Input Cost/ha, "IC/ha"* intensity indicator) and their land uses (Fig. VII.s3, p-value< 0.001). This correlation was not perfect ($r^2 = 0.29$) because the there was differences in input levels within the land uses (*e.g.* between two small agricultural regions dominated by arable lands) besides differences between land uses (*e.g.* between a grassland dominated and an arable land dominated small agricultural region).

s4 Detectability of the bird species

Detectability of the bird species in extensive *vs* intensive Small Agricultural Regions.



	Species
1	*Perdix perdix*
2	*Motacilla flava*
3	*Vanellus vanellus*
4	*Miliaria calandra*
5	*Carduelis chloris*
6	*Coturnix coturnix*
7	*Alauda arvensis*
8	*Carduelis carduelis*
9	*Alectoris rufa*
10	*Carduelis cannabina*
11	*Corvus frugilegus*
12	*Anthus pratensis*
13	*Sylvia communis*
14	*Falco tinnunculus*
15	*Emberiza citrinella*
16	*Saxicola torquata*
17	*Emberiza cirlus*
18	*Buteo buteo*
19	*Saxicola rubetra*
20	*Upupa epops*
21	*Lanius collurio*
22	*Lullula arborea*

Figure VII.s4: Detection probability of the 22 species in extensive *vs* intensive Small Agricultural Regions (SARs) (first and last quartile of intensity value, respectively). Green = grassland species, yellow = arable species, blue = mixed habitat species. For tree species, samples were too low to compute detectability in one of the two SAR groups: *Saxicola rubetra*, *Coturnix coturnix* and *Vanellus vanellus*. Dotted line: y = x

Chapter VIII

Optimal targeting of agricultural intensity allocation to reconcile production, economy and biodiversity at the countrywide scale

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In preparation

Abstract

Higher agricultural intensities enhances food production but are often detrimental to biodiversity conservation. Planning the allocation of intensity on a large scale will be crucial to reconciling these two objectives. This study is aimed at exploring whether intensity allocation could modulate the trade-offs between production, economy, and biodiversity. We developed a spatially explicit optimization model for intensity allocation at the whole-of-France scale, with the resolution of Small Agricultural Regions (SARs, mean width = 22.4km, n = 708 for the whole country). Multi-criteria optimization was conducted on production, economic, and biodiversity performances. Three intensity scenarios (intensification, extensification, and reallocation) were explored with random and optimized allocations. Biodiversity was assessed by measuring the composition of a farmland bird community. The model incorporates several novelties. Intensity was described with a continuous indicator that was based on input costs and was relevant for both crop and livestock production types. We accounted for an interacting effect on the bird community between intensity and intensity aggregation. We show that optimal allocations led to more efficient solutions. Furthermore, we revealed “win-no-lose” solutions: optimal intensification increased production with almost no harm to biodiversity; optimal reallocation benefited biodiversity at almost no loss to production. Optimal allocations consisted of targeted intensity modifications. Opposite targeting was necessary when extensifying (promoting large, homogeneous clusters of extensive SARs) *vs* when intensifying (concentrating intensification in few SARs and promoting heterogeneity). This opposite targeting suggests that accounting for the effect of the spatial intensity arrangement on biodiversity leads to more complex optimal allocation strategies than do the land sparing/land sharing extremes. Spatial targeting has been proposed to improve the effectiveness of European conservation policies. Our model could be an adequate tool to achieve this targeting. New policy mechanisms would have to be developed.

1 Introduction

Agricultural intensity drives a trade-off between food production and biodiversity conservation. During the past decades in Europe, the productivity of agriculture has increased considerably. Although yields depend on pedo-climatic conditions, this augmentation has mainly been due to higher intensities of management practices (Tilman *et al.*, 2002). Intensity is also an important driver of biodiversity loss (Donald *et al.*, 2001). Intensive management practices are responsible for a direct impact on biodiversity and for the alteration of species habitats (McLaughlin & Mineau, 1995; Robinson & Sutherland, 2002). Because intensity is a key variable linking production and biodiversity, the thoughtful management of intensity levels and their allocation could help to reconcile these two objectives.

Several recent studies have highlighted the importance of the spatial distribution of intensity in addition to its level. Indeed, the intensities of surrounding habitats affect biodiversity. For farmland species mainly using semi-natural habitat patches (*e.g.*, grassland, tree clumps, and hedgerows) present within the landscape, the intensity of the surrounding agricultural matrix is important. The matrix has an impact on adjoining semi-natural habitats through pesticide drift, foraging opportunities in fields, and dispersal abilities of mobile species (Freemark, 1995; Donald & Evans, 2006; Vandermeer & Perfecto, 2007). Other species live in cultivated habitats and the landscape represents a mosaic of land use and intensities, offering different resources with various qualities (Bennett *et al.*, 2006). The spatial arrangements of land uses and their intensities influence the availabilities of complementary resources within the species habitat ranges (Dunning *et al.*, 1992). Devictor & Jiguet (2007) showed that farmland birds were impacted by the various intensity levels of the surrounding land uses. Recently, Teillard *et al.* (In prep.) computed the relationship between the composition of a farmland-bird community and agricultural intensity. They accounted for an interacting effect of the spatial aggregation of intensity. Their study demonstrated that the effect of intensity was stronger in extensive areas, and was reinforced by spatial aggregation.

Understanding the relationship between biodiversity, intensity, and the spatial aggregation of intensity could be a way to improve the effectiveness of conservation policies. Although the budgets of agri-environment schemes (AESs) have been significantly increased over the past 20 years in Europe, several studies point out the great need to improve their effectiveness on large scales (Kleijn *et al.*, 2006; Whittingham, 2007). Targeting the allocation of policy measures promoting more extensive farming practices should be an important way to achieve this improvement. If the biodiversity/intensity relationship is exponentially declining, policy measures targeting extensive areas may yield higher biodiversity gains (Kleijn & Sutherland, 2003). Gains could be further increased where surrounding areas are also extensive, if the spatial aggregation reinforces its effect (Teillard *et al.*, In prep.). Targeting policy measures at the countrywide scale is crucial, because the allocation of agricultural intensity is already very spatially structured at that scale. Teillard *et al.* (2012) revealed clusters in France of homogeneous intensities within the extremes and suggested that they could be opportune targets for policy measures. Gabriel *et al.* (2009) showed regions where organic farming is aggregated in the UK, and proposed that organic conversion should be endorsed in these regions to strengthen their conservation value. The existing spatial structure of intensity raises the question of how policy measures should modify it.

In order to answer this question, tools are needed to explore alternative allocations of farming intensity with the aim of enhancing the conciliation between production and biodiversity objectives. Most models focus on the effects of agricultural land-use changes on biodiversity (*e.g.*, Swetnam *et al.* 2005 on landscape scale; Scholefield *et al.* 2011 on European scale). Butler *et al.* (2007; 2010) developed frameworks linking agricultural land uses and farmland birds through detailed mechanisms of impact, and used them to predict the effects of land use change scenarios. The authors argued that their framework could help the development of AESs targeting key drivers of farmland-bird decline. Although very relevant in their ecological aspects, the previous studies did not assess the consequences of their scenarios on agricultural production. Other models used multi-criteria (Pareto-based) optimization procedures to find the land use allocations that draw the efficiency frontier between production (or economic) and biodiversity performances (Drechsler *et al.*, 2007; Polasky *et al.*, 2008; Groot *et al.*, 2010; Wilson *et al.*, 2010). Pareto-based approaches could be particularly useful to point out effective policy targeting solutions, because they reveal a set of solutions without hierarchy between criteria, which can inform policy makers. Multi-criteria optimization models have, however, mainly been used as conservation planning tools for small areas and particular species.

In this study, the objective was to assess the performances of a large set of alternatives for intensity allocation on the scale of the whole of France. We modeled scenarios of intensity allocation and made apparent the trade-offs between production, economy, and biodiversity on this nationwide scale. We considered three intensity scenarios: intensification, extensification, and reallocation. For each scenario, we ran an optimization procedure to find the efficiency frontier between the three performance criteria. Furthermore, we sought spatial allocations that simultaneously promoted production and biodiversity.

2 Methods

2.1 Conceptual model

Fig. VIII.1 presents the conceptual model. The model considers bird conservation as a multi-criteria optimization problem. Agricultural intensities constitute the decision variable. Intensity allocation is defined on a France-wide scale with the resolution of Small Agricultural Regions

(SARs). SARs are homogeneous units in terms of agricultural systems and pedo-climatic conditions (Klatzmann, 1955); their mean width (± standard deviation) is 22.4±13km (mean area = 669.6km^2). The whole of France is covered by 708 SARs. We simulated three scenarios of intensity allocations that represent intensity changes of the real allocations from the year 2006 (the reference state): intensification, extensification, and reallocation. Within each scenario, we first generated intensity allocations as random modifications of the reference state. Then, we assessed random modifications for their national performances based on three criteria: production, economy, and biodiversity. All three criteria were expressed as functions of agricultural intensity calibrated with national databases (Sections 2.2 and 2.3). An optimization procedure selected the allocations based on the three criteria (Section 2.4). Optimal allocations drew the efficiency frontier between criteria.

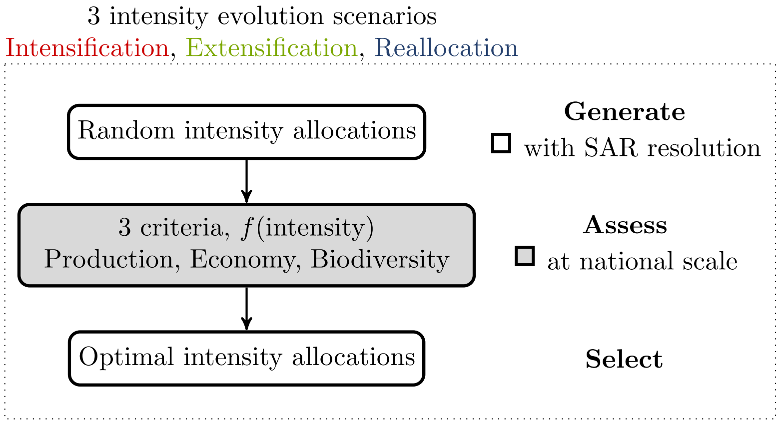


Figure VIII.1: Conceptual model for the simulation and optimization of intensity allocations. Within each scenario, three steps were conducted: generate random intensity allocations on the scale of France with the resolution of Small Agricultural Regions, assess the national performance of these allocations on three criteria (expressed as functions of intensity), and select optimal allocations.

2.2 Data

Agriculture

Agricultural intensity is described with the *Input Cost/ha* (IC/ha) intensity indicator (expressed in €/ha) (Teillard *et al.*, 2012), which is defined as the ratio between the sum of different categories of input costs and the total Utilized Agricultural Area (UAA) of the farm. Input-cost categories include fertilizers, feedstuffs, pesticides, seeds, fuel, veterinary products, and irrigation water. In order to overcome year-to-year variation in price and stock, the IC/ha corresponds to a three-year averaged value. The IC/ha provides a measure of intensity for five production types: industrial crops, cereals, dairy cattle, beef cattle, and mixed crop-cattle. Together, they account for 67% of French farms and cover 80% of French agricultural lands. SARs where the five production types covered less than 2/3 of the total agricultural area were excluded from the analyses (calibrations and simulations) (590 out of 708 SARs were kept).

The French Farm Accountancy Data Network (FADN) was used to calibrate the relationships between the IC/ha values, the production performances (volumes of agricultural products in liters or quintals, per ha of UAA), and the economic performances (gross margins, *per* ha of UAA). The production performances were normalized within each production type (min max normalization). These calibrations were made for each production type at the national scale, where the FADN data are statistically representative.

The French Observatory of Rural Development (ODR) provides a dataset where the IC/ha value is available at the resolution of SARs for the year 2006 (ODR, 2011; Teillard *et al.*, 2012). This dataset was used to represent the reference state of all simulations, and to calibrate the relationships between the bird communities and agricultural intensities.

We computed the intensity aggregation index of any SAR i (AI_i) as the difference between its IC/ha and the mean IC/ha of its contiguous neighbors:

$$\mathrm{AI_i} = \left| \mathrm{X_i} - \frac{1}{\sum_{\mathrm{j}} \mathrm{w_{i.}}} \sum_{\mathrm{j}} \mathrm{w_{ij} X_j} \right| \tag{VIII.1}$$

where X_i is the IC/ha value of SAR i and w is the connectivity matrix of all SARs: $w_{ij} = 1$ if SARs i and j are contiguous neighbors; otherwise $w_{ij} = 0$. Spatial aggregation is indicated by low values of the AI. We distinguished between aggregated and non-aggregated SARs: aggregated SARs had an AI value lower than the national average value.

Bird community

Bird data were collected by the French Breeding Bird Survey (FBBS, Jiguet *et al.* 2011). The FBBS is a standardized monitoring program in which skilled volunteer ornithologists identify breeding birds in randomly selected sites ($2 * 2$km) twice each spring. In these sites, every bird (heard or seen) is recorded at ten sample points during 5-min counts. We only kept sites with at least five points located in farmland, and we randomly selected five of them. Yearly relative abundances of each species were computed as the maximum of the two counts and the sum of the five points. In order to compare with the 2006 IC/ha values, we averaged yearly relative abundances of birds for years 2006 to 2008 to account for potential delayed effects of agricultural intensity.

We focused on a community of 22 species classified as farmland birds (species list in Table s1 in Appendix). Given that agricultural intensity has been shown to impact the composition rather than the size of this community (Teillard *et al.*, In prep.), we computed a community composition indicator: the community-specialization-for-grassland index (CSIg),

$$\mathrm{CSIg} = \sum_{\mathrm{i}} \frac{\mathrm{N_i}}{\mathrm{N_{tot}}} * \mathrm{SSIg_i} \tag{VIII.2}$$

where $SSIg_i$ is the specialization-for-grassland index of each species i, weighted by its abundance N_i, and divided by the summed abundances of all 22 species N_{tot}. The SSIg was computed as a weighted mean of species abundances among four sub-habitats of the farmland habitat: unimproved grasslands, improved grasslands, mixed grasslands/arable lands, and arable lands (Teillard *et al.*, In prep.). Weighting coefficients were 4, 3, 2, and 1, respectively. These sub-habitats were recorded by the FBBS observers along with the bird survey. All farmland FBBS sites surveyed between 2006 and 2008 were included in this computation. At the community level, the CSIg is high when grassland-specialist species are dominant in the community and low when arable specialists are dominant.

2.3 Statistical calibrations

Generalized additive models (GAMs) were used to calibrate the relationships between the production (production volume/ha) and economic (gross margin/ha) performances and intensities. Because our model was based on SARs, we excluded the FADN farms whose intensities did not match the intensity range of the SARs. The continuous IC/ha intensity indicator, integrated in the GAMs as a spline function, was the only explanatory variable. The numbers of degrees of freedom of the spline function were chosen by minimizing the cross-validation error (Zuur *et al.*, 2007). Relationships were calibrated separately for each production type, except for FADN farms belonging to industrial crops and cereal crops, which were pooled together.

GAMs were also used to calibrate the relationship between the bird-community composition and intensity. We compared the IC/ha value of a given SAR with the bird communities of FBBS sites located within the SAR. The response variable was the CSIg. The continuous IC/ha intensity indicator was integrated in the GAMs as a spline function. Other continuous explanatory variables were also included in the models: mean temperature and precipitation in the SAR (climate variables), and the relative amounts of forests and urban land in the SAR (land use variables). The sources of these data were Météo France (French meteorological institute, value averaged from 2006-2008) for climate and CORINE land cover (CLC 2006, 2006 value) for land uses.

We divided the sample of SARs into aggregated and non-aggregated SARs, to calibrate the interacting effect of aggregation around the mean-intensity effect on CSIg. Because the sample was divided, we used Generalized Linear Models rather than GAMs to avoid over-fitting. The CSIg was the response variables and the continuous explanatory variables were the same as in the GAMs (IC/ha, climate, and land use variables). In addition, the aggregation/non-aggregation of each SAR was added as a factor parameter, as was its interaction with the IC/ha.

All calibrations were performed with the R statistical software (R Development Core Team, 2007). GAM models were computed with the *mgcv* package. The details of the calibrations is presented in Appendix s2.

2.4 Simulations

Generating random allocations

Within each scenario, we first generated 1000 random allocations. They corresponded to random intensity modifications from the reference state. Intensification corresponded to an intensity increase, extensification corresponded to an intensity decrease, and reallocation corresponded to a coupled increase and decrease in separate SARs without change in the national-average intensity.

To generate each random allocation, we first sampled the total amount of intensity modification, between 0 and 30% of the national-average intensity, from a uniform distribution (step 1). We then sampled the number of SARs affected by the intensity modification, their identities, and how the total amount of intensity modification was distributed among them (step 2). The only constraint was that the intensity in any of the SARs could not exceed the minimum and maximum intensity values of the reference state (*i.e.*, 20 and 1080€/ha). Within the intensification and extensification scenarios, steps 1 and 2 were conducted to generate each of the 1000 random allocations. For the reallocation scenario, step 2 was conducted twice (to intensify and to extensify) with half of the total amount of intensity modification.

Assessing allocations for multiple criteria as functions of intensity

The performance of the intensity allocations at the national scale was assessed according to three criteria: production, economy, and biodiversity. These three performance criteria were expressed as functions of agricultural intensity.

The national production performance was the production volume averaged across all n SARs:

$$\mathrm{F_{Prod}(X)} = \sum_{\mathrm{i}} \frac{1}{\mathrm{n}} \sum_{\mathrm{j}} \mathrm{p_{ij} f^{j}_{Prod}(X_i)} \tag{VIII.3}$$

For a given SAR i, the production volume was computed from its intensity value (X_i), through the relationships calibrated between these two variables (f_{prod}), for each production type j (see Sections 2.2 and 2.3). The proportion (p_{ij}) of the production type j in SAR i corresponds to the ratio between the agricultural area of the farms of type j and the total agricultural area of all production types (for any given SAR i, $\sum_j p_{ij} = 1$).

Similarly, the national economic performance was the gross margin averaged across all n SARs:

$$\mathrm{F_{Econ}(X)} = \sum_{\mathrm{i}} \frac{1}{\mathrm{n}} \sum_{\mathrm{j}} \mathrm{p_{ij} f^{j}_{Econ}(X_i)} \tag{VIII.4}$$

where f_{econ} is the relationship calibrated between gross margin and intensity for each production type j.

The national biodiversity performance was the coefficient of variation of the bird CSIg between SARs. Therefore, the biodiversity performance was high when the bird communities were very diverse among SARs and low when they were similar among SARs:

$$\mathrm{F_{Biodiv}(X) = CV\Big(f_{CSIg}(X, Aggreg(X), Clim, LU)\Big)} \tag{VIII.5}$$

where f_{CSIg} is the relationship calibrated between the CSIg and the intensity value, which also accounts for the effect of spatial aggregation of intensity ($Aggreg(X)$), as well as climatic ($Clim$) and land use (LU) variables (see Section 2.3). CV stands for the coefficient of variation (*i.e.*, standard deviation/mean ratio) of the CSIg between SARs.

Selecting the optimal allocations with a non-weighting Pareto-based procedure

Exploring the trade-offs between the production, economic, and biodiversity performance criteria among various intensity allocations is a multi-objective optimization problem. It can be written as:

$$\mathrm{\max F(X) = \Big(F_{Prod}(X), F_{Econ}(X), F_{Biodiv}(X)\Big)} \tag{VIII.6}$$

$$\mathrm{X = (X_1, X_2, ..., X_n)} \tag{VIII.7}$$

where $F_{prod}(X), F_{econ}(X)$ and $F_{Biodiv}(X)$ are the three objective functions (described in Eq. VIII.3, VIII.4 and VIII.5) that are simultaneously maximized. The decision variable is X; *i.e.*, the intensity in the n SARs spatial units ($n = 590$).

The multi-objective optimization was performed with the NSGA-II (Non-dominated Sorting Genetic Algorithm-II; detailed description in Deb *et al.* 2002). Genetic algorithms are efficient heuristic techniques based on the the principles of natural evolution. One optimization procedure was conducted separately for each of the three scenarios. The algorithm was initiated with the random set of allocations described in Section 2.4. The genetic algorithm considers this set as a population where each intensity allocation at the France-wide scale is an individual with a genotype. The alleles in the genotype encode the continuous intensity values at each SAR. The quality of the initial population was improved over 10 generations. At each generation, a competitor is generated for each individual by allele mutation (probability = 0.1) and recombination (probability = 0.7). The qualities of the individuals and their competitors are assessed by Pareto ranking in order to approach the trade-off frontier. Within the same rank, quality is further assessed by crowdedness in order to promote spreading over the solution space. According to their qualities, either the original individual or its competitor is selected for the next generation.

The optimization procedure was performed with the *optim_nsga2* function in the Scilab 5.1.3 software (Scilab Consortium, 2007).

3 Results

3.1 The trade-offs between criteria among all intensity allocations

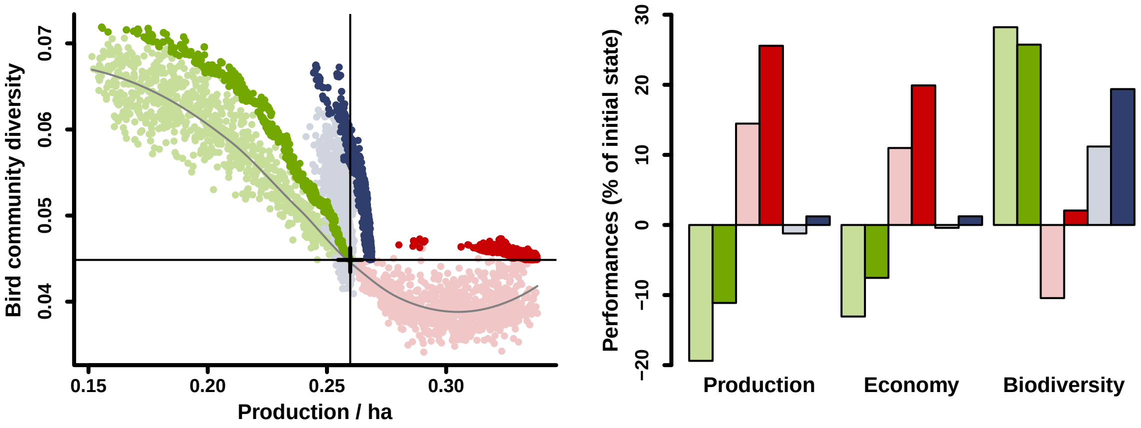
Fig. VIII.2a reveals the trade-off, between production and biodiversity performances, among allocations at the national scale. The random allocations of the extensification and intensification scenarios displayed a global trade-off shape similar to that of a negative sigmoid function. At the reference state, the bird community diversity was already close to its minimum; therefore its variation was stronger in the extensification scenario than in the intensification scenario.

Production and economy were closely linked (Fig. VIII.2b); a very similar pattern was observed for the trade-off between biodiversity and economy (Fig. VIII.s3a in the Appendix). The bird community diversity value (coefficient of variation of the CSIg, Eq. VIII.5) could theoretically range from 0, if all SARs had the same intensity, to 0.14, if half of the SARs were at the lowest IC/ha value and the other half were at the highest IC/ha value. The CSIg was already close to its lowest value at the average intensity of the initial state (Fig. VIII.s2c in the Appendix). Increasing the CSIg diversity was thus made possible by increasing the CSIg itself. A similar pattern was observed at the national scale for the trade-off between the mean CSIg and production (Fig. VIII.s3b in the Appendix).

Optimal allocation improved the efficiency of extensification; *i.e.*, for a given production loss, higher biodiversity benefits were reached with optimal allocations versus random allocations (Fig. VIII.2a). On average, the optimal allocations in the extensification scenarios led to slightly lower biodiversity levels, but at half the production loss (Fig VIII.2b). Therefore, the optimization procedure within the extensification scenario tended to select the allocations that maximized production for a given biodiversity level (*i.e.*, moving points to the right in Fig. VIII.2a) rather than the opposite (*i.e.*, moving points upward). Optimal allocations in the intensification and reallocation scenarios revealed “win-no-lose” allocation solutions in which one criterion was increased while the other was not decreased. Within intensification, optimal allocations made it possible to have both higher production and higher economic benefits while annulling the biodiversity losses. Reallocation overcame the trade-off drawn by the extensification and intensification scenarios. Biodiversity benefits could be reached at very low production losses. However, these biodiversity benefits were smaller than those within the extensification scenario.

3.2 The targeted intensity changes leading to optimal allocations

Intensity allocation scenarios were analyzed by focusing on the distributions of three properties of intensity change: the mean intensity change per SAR, the mean national aggregation of the SARs, and the percentage of extensive SARs. Fig. VIII.3 compares these three properties between the extensification and intensification scenarios (with random and optimal allocations).

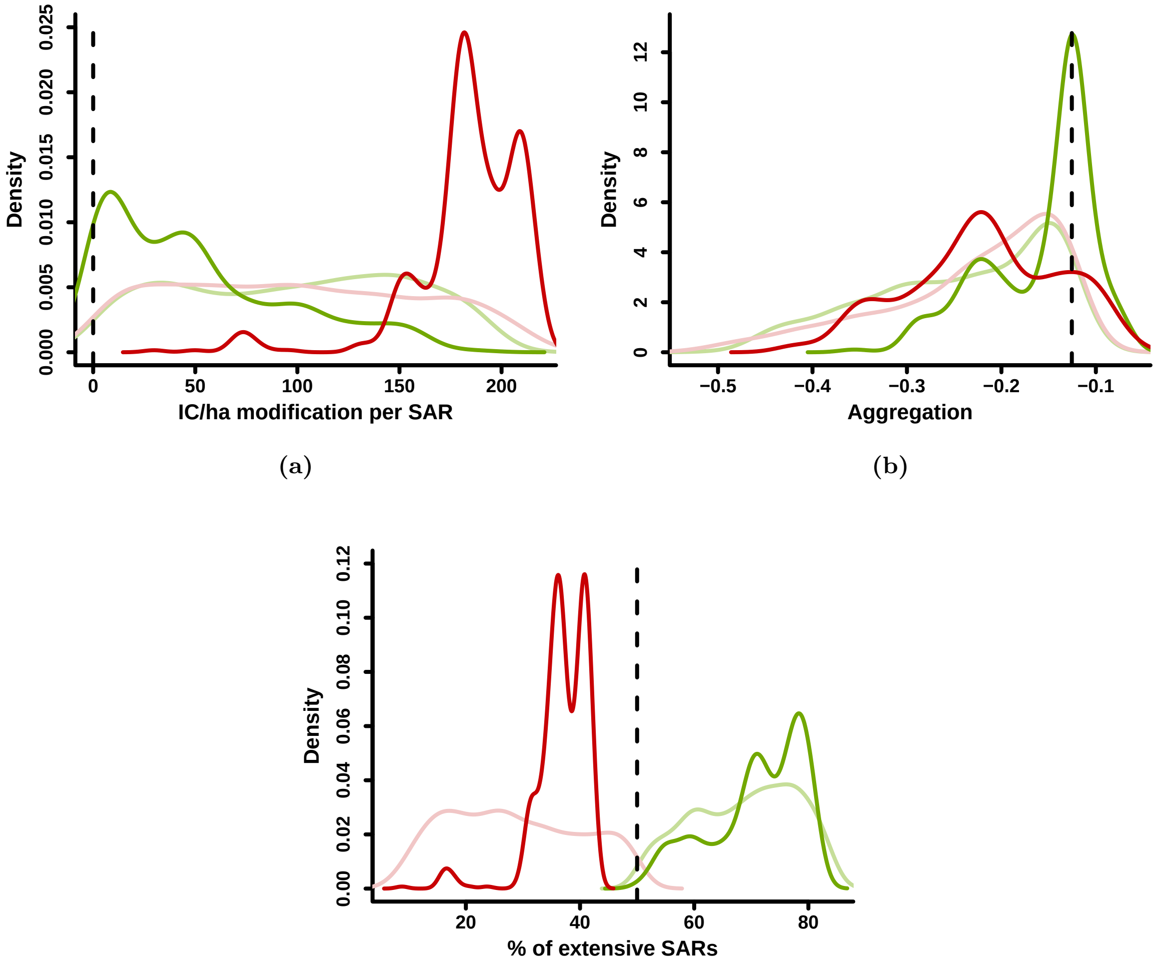


(a) (b)

Figure VIII.2: National performances of all intensity allocations according to the three criteria (production, economy, and biodiversity). Red: intensification scenario, green: extensification scenario, blue: reallocation scenario. Pale colors: random allocations, bright colors: optimal allocations. The production performance is the national mean production (production volume/ha), the economic performance is the national mean gross margin (€/ha), and the biodiversity performance is the national coefficient of variation of the bird community specialization for grassland (see Eq. VIII.3, VIII.4 and VIII.5). (VIII.2a) Performance trade-off between the the production and biodiversity criteria across all allocations. The cross is the reference allocation. (VIII.2b) Average performances among the three criteria (in terms of % of the reference allocation) for the random and optimal allocations in the three scenarios.

Random allocations resulted in rather uniform distributions of these three properties and in the same (or symmetric) intensity changes between the extensification and the intensification scenarios. Conversely, optimal allocations displayed asymmetric distribution patterns of the three properties. These patterns corresponded to the targeting of intensity changes. For most properties, the targeting was opposite between optimal extensification and intensification.

Random intensification and extensification produced the same uniform distribution of intensity modification per SAR (Fig. VIII.3a). Optimal extensification involved allocating smaller changes per SAR and thus changing the intensities of a higher number of SARs (the total amount of modification being constant). The opposite solution was optimal for intensification: concentrating larger intensity changes in a lower number of SARs. Random allocation in both scenarios led to a decrease in the overall levels of spatial aggregation (Fig. VIII.3b) compared with the reference state. Optimal intensification slightly accentuated this decrease. Less spatial structure can also be observed in the average map of optimal intensification (Fig. VIII.4c, compared with the reference state, Fig. VIII.4a). Conversely, optimal extensification increased aggregation back to the level of the reference state. A large, homogeneous cluster of extensive SARs can be observed in Fig. VIII.4b. Random intensification decreased the percentage of extensive SARs while random extensification increased it, as could be expected. Optimal solutions



(a) (b)

(c)

Figure VIII.3: Properties of the intensity allocations between the random and optimal allocations of the intensification and extensification scenarios. The densities (smoothed distributions) of the allocations are shown for three properties. (VIII.3a) Mean intensity (*Input Cost/ha*, IC/ha) change *per* Small Agricultural Region (SAR). (VIII.3b) Mean national aggregation (with aggregated SARs = 1 and non-aggregated SARs = −1). (VIII.3c) % of extensive SARs (with intensity value lower than the mean intensity at reference state). Red: intensification scenario, green: extensification scenario. Pale colors: random allocations, bright colors: optimal allocations. Dotted line: value at reference state.

of both intensification and extensification, however, led to higher percentages of extensive SARs than did the random allocations (Fig. VIII.3c).

The optimal solutions of the reallocation scenarios combined the optimal intensification and extensification allocations: (i) keep a rather high number of extensive SARs, (ii) intensify by concentrating intensity modifications and promoting spatial heterogeneity of intensity in intensive areas, and (iii) extensify by touching a high number of SARs and promoting spatial aggregation of intensity in extensive areas (Fig. VIII.4d).

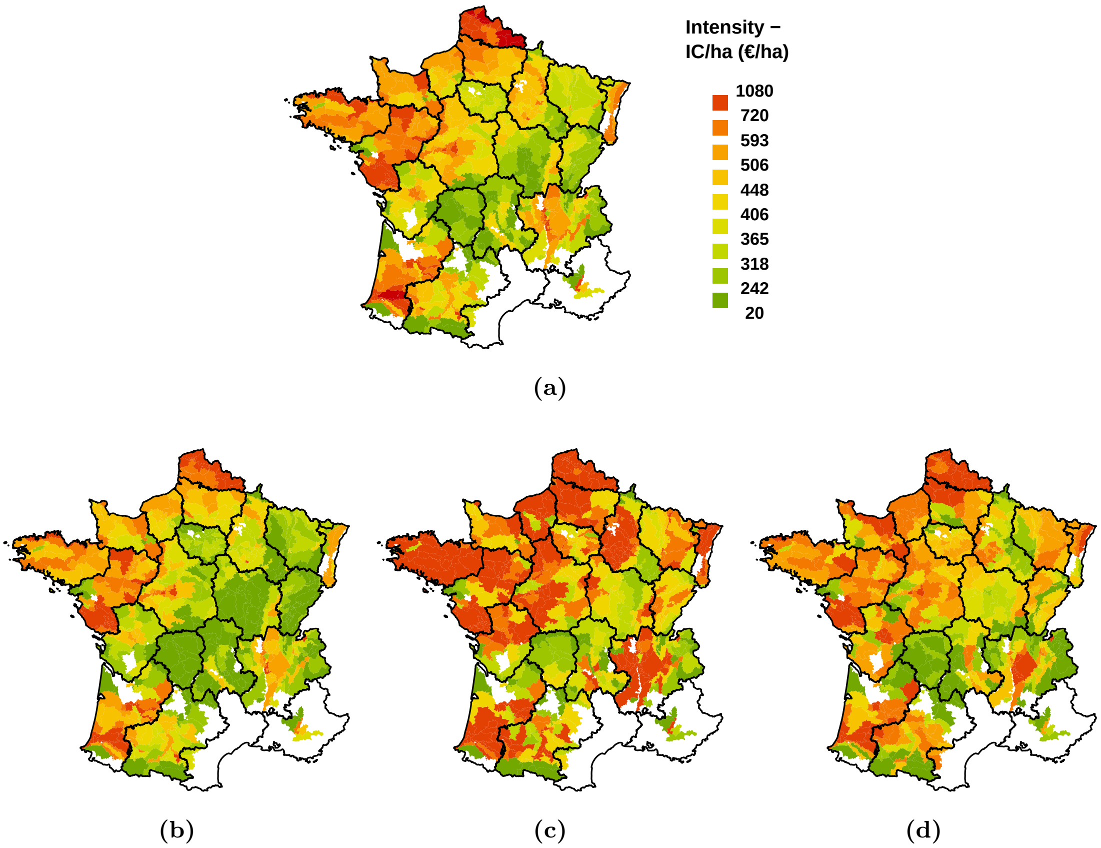


Figure VIII.4: Maps of the intensity (*Input Cost/ha*, IC/ha) at the reference state (VIII.4a) and for the mean optimal allocations of the three scenarios: (VIII.4b) extensification, (VIII.4c) intensification, and (VIII.4d) reallocation. Continuous intensity values are represented in color classes from green (extensive) to red (intensive). The legend is shown in Fig. VIII.4a, intensity intervals for all the color classes correspond to the deciles $0, 0.1, 0.2 ... 1$.

4 Discussion

In this study, we showed that the allocation of intensity was key to reconciling the production, economic, and biodiversity performances of agriculture at the national scale. We revealed that optimal allocations of agricultural intensity exist that improve the efficiency frontier between production, economy, and biodiversity. Some allocations even revealed win-no-lose solutions. The optimization of intensity allocation was achieved through the spatial targeting of intensity changes. Interestingly, opposite targeting was needed for maximizing biodiversity at a given production loss *vs* increasing production while limiting biodiversity losses.

4.1 Variables used

Agricultural intensity was described with the IC/ha indicator, which combined several categories of inputs. We simulated changes of the whole IC/ha, but changes could also be considered as modifications of specific input categories. The same reduction of IC/ha caused by the reduction of two different input categories, however, may not have the same effects on biodiversity and production. The IC/ha includes input categories, like fertilizers and pesticides, that have direct, negative effects on biodiversity and habitats (Stoate, 2001; Vickery *et al.*, 2001). Other categories are expected to have indirect effects. For instance, higher feed costs are associated with higher livestock densities and nitrogen dissipation (Dalgaard *et al.*, 1998; Bleken *et al.*, 2005). The different input categories are not all equally necessary for production. The use of feed concentrates is essential to increase production beyond a certain threshold (Puillet *et al.*, 2011). Conversely, pesticides could be reduced without production loss when they are used for preventive purposes at higher levels than necessary (Pimentel *et al.*, 1991). Considering IC/ha modifications by specific input categories could be an interesting perspective, but it would require new calibrations of the relationships between separate categories and the performance criteria.

In the trade-offs between criteria, the yield (production volume/ha, used to describe production performance) was strongly correlated with the gross margin (/ha, used to describe the economic performance). Other variables reflecting economic performance may be less correlated with production; for instance, the added value or the net-margin account for additional cost categories (*e.g.*, structural costs), which may be detrimental to the economic performance of the intensification scenario.

The biodiversity component was assessed through an indicator of the composition of a farmland bird community. In Europe, numerous bird species are specialists for the farmland habitat (Robinson & Sutherland, 2002). Agricultural intensification largely explains why populations of farmland birds have suffered a more severe decline than other bird groups (Gregory *et al.*, 2005; Jiguet *et al.*, 2011). Farmland birds are thus an important conservation issue and the Farmland Bird Index (FBI, Gregory *et al.* 2009) is recognized as an indicator of structural biodiversity changes at the European Union (EU) level. Although we could not study the FBI because we did not address temporal changes, our community shared 20 species with the French FBI (Jiguet *et al.*, 2011). Several studies have shown that the compositions of bird communities, rather than their total sizes, changed along a gradient of intensity or habitat disturbance (Devictor *et al.*, 2008; Doxa *et al.*, 2010). Teillard *et al.* (In prep.) found the relative abundances of grassland and arable species to be the most impacted by the French gradient of intensity and its spatial aggregation. The CSIg reflects whether grassland or arable birds dominate the bird community, and we showed its strong link with intensity. From the conservation viewpoint, this indicator is relevant because the exponential decline of grassland species with intensity indicates that these species suffer disproportionately as a result of increased intensity. At the national scale, we used the coefficient of variation of the CSIg between SARs as a biodiversity performance criterion. Thus, biodiversity performance was high if the bird communities were diverse among SARs. Because the CSIg was already low at the national mean intensity of the initial state, increasing the CSIg diversity also implies increasing its value in several SARs, thus favoring the most disadvantaged species. Further studies could assess the biodiversity performances of intensity allocations through other relevant descriptors (*e.g.*, generalist species or trophic levels, see Mouysset *et al.* 2012).

On the whole-of-France gradient, different agricultural intensities (IC/ha) correspond both to different land uses and to different input levels with the same land uses. These two mechanisms impact the bird communities. In particular, land uses determine habitat extent while input levels determine its quality (*e.g.*, via direct toxicity and resource availability) (Robinson & Sutherland, 2002). SARs are larger than the habitat ranges of the studied species, but the aggregation of intensities between contiguous SARs matches the scale at which the bird metapopulation dynamics take place (Devictor & Jiguet, 2007). Intensified and extensified allocations will impact the bird communities through these mechanisms. Moreover, the reallocation scenario could increase the bird community diversity by segregating communities dominated by intensity winner species in intensive SARs from those dominated by intensity loser species in extensive SARs.

4.2 Complementarity with other approaches

To date, existing scenarios of the evolution of European agriculture have been concerned with climate (Smith *et al.*, 2000; Maracchi *et al.*, 2005) and land use changes (Ewert *et al.*, 2005; Rounsevell *et al.*, 2005; Verburg *et al.*, 2006). The effects of such scenarios on biodiversity have been assessed in several studies (Butler *et al.*, 2010; Scholefield *et al.*, 2011; Barbet-Massin *et al.*, 2012; Devictor *et al.*, 2012). Scenarios of intensity evolution have not been tested, hence our study could be complementary to the previous approaches. We considered three scenarios of intensity changes at the national scale: intensification, extensification, and reallocation. Our focus on input intensity makes it possible to explore strategies for pesticide reduction, which are important at both the EU-wide (2007 resolution) and France-wide levels (plan for a twofold reduction in pesticide use by 2018, Butault *et al.* 2010). Pesticides are part of the IC/ha, and such a twofold pesticide reduction could easily be translated into an IC/ha reduction. As mentioned above, however, it would require additional calibration between pesticides and the various performance criteria. Other databases, such as the French Network for Sustainable Agriculture (RAD), which promotes a lower and more efficient use of inputs (Rohellec & Mouchet, 2008), could be used to calibrate the extensification scenarios. Those authors have shown that, compared with conventional farms, production performances of RAD farms are slightly lower while the savings in input expenses yield great gains in economic performance.

Whether the intensification and reallocation scenarios could be realistic for Europe is unclear. Although policy measures promoting extensive practices are of growing importance, the majority of agricultural subsidies still encourage production. Europe, however, may not need to increase or even maintain food production (Krebs *et al.*, 1999). The reallocation scenario made it possible to improve biodiversity at very low production costs because the positive effects in extensified areas compensated for the negative effects in intensive areas. Such a compensation mechanism would not exist for other environmental components like pollution or soil deterioration (Matson, 1997).

We considered that the relative percentages of the four production types remained constant at the SARs level. Agriculture intensification has been accompanied by the abandonment of less productive production types (*e.g.*, grassland to arable land conversion, (Duncan *et al.*, 1999)). Coupling models addressing production types and production intensity may be an interesting perspective. Bio-economic models where the relative percentages of production types at the SAR level change according to policy scenarios Mouysset *et al.* (2011) offer another area for incorporating economic complexity.

4.3 Policy implications

Land sparing and land sharing are two theoretical and contrasted strategies for intensity allocation. They can be seen as the two endpoints of a gradient of spatial intensity aggregation (Fischer *et al.*, 2008). Land sparing corresponds to maximal intensity aggregation because the two intensity extremes are spatially segregated into large clusters. In a theoretical model, Green *et al.* (2005) proposed that the shape of the relationship between biodiversity and intensity helps to determine the best strategy for reconciling biodiversity and production performances. We calibrated this relationship on data linking intensity to a farmland bird community at the countrywide scale. We added further complexity by accounting for the influence of spatial intensity aggregation on this relationship, the importance of which has recently been demonstrated (Devictor & Jiguet, 2007; Teillard *et al.*, In prep.). We also calibrated the links between intensity, production, and economy. We did not compare the land sparing/sharing extreme strategies, but we revealed how to optimize modifications of intensity allocation from its current state. Like Polasky *et al.* (2005), we found that optimal allocation made it possible to achieve benefits to one criterion at little loss to the other criteria (win-no-lose solutions). For instance, reallocating intensity increased biodiversity with almost no losses to production and economy. It might be tempting to qualify this reallocation as land sparing, because it segregated intensity modifications and intensification compensated for extensification in different areas. Unlike in land sparing, we showed that reallocation led to homogenization of extensive areas but allowed intensive areas to become more heterogeneous. Accounting for the effect of the spatial intensity arrangement on biodiversity leads to optimal allocation strategies being more complex than the land sparing/sharing extremes.

In Europe, Agri-Environmental Schemes (AESs) are the main policy mechanisms for promoting extensive practices and favoring biodiversity. AESs are mainly implemented at the national scale. Their uptake, based on voluntary compliance, results in a spatial distribution that is either random or biased toward higher rates where adoption costs are lower (Osterburg *et al.*, 2001; Kleijn & Sutherland, 2003). Such random and diffuse uptake has been pointed out as a cause of their limited effectiveness in promoting biodiversity (Kleijn *et al.*, 2006; Whittingham, 2007). Conversely, the spatial targeting of AESs has been suggested as a way to improve their effectiveness (Latacz-Lohmann & Hodge, 2003; V Haaren & Bathke, 2008; Matzdorf *et al.*, 2008). Uthes *et al.* (2010) define targeting as applying conservation measures to the most vulnerable or suitable areas, where environmental effects are provided at lower costs than if conducted elsewhere. This is also achieved by the optimization procedure in our model. The model did show that optimal intensity allocations consisted of targeted intensity modifications, compared with a random distribution of modifications. Models like ours could thus be adequate tools to determine effective targeting of AESs.

Both optimal intensification and extensification tended to spare more extensive areas than did the random allocations. This result is in line with the crucial role of extensive habitats in maintaining a rich and uniquely adapted biodiversity (Bignal & McCracken, 1996; Benton, 2003). The optimal targeting of extensification led to a broadening of the initial cluster of extensive SARs. Other authors have proposed that reinforcing the quality of extensive areas would be the most effective way to promote farmland biodiversity (Kleijn & Sutherland, 2003; Feehan *et al.*, 2005; Whittingham, 2007). Gabriel *et al.* (2010) showed biodiversity measure to be more effective when there was a greater area under AESs at a $10 * 10$km scale. Other studies found AESs to be more effective in more extensive countries (Kohler *et al.*, 2007; Batáry *et al.*, 2010). Interestingly, the optimal intensification allocation involved the opposite targeting: concentrate the intensity modification in certain SARs and promote more heterogeneity. Primdahl *et al.* (2003) proposed that *protection measures* should target extensive areas in order to protect their high biodiversity values, whereas *improvement measures* should achieve positive changes in intensive areas. Our results show that it can be more effective to improve biodiversity in extensive areas and to mitigate its losses in intensive areas.

A question that is complementary to finding optimal intensity allocations is: what policy mechanisms would allow them to be reached? Today, no general policy mechanisms exist to target intensity changes or reallocations at the national scale. The trade-off between production and environmental performance drawn by various intensity allocations has been formalized as a trade-off between private and public benefits (Parra-López *et al.*, 2009; Groot & Rossing, 2011). This formalization underlines the need to use the policy design framework of Pannell (2008) for reflecting on the appropriate policy instrument to encourage a given allocation. The win-no-lose situation that we reveal (optimal intensification and reallocation) would thus require an *extension* mechanism through which education, communication, and support for community networking would support the coordination needed to reach the optimal allocations.

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Supplementary material

s1 Species list of the farmland bird community

Species	Grassland specialization index
Perdix perdix	1.25
Motacilla flava	1.33
Miliaria calandra	1.56
Vanellus vanellus	1.56
Carduelis chloris	1.58
Coturnix coturnix	1.59
Alauda arvensis	1.6
Carduelis carduelis	1.66
Alectoris rufa	1.84
Carduelis cannabina	1.85
Corvus frugilegus	1.94
Anthus pratensis	2
Sylvia communis	2.04
Falco tinnunculus	2.12
Emberiza citrinella	2.26
Saxicola torquata	2.29
Emberiza cirlus	2.37
Buteo buteo	2.42
Saxicola rubetra	2.44
Upupa epops	2.53
Lanius collurio	2.58
Lullula arborea	2.61

Table VIII.s1: List of the species included in the farmland bird community, along with their specialization-for-grassland indexes (SSIg).

s2 Calibrated relationships between the three criteria and intensity

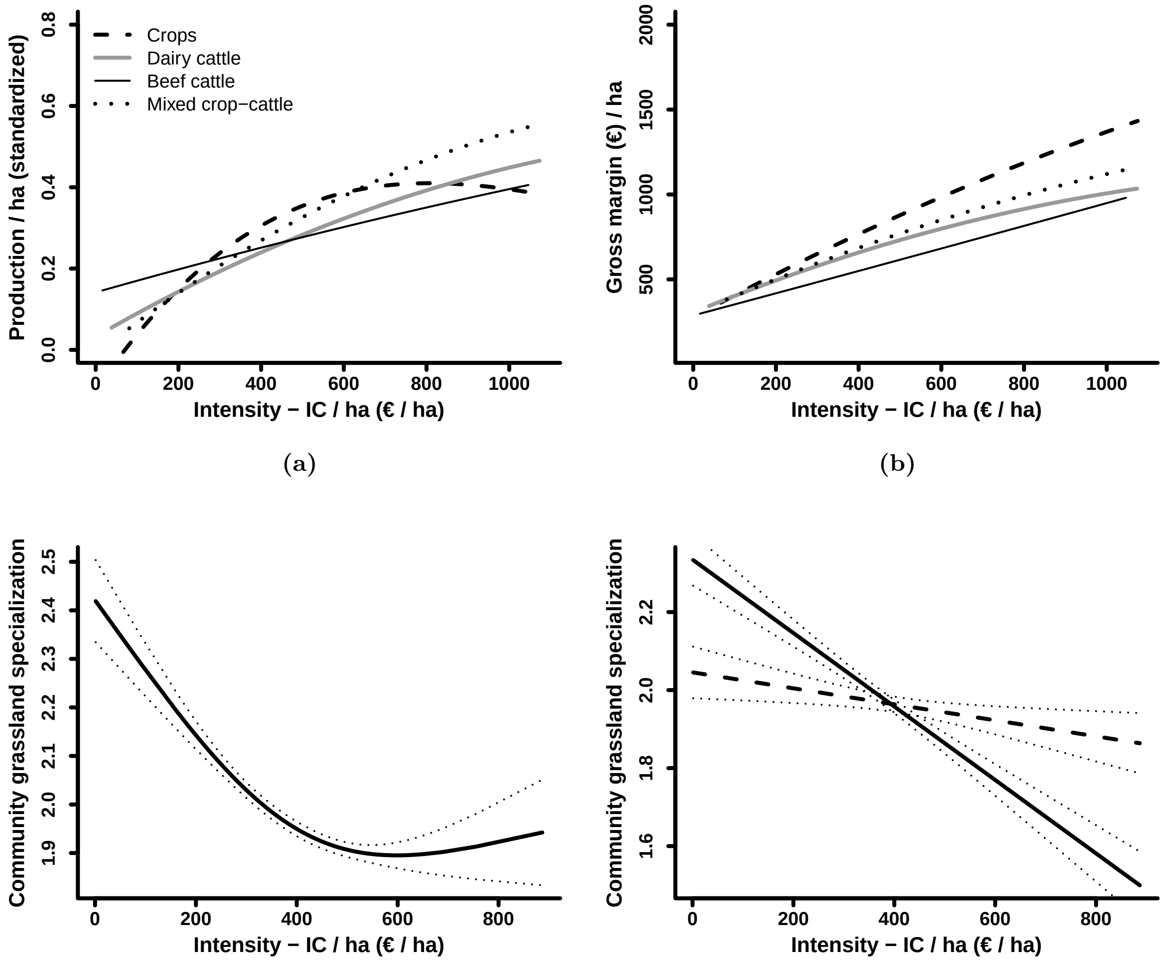
	n	*F*	*P-value*	% Deviance
Production				
Crops	1805	137.64	<0.001***	19
Dairy cattle	948	509.76	<0.001***	52
Beef cattle	570	39.28	<0.001***	12
Mixed crop-cattle	547	163.93	<0.001***	37
Gross Margin				
Crops	1805	379.89	<0.001***	30
Dairy cattle	948	400.6	<0.001***	46
Beef cattle	570	210.12	<0.001***	42
Mixed crop-cattle	547	245.1	<0.001***	47
Bird community				
Intensity	330	59.49	<0.001***	18
Aggregation (intercept)	193/137	-5.39	<0.001***	6
Aggregation (slope)	193/137	5.99	<0.001***	7

Table VIII.s2: Summary of the Generalized Additive Models (GAMs) used to calibrate the relationships between production (production volume/ha), economy (gross margin/ha), biodiversity (bird community specialization for grassland), and intensity (*Input Cost / ha*, IC/ha intensity indicator). For production and economy, GAMs are calibrated on FADN farms separately for each production type. For the bird community, GAMs were calibrated with the IC/ha value at the SAR level, and we accounted for an effect of the intensity spatial aggregation.

For most production types, the production and economic performances of the FADN farms showed a strong positive correlation with their intensity values. All relationships were highly significant (p-value< 00.001) and the percentages of variance explained by the IC/ha ranged from 12% to 52% (Table VIII.s2). It was higher than 30% except for the crops and beef cattle production types. For both production and economy, the relationships with intensity were similar among production types. For all production types except beef cattle, the positive correlations between production and intensity tended to slightly attenuate at high intensities (Fig. VIII.s2a). The positive correlations between economy and intensity were rather linear for all production types (Fig. VIII.s2b).

The relationship between the community grassland specialization (CSIg) and agricultural intensity was negative, with a non-linear, convex shape (Fig. VIII.s2c). The correlation was very significant (p-value< 0.001) and the percentage of variance explained by the IC/ha was 18% (Table VIII.s2). On an increasing intensity gradient, grassland birds were thus "loser" species and were replaced by arable birds ("winners"). The convex shape indicates that the effect of agricultural intensity on the bird community was sharper at low intensities and became null at high intensities. The average value of the French intensity was 464.1€/ha. This value was close to the point where the the CSIg reached is minimum and was no longer impacted by increasing intensity.

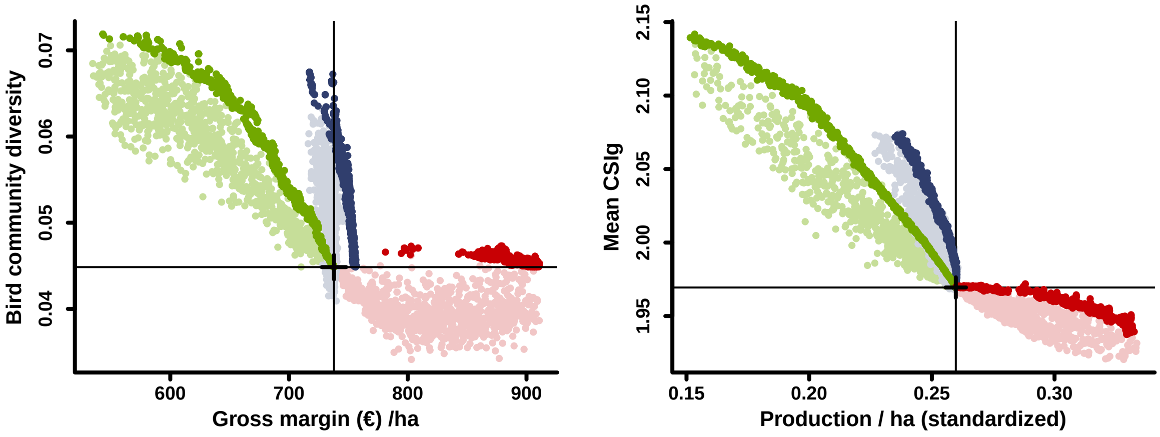
The effect of agricultural intensity on the bird community was stronger when intensity was spatially aggregated (Fig. VIII.s2d), *i.e.*, in SARs aggregated with contiguous neighbors having similar intensity values. The responses of the community-grassland specialization to intensity had significantly different intercepts and slopes (both p-values< 0.001, Table VIII.s2) in aggregated *vs* non-aggregated SARs. However, this interaction had a lower magnitude than the effect of intensity itself had (the aggregation + intensity*aggregation interaction explained a variance of 7% of the community-grassland specialization, vs 18% for the intensity). Fig. VIII.s2d also reveals that spatial aggregation had a positive effect on CSIg in extensive SARs, but a negative effect in intensive SARs.



(a) (b) (c) (d)

Figure VIII.s2: Calibrated relationships between the production, economic, and biodiversity criteria and agricultural intensity (*Input Cost/ha* indicator, IC/ha). (VIII.s2a) Relationship with production (production volume/ha, min max standardized within each production type). (VIII.s2b) Relationship with economy (gross margin/ha). For production and economy, relationships were calibrated on FADN farms, separately for the four production types (see legend). (VIII.s2c) Relationship with the farmland bird community composition (specialization for grassland index, CSIg). The relationship (black curve) is plotted along 95% confidence intervals (dotted lines). (VIII.s2d) Relationship between the CSIg and intensity in Small Agricultural Regions aggregated with neighbors showing similar intensity (full line) or non-aggregated (dashed line). 95% confidence intervals are plotted as dotted lines. For details of the calibration performances see Table VIII.s2.

s3 The trade-offs between the economy and alternative biodiversity criteria



(a) (b)

Figure VIII.s3: National performances of all intensity allocations according to the three criteria (production, economy, and biodiversity). Red: intensification scenario, green: extensification scenario, blue: reallocation scenario. Pale colors: random allocations, bright colors: optimal allocations. (VIII.s3a) Performance trade-off between the economic (national mean gross margin/ha) and biodiversity (coefficient of variation of the bird community specialization for grassland, CSIg) criteria across all allocations. (VIII.s3a) Trade-off between the production (national mean production volume/ha) and an alternative biodiversity criteria (national mean CSIg).

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Résumé

L'intensification de l'agriculture a joué un rôle crucial pour augmenter la production alimentaire au cours des dernières décennies. Plusieurs processus liés à l'intensification ont aussi causé d'importants dommages environnementaux, sur la biodiversité en particulier. L'agriculture doit aujourd'hui faire face au défi de satisfaire à une demande alimentaire croissante tout en améliorant son impact environnemental et sa durabilité. Il est nécessaire de connaître la forme de la relation entre biodiversité et intensité agricole pour déterminer où les politiques de conservation seront les plus efficaces et quelles allocations spatiales de l'intensité permettront de concilier production et biodiversité. Il existe peu de preuves empiriques de la forme de cette relation, de plus, l'influence de l'arrangement spatial de l'intensité sur la biodiversité demeure inconnue. Cette thèse avait pour objectif de déterminer comment cibler l'intensité agricole et son allocation spatiale afin d'atteindre des objectifs à la fois productifs et environnementaux.

Afin de répondre à cette question, nous avons adopté une approche à l'échelle de la France entière, en couplant des bases de données décrivant l'agriculture et des oiseaux spécialistes des milieux agricoles à cette échelle. Nous avons caractérisé un gradient d'intensité à l'échelle du pays et étudié une communauté d'oiseaux spécialistes des milieux agricoles tout au long de ce gradient. Plusieurs descripteurs de cette communauté ont été utilisés, renseignant sa taille (richesse spécifique) mais aussi sa composition (spécialisation, niveau trophique, habitat). L'intensité agricole et les communautés d'oiseaux ont été reliées au niveau de la Petite Région Agricole (PRA; largeur moyenne = 22.4 km).

Tout d'abord, nous avons développé une méthode permettant d'estimer un indicateur d'intensité agricole basé sur le coût intrant par hectare, au niveau de la PRA. Cet indicateur fournit une valeur d'intensité continue, pertinente à la fois pour les systèmes d'élevage et de culture. Ensuite, nous avons examiné les effets d'un gradient d'utilisation des sols (des prairies aux grandes cultures) et de leur hétérogénéité, sur la communauté d'oiseaux. L'hétérogénéité a un effet négatif sur les espèces spécialistes car elle entraine la perte de leur habitat. En revanche, elle avantage les espèces généralistes. Lors d'une troisième étape, nous avons montré que la communauté d'oiseaux était significativement influencée par l'intensité. Le long du gradient des espèces "gagnantes" remplacent des espèces "perdantes", ce changement étant plus marqué aux faibles intensités. L'effet de l'intensité sur la communauté d'oiseaux est renforcé par son agrégation spatiale. Enfin, les relations entre l'intensité, la communauté d'oiseaux, et les performances productives et économiques ont été intégrées dans un modèle d'optimisation de l'allocation de l'intensité. Les allocations optimales révèlent des solutions gagnant-non-perdant entre les trois critères de performance (biodiversité, production et économie). Ces allocations optimales correspondent à des modifications d'intensité ciblées: beaucoup de petits changements, favorisant des zones homogènes et extensives dans le cas d'un scénario d'extensification, à l'opposé de changements importants et moins nombreux, favorisant plus d'hétérogénéité, dans le cas d'un scénario d'intensification.

Cette thèse apporte une des premières démonstrations de l'influence de l'agrégation spatiale de l'intensité sur la relation entre biodiversité et intensité. Nos résultats révèlent une opportunité pour améliorer l'efficacité des politiques de conservation de la biodiversité à l'échelle nationale. Il s'agit d'un ciblage de ces politiques, qui devra être différent pour maximiser la biodiversité à coût productif réduit ou pour augmenter la production tout en limitant les dommages sur la biodiversité. Nos résultats soulignent aussi l'importance de considérer des stratégies d'allocations intermédiaires, entre les deux extrêmes que sont le *land sparing* (ségrégation) et le *land sharing* (coexistence). Afin de tirer profit de ces opportunités, de futures recherches devront dévoiler les solutions techniques permettant de modifier l'intensité au niveau des exploitations agricoles, et concevoir les politiques ciblées permettant de bénéficier à la biodiversité et à d'autres critères environnementaux.

Mots-clés : biodiversité, intensité, allocation, arrangement spatial, oiseaux agricoles, communauté, mesures agro-environnementales, ciblage, indicateur, optimisation multicritères

Abstract

During the past several decades, agricultural intensification has been crucial to increase the food supply. Several processes related to intensification are very detrimental to the environment, particularly biodiversity. Today, agriculture is facing the challenge of satisfying its demand for food while improving its environmental sustainability. Knowledge of the shape of the relationship between biodiversity and intensity is necessary to determine both where conservation policies will be most effective and how to allocate intensity to reconcile production and biodiversity. Few empirical studies on this relationship exist, and the influence of the spatial arrangement of intensity on biodiversity remains untested. This Ph.D. thesis determined how to target both agricultural intensity and its spatial allocation for meeting production and conservation objectives of farmlands.

To answer this research question, we used a country-scaled approach that combined two France-scaled databases that describe agriculture and farmland birds. We characterized a nationwide gradient of agricultural intensity and studied a farmland bird community along this gradient, using several trait-based descriptors (specialization, trophic level, and species main habitat). Agricultural intensity and bird communities were described at the Small Agricultural Region (SAR; mean width = 22.4 km) level.

As a first step, we developed a novel method to estimate an intensity indicator that was based on Input Costs/ha, with SAR resolution. This indicator provides a continuous intensity measure that is relevant across different types of agricultural systems. Secondly, we investigated the effects of a gradient of land uses (grassland to arable land) and its heterogeneity on the bird community. We found habitat specialists suffered from habitat loss, while generalists benefited from heterogeneity. Thirdly, we showed that the community responded significantly to intensity, with winner species replacing loser species along the gradient. The shift between losers and winners was sharper at low intensities. Interestingly, spatial aggregation of intensity had a strengthening effect on the bird community. Finally, the relationships linking intensity to the bird community, food production, and economic performance were integrated into a model aimed at optimizing intensity allocation. Optimal allocations reached win-no-lose solutions with the three criteria. They corresponded to targeted intensity modifications: many small changed, favoring homogeneous, extensive clusters, were optimal within an extensification scenario; while a few large changes, favoring heterogeneity, were optimal within an intensification scenario.

We provide one of the first studies demonstrating that spatial aggregation of intensity can influence the biodiversity/intensity relationship. Our results also provide an opportunity to improve the effectiveness of conservation policies, at national scales, with spatial targeting: opposite targeting should be performed either to maximize biodiversity benefits or to increase production, while mitigating biodiversity impacts. Our results highlight the importance of mixed allocation strategies between land sparing/sharing extremes. In order to put these opportunities into effect, further research should address the technical solutions that achieve intensity modification at the farm level and design targeted policies that benefit biodiversity and other environmental criteria.

Keywords: biodiversity, agriculture, intensity, allocation, spatial arrangement, farmland birds, community, agri-environment schemes, targeting, indicator, multi-criteria optimization