

# Chapter 1

## Ecology for Sustainable and Multifunctional Agriculture



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**Abstract** The Green Revolution and the introduction of chemical fertilizers, synthetic pesticides and high yield crops had enabled to increase food production in the mid and late 20th. The benefits of this agricultural intensification have however reached their limits since yields are no longer increasing for many crops, negative externalities on the environment and human health are now recognized and economic inequality between farmers have increased. Agroecology has been proposed to secure food supply with fewer or lower negative environmental and social

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impacts than intensive agriculture. Agroecology principles are based on the recognition that biodiversity in agroecosystems can provide more than only food, fibre and timber. Hence, biodiversity and its associated functions, such as pollination, pest control, and mechanisms that maintain or improve soil fertility, may improve production efficiency and sustainability of agroecosystems. Although appealing, promoting ecological-based agricultural production is not straightforward since agroecosystems are socio-ecosystems with complex interactions between the ecological and social systems that act at different spatial and temporal scales. To be operational, agroecology thus requires understanding the relationships between biodiversity, functions and management, as well as to take into account the links between agriculture, ecology and the society. Here we review current knowledge on (i) the effect of landscape context on biodiversity and ecosystem functions and (ii) trophic and non-trophic interactions in ecological networks in agroecosystems. In particular, many insights have been made these two previous decades on (i) the interacting effects of management and landscape characteristics on biodiversity, (ii) the crucial role of plant diversity in delivering multiple services

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and (iii) the variety of ecological belowground mechanisms determining soil fertility in interaction with aboveground processes. However, we also pinpointed the absence of consensus on the effects of landscape heterogeneity on biodiversity and the need for a better mechanistic understanding of the effects of landscape and agricultural variables on farmland food webs and related services. We end by proposing new research avenues to fill knowledge gaps and implement agroecological principles within operational management strategies.

**Keywords** Agroecology · Ecological intensification · Ecosystem services  
Eco-evolutionary dynamics · Biotic interactions · Landscape heterogeneity  
Socio-ecological systems

## 1.1 Introduction

Contemporary agriculture faces conflicting challenges due to the need of increasing or expanding production (i.e. food, feed, bioenergy) while simultaneously reducing negative environmental impacts. The heavy agricultural reliance on synthetic chemical pesticides or fertilizers for crop protection and crop nutrition is leading to soil, air and water pollution (agriculture represents 52 and 84% of global methane and nitrous oxide emissions, Smith et al. 2008; more than 50% of the nitrogen applied to fields is not taken up by crops, Hoang and Allaudin 2011), as well as a dramatic decline of biodiversity (67% of the most common bird species in Europe, i.e. mainly farmland species, Inger et al. 2014), soil degradation concerning about 40% of cropped areas worldwide (Gomiero et al. 2011)) and the degradations in ecosystem functioning (Tilman et al. 2001; Cardinale et al. 2012). Agroecology principles suggest that strengthening ecosystem functions will improve the production efficiency and sustainability of agroecosystems, while decreasing negative environmental and social impacts (Gliessman 2006; Altieri 1989; Altieri and Rosset 1995; Wezel et al. 2009). One generic term grouping approaches that rely on strengthening ecosystem functions, such as pollination, pest control, and mechanisms that maintain or improve soil fertility, is ‘ecological intensification’ (Doré et al. 2011; Bommarco et al. 2013; Tittonnell et al. 2016, but see Godfray 2015). Such an approach fits the aim of adopting a sustainable and multifunctional agriculture, i.e. an agriculture that delivers multiple ecosystem services (Fig. 1.1). However, it constitutes a knowledge challenge as it requires to both understand and manage ecosystem functions and also to take into account the relationships between agriculture, ecology and the society.

Agroecosystems are commonly defined as ecological systems that are modified by humans to produce food, fibres or other agricultural products (Conway 1987). They are prime examples of social-ecological systems (Redman et al. 2004; Collins et al. 2007; Mirtl et al. 2013): multiple interactions between farmers, societies and ecological systems are indeed involved in the sociological and ecological dynamics. However, until fairly recently, social and biophysical processes were most often



**Fig. 1.1** Example of a technique delivering multiple ecosystem services. This multifunctional cover crop is composed of *Vicia sativa*, *Trifolium alexandrinum*, *Phacelia tanacetifolia* and *Avena strigosa* and is designed to enhance soil fertility (nitrogen supply via legumes, nitrogen retention through *A. strigosa*, erosion control and soil organic matter enhancement thanks to biomass production), to support some pollinators (thanks to flowering *P. tanacetifolia* and *T. alexandrinum*) and to maintain natural enemies between successive crops (thanks to legumes providing alternative hosts to aphid predators and *V. sativa* providing extrafloral nectar)

considered separately. For instance, questions regarding agricultural production on one hand, and those regarding social needs and diets on the other hand, were treated apart. Hence one avenue to improve sustainability in agriculture is to treat agriculture ecological impacts with the same attention than question of optimal food production. This requires to adopt an ecological perspective with interactions and networks as core concepts. Research is currently dealing with many issues, from ecological point of view, such as: *How can greenhouse gas emissions be minimized? How can the impacts on biodiversity be reduced? Where and how should biofuels be produced to avoid or limit impacts on biodiversity? How can we solve the land-sharing/land-sparing debate (Green et al. 2005) regarding biodiversity conservation? How to design efficient biodiversity based agricultural systems to ensure the availability of natural resources (water, fossil resources, phosphorus...)? How production types and biodiversity interact with social issues? How can we alleviate poverty and hunger through innovative food production systems (Griggs et al. 2013), as well as appraise the new diet challenges of developed countries?* All these burning questions require to be addressed together and to solve

the nexus between provisioning goods, climate, social context and biodiversity (Tomish et al. 2011).

A better understanding of the interactions within and between the ecological and social templates, and processes underlying them will help to improve the analysis of farming system and public policies (Cumming et al. 2013). Yet, both the ecological and the social templates have their own and peculiar characteristics, that must be accounted for. For example, arable fields are dominated by one single plant species (the crop), and both the abiotic and biotic environment are modified to increase biomass production by human practices (Swift et al. 2004), which thereafter affects nutrients and ecological processes (e.g. competition for resources). The conventional practices tend to reduce the magnitude of ecologically-driving mechanisms beneficial for crop production: for instance, pesticides may reduce tri-trophic interactions between pest and their predator or parasitoid by killing non-targeted potentially beneficial organisms (Potts et al. 2010; Pelosi et al. 2014); losses of soil organic matter and tillage practices tend to reduce the abundances of soil fauna and microorganisms (Kladivko 2001; Roger-Estrade et al. 2010) and thereafter their beneficial effect on soil fertility.

Biodiversity is one of the mostly affected dimension of ecosystem due to intensively managed agroecosystems: in croplands, the plant biodiversity is strongly biased towards short-lived disturbance-tolerant plant strategies. Together, tillage impedes the development of a structured soil profile with organic-rich layer at the soil surface. As a consequence of selection of new crop varieties through intensive breeding technics for fast growth rates in nutrient and water rich environment, crop plants have evolved from resource-conservation towards resource-acquisition traits in comparison to wild species (Tribouillois et al. 2015; Delgado-Baquerizo et al. 2016; Milla et al. 2015). This contributes to nutrients' leaching from agroecosystems (Gardner and Drinkwater 2009). Rather to make the most of ecological processes, the current practices thus limit ecological interactions and keep them as neutral as possible to reduce their imponderable effects on crop production.

Ecological and socioeconomic processes act at different spatial scales, since field or farm scales are rarely ecologically meaningful (Cummings et al. 2013). Agroecosystems are complex, in particular because they are driven by spatially nested decision-making that range from farmer decisions at local scale (e.g. field) to societal management and political decisions at regional and national scales. Given that complexity, it is perhaps not surprising that in several cases ecological laboratory studies do not reflect the results obtained in long-term field studies. This is the case for the study of the impact of genetically modified (GM) crops on natural enemies (Lövei, Andow, and Arpaia (2009); Box 1) and biological control (Frank van Veen et al. 2006). Taken together, these arguments suggest that studying the relationships between agricultural practices and ecological processes (i.e. biotic interactions related to pest control, pollination, biogeochemical cycles and soil fertility) at nested scales (field, farm, landscape) is mandatory to develop sustainable and multifunctional agriculture.

**Box 1: Technology, Agro-Ecological Engineering, and Socio-Cultural Mismatch: The Case of Genetically Modified Crops**

Technologies can reshape interactions between humans and ecosystems, namely between agro-ecosystems, the agri-food system and the overall socio-ecological system. Since the green revolution, modern food production has become highly dependent on agricultural technological advances (Altieri and Nicholls 2012). Despite its numerous claimed benefits and widespread adoption (Lu et al. 2012; Klümper and Qaim 2014), no other agriculture technological advance has been as controversial as the development of GM crops (Stone 2010). There is still intense discussion in the research community on whether the use of this technology in agriculture may contribute to a sustainable agriculture reaching the world nutritional demand (Ervin et al. 2011; Godfray et al. 2010). The arguable environmental uncertainty of GM crops allied with the feasibility (or even ethicality) of food monopolization, and the enormous economic interests at stake for the biotechnology industry make this topic rather complex (Glover 2010). Besides the conceivable ecological risks directly caused by the employment of GM crops (Dale et al. 2002) and the dispersion of its contents (Piñeyro-Nelson et al. 2009), which may take several years to manifest (Catarino et al. 2015), other questions and challenges have arose.

Biotechnology companies and some academic proponents claim that GM crops are a crucial scientific step forward in order to meet food security demands (Tester and Langridge 2010; Qaim and Kouser 2013), however some evidence dispute these assertions. Research and political priorities, and the consequent employment of new plant strains usually occur with little knowledge on the intricacies of their impact on the complex socio and agri-food systems of small-scale farmers (Glover 2010; Altieri and Rosset 2002). A key example is the case of the Golden Rice (for details see Stein et al. 2006 and Paine et al. 2005), more than a decade after its development, is still not available (Whitty et al. 2013). Instead, in developing countries, two plants dominate the GM market, *Bt* Cotton and *Bt* Maize (James 2014). Since the intellectual property rights system implemented in many countries promote a restricted number of private companies with an excessive dominance (Rao and Dev 2009; Russell 2008), it has been argued that strong adoption of GM crops in developing countries, such as *Bt* maize in South Africa, may actually result from a lack of choice rather than being a direct benefit of the technology (Witt et al. 2006), or as Gouse et al. (2005) claim “a technological triumph but institutional failure”.

In addition, evaluating the suitability of this technology has mainly focused on immediate ecological and economic impact (Fischer et al. 2015). There is a clear lack of knowledge regarding the actual social impacts of GM crops introduction, particularly within smaller-scale and resource-poor farmers (Fischer et al. 2015; Stone 2011). Still, it is clear that the amalgamation of these factors create a technological regime and a lock-in situation

that delays the development of alternative agriculture solutions (Vanloqueren and Baret 2009; Dumont et al. 2016) and limited food sovereignty (Jansen 2015). Thus, the sustainability of an agriculture innovation, including biotechnology, is dependent on the relationship between economic performance while addressing key social, ecological and political challenges facing the adopting farmers (Ervin et al. 2011). The latest gene editing techniques, including CRISPR-Cas 9 method, relaunch this debate and highlight the importance to focus on broad issues on sustainability rather than on technologies (Abbott 2015).

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Here, we review ecological theories and concepts, that may be useful to understand and enhance biodiversity and ecosystem functions in agroecosystems. We first discuss the specific characteristic of agroecosystems as social-ecological



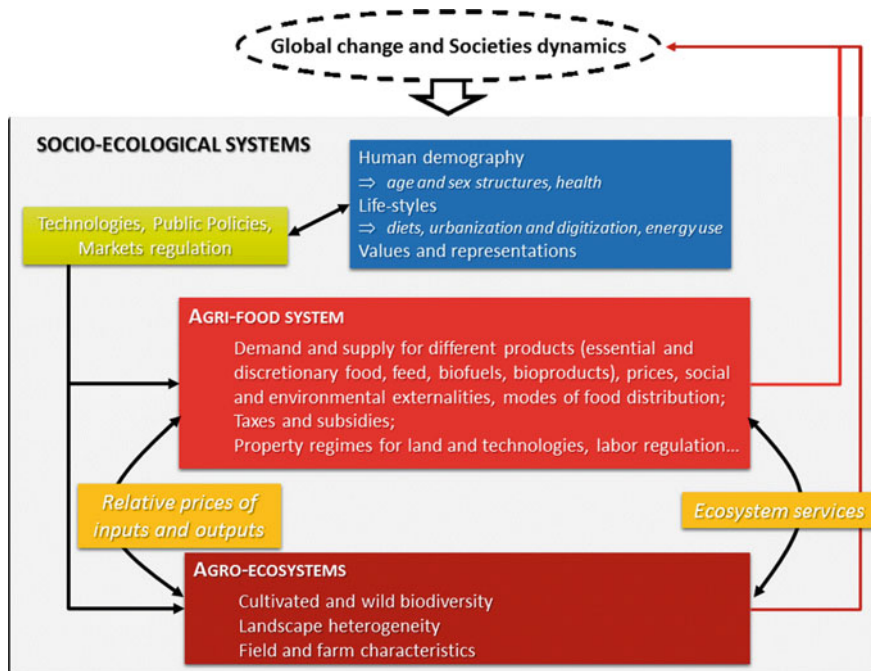
systems in order to highlight the need to study ecological processes in interaction with management and human decisions, while taking into account the socio-economic context. We then present several contributions of ecological sciences on (i) the effect of landscape on biodiversity and ecosystem functions and (ii) biotic interactions in ecological networks in agroecosystems. Finally, we discuss relevant perspectives to fill current knowledge gaps to implement agroecological principles in agriculture and to go from theories to practices.

## 1.2 Agroecosystems are Social-Ecological Systems at Work

Dynamics of social-ecological systems depend on interactions and feedbacks between environmental and social processes (Oström 2007). Feedbacks result from human actions on one side, and from amenities and ecosystem services, environmental constraints, stochastic events or vulnerabilities on the other side. Various socio-ecosystem models (e.g. DPSIR, MEFA, HES...) emphasize different interactions, or feed-backs (Binder et al. 2013). To understand these feed-backs in the case of agriculture, different systems may be considered, agroecosystems (Loucks 1977), agri-food system (Busch and Bain 2004), and the overall socio-ecological system, emphasizing different entities, processes (Fig. 1.2). Public policies, markets and technologies determine relationships between agroecosystem and the agri-food system (Fig. 1.2). These two systems further interact with the overall socio-ecological system, through global change and society dynamics. Considering these three systems and their interactions, is necessary to analyze the nexus between food-price-, energy, available land and sustainable development goals (Obersteiner et al. 2016), or at a finer scale the relation between biodiversity conservation and poverty traps (Barrett et al. 2011).

Given their environmental impact, the way public policies are scrutinized and evaluated by the different stakeholders, is a major feedback mechanism. Agricultural policies are technically quite complex, involving at least four strata of decision-makers, from voters to politicians, administration and managers, related through a principal-client relationship (Wolfson, 2014). As a result, social choice to change agricultural modes of production faces many complexities, uncertainties, and rigidities. Indeed, social and environmental consequences of decisions, involve path-dependence and lock-in processes, particularly between technologies and social organizations (Vanloqueren and Baret 2009), accounting for difficulties to decide technical changes, even though detrimental environmental effects of the present techniques have been shown.

Beyond public policies, social processes having major environmental effects involve human demography, life-styles, including urbanization and, more specifically in regards to agriculture, types of food distribution, consumption (Seto and Ramankutty 2016) and diets overall (Bonhommeau et al. 2013), but also related



**Fig. 1.2** Interaction between Agro-ecosystems, Agri-food systems and Socio-Ecosystems (adapted from Hubeau et al. 2016)

institutions (Kessler and Sperling 2016). That concerns social norms, through representations and preferences relative to diets, for example preferences for discretionary food (sensu Hadjikakou 2017). These processes determine the relationship between supply and demand, through the agri-food system, relating different kinds of producers and consumers, affecting the dynamics of local, regional and global agroecosystems. In this regard, understanding and integration of environmental impacts of diets by consumers is a major mechanism determining the relationship between societies and agro-ecosystems, promoting some types of agricultural production such as conventional, agro-ecological or organic farming, at the expense of others. For example, changes in social norms require knowledge on the relationships between the local effects on food preference induced by the global agricultural markets (Lenzen et al. 2012) and the dietary information according to nutritional requirements (deFries et al. 2015). Such information depends on life-cycle analyses (LCA, e.g. Kareiva et al. 2015; Schouten and Bitzer 2015) that can estimate the impact of market including economic incentives, such as taxes and subsidies, on agroecosystem dynamics. Then, the effect of incentives such as public policies, designed beyond the national levels and mediated through international treaties, can be evaluated on local agro-ecosystems (Friedmann 2016). Rules or guidelines may specify a desired environmental state or limit to alterations of the

environment by human activities. Competition between different standards, could thus become a major determinant of the dynamics of agro-ecosystems, in the context of rigid public policies (see above). Such standards were developed first by non-governmental organisations (NGOs), in close collaboration with northern retailer actors, based at first on environmental criteria. Southern countries production actors now propose competing standards, putting more emphasis on socio-economic criteria (Schouten and Bitzer 2015), potentially leading to a different kind of agro-environmental changes. In other words, through its input on the making of environmental standards of food products, ecology could have a major impact on the dynamics of agro-ecosystems.

### **1.3 Reconciling Production and Biodiversity Using the Concept of Ecosystem Services**

Ecosystem services concept formalizes the dependency of human societies to ecosystem functioning, between social-ecological and agro-ecosystems (Fig. 1.2). From this, ecosystem services have an operational value for rethinking the links between ecological processes and functions and expected agriculture-related services. As such, ES embraces all complexity and interactions involved and present promising avenues for addressing the sustainable production challenges, more generally to consider sustainable livelihoods.

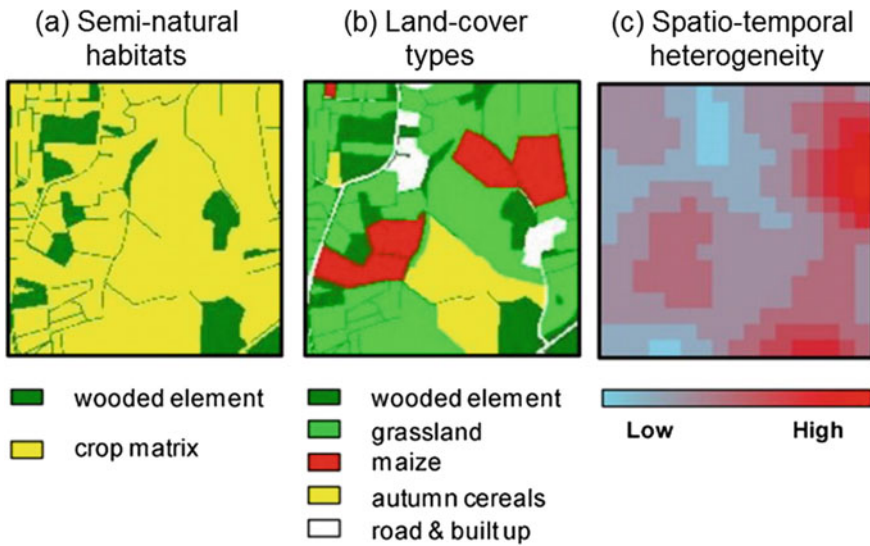
This concept emerged during the 70's and the 80's in the scientific literature, but grew faster since 1997 and the seminal publications of Daily et al. (1997) and Costanza et al. (1997). The Millennium Ecosystem Assessment (MEA 2005) ratified a definition of ecosystem services (ES) actually proposed by Daily et al. (1997). The concept has, since then, been used as a framework in numerous initiatives and international platforms such as IPBES (Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Assessment) or SGA-Network (Sub-Global Assessment Network, operated by the United National Environment Program, UNEP) (Tancoigne et al. 2014). As being part of a socio-ecological system (SES) framework (e.g. Collins et al. 2007), ecosystem service concept emphasizes the interdependency between economic systems and ecosystems. It also offers a common framework to initiate debates between the different stakeholders, allowing operational ways of thinking for collective design and assessment of management options. For agriculture issues, the evaluation of ecosystem services requires considering, regulating and cultural services jointly to provisioning services (Bateman et al. 2013). The analyses of bundles of services relying on processes acting at different spatial scales require landscape-scale investigations (see for an example Nelson et al. 2009).

## 1.4 Landscape Scale, Key Scale for Agroecology

Landscape is a level of organization of ecological systems that is characterized by its heterogeneity and its dynamics that are partly driven by human activities (Burel and Baudry 2003). Agricultural landscapes are spatially heterogeneous because of the variety of cultivated land-cover types that are distributed in a complex spatial pattern and interspersed with semi-natural and/or uncultivated habitats like woodlands, hedgerows, field margins or permanent grasslands. Farmers' decision rules about cropping systems led to the highly variable of landscape mosaic in time with a diversity of crop types, organized in inter-annual sequences and with within-year management practices (Vasseur et al. 2013). In agricultural landscapes, farming activities generally operate at the field scale but their type and intensity strongly depend on processes acting at larger scales such as the farm such as type of agriculture or availability of agricultural material, the territory such as agricultural cooperatives and agri-food market, and administrative scales relevant for policy making such as national or European levels. Biodiversity patterns and their associated ecosystem functions occur at several spatial scales from some few mm<sup>2</sup> (e.g. soil micro-organisms) to worldwide (e.g. carbon cycle). Accordingly, ecological processes act at a variety of spatial and temporal scales, and they generate patterns at scales that may differ from that at which processes act (Levin 1992). Such nested patterns in the ecosystems drivers bring complexity that need to be taken into account for the management of biodiversity and ecosystems functions. There are therefore mismatches between the scales of ecological processes and the scale of management (Pelosi et al. 2010).

### *1.4.1 Absence of Consensus About the Effects of Landscape Heterogeneity on Biodiversity and Ecosystem Services*

Landscape heterogeneity, defined as the composition (diversity, quality and surface of habitats) and configuration (spatial arrangement of habitats) of a landscape (Fahrig et al. 2011), has been recognized as a key driver of biodiversity and ecological processes in most agro-ecological studies (Benton et al. 2003; Bianchi et al. 2006). Landscape heterogeneity influences a variety of ecological responses, including animal movement (reviewed in Fahrig 2007), population persistence (Fraterrigo et al. 2009), species diversity (Benton et al. 2003), species interactions (Polis et al. 2004), and ecosystem functions (Lovett et al. 2005). In relation with the island biogeography theory (MacArthur and Wilson 1967), studies investigating the effects of landscape heterogeneity on ecological processes have traditionally focused on the role of semi-natural habitats viewed as embedded in a hostile agricultural matrix (Fig. 1.3).



**Fig. 1.3** Different representations of spatio-temporal heterogeneity, adapted from Vasseur et al. (2013): **a** spatial heterogeneity related to semi-natural habitats, **b** spatial heterogeneity related to land-cover types, and **c** spatio-temporal heterogeneity related to shift intensity in the relative crop composition of crop successions over years

Meanwhile, studies have measured landscape heterogeneity, also called “landscape complexity”, as the amount or surface area of semi-natural habitats in agricultural landscapes (Benton et al. 2003). They have highlighted its role in maintaining farmland biodiversity (Baudry et al. 2000; Tscharntke et al. 2005) and enhancing ecosystem functions of economic importance such as pest predation and parasitism (Bianchi et al. 2006; Rusch et al. 2011). Indeed, semi-natural habitats provide resources (e.g. food, nesting places, shelters) for many taxa, and are often considered as “sources” of pest natural enemies in the landscape (Landis et al. 2000; Médiène et al. 2011). However, several empirical evidence also demonstrated that semi-natural habitats might fail to enhance biological control of crop pests in various context (Tscharntke et al. 2016). Generalist predators, such as aphidophagous coccinellids, may also spillover from crops to semi-natural habitats, as they exploit resources (i.e. aphid resources, overwintering sites) in both habitats (Tscharntke et al. 2005). Other studies have underlined the detrimental effect of spatial isolation of semi-natural habitats on the diversity and abundance of many taxa such as invertebrates, plants or birds (Steffan-Dewenter and Tscharntke 1999; Tewksbury et al. 2002; Petit et al. 2004; Bailey et al. 2010). Indeed, spatial isolation of semi-natural habitats alters the physical continuity of resources. The abundance and richness of species inhabiting semi-natural habitats varied with the success of finding a patch, which decreases with isolation (Goodwin and Fahrig 2002). Thus,

decreasing isolation by increasing spatial connectivity<sup>1</sup> of semi-natural habitats with ecological corridors is a way to promote biodiversity and associated functions as demonstrated for insects (Petit and Burel 1998; Holland and Fahrig 2000) or birds (Hinsley and Bellamy 2000).

Habitat fragmentation might not only affect biodiversity but also important ecosystem functions (Tschamtko et al. 2005; Ricketts et al. 2008). For instance, there are empirical evidences that habitat fragmentation may lead to the reduction of pest control as a consequence of stronger impacts on natural predators than on their herbivore preys (Kruess and Tschamtko 1994; Bailey et al. 2010). Despite a consensus about the negative impact of habitat loss, landscape ecologists often disagree about the impact of habitat fragmentation per se (patch size reduction and isolation). This controversy has resulted in the SLOSS (Single Large Or Several Small) debate regarding how species should be conserved in fragmented landscape, i.e. through the promotion of “Single Large” or “Several Small” habitat patches (Diamond 1975; May 1975). It has been reinforced by the difficulty to quantify the relative effects of both aspects of fragmentation that are often strongly correlated in non-manipulative studies (Fahrig et al. 2011).

Semi-natural habitats play a key role in agricultural landscape. For instance, pollinators, crop pests and their natural enemies use alternatively semi-natural habitats (e.g. overwintering in hedgerows or forest edges) and crop fields to complement or supplement their resources during their life cycle for example. feeding and breeding in crop fields (Kromp 1999; Westphal et al. 2003; Rand et al. 2006; Macfadyen and Muller 2013). Other species may also interact with the whole agricultural mosaic whilst simply moving between semi-natural habitats (Vos et al. 2007). The growing awareness that the “matrix matters” for ecological processes (Ricketts 2001; Jules and Shahani 2003; Kindlmann and Burel 2008) has resulted in growing consideration of the heterogeneity of the agricultural mosaic itself. Characterizing the mosaic is not straightforward because of the strong correlation between landscape composition and configuration (Box 2). Fahrig et al. (2011) has proposed a framework to decorrelate these features (Box 2), and its use led to contradictory results about the effects of crop heterogeneity on biodiversity. For instance, Fahrig et al. (2015) have found a higher effect of crop configurational heterogeneity on multi-taxa diversity while Duflo et al. (2016) showed that carabid diversity was more affected by crop compositional heterogeneity and Hiron et al. (2015) did not find any effect of crop heterogeneity on bird diversity. The effects of crop heterogeneity thus appear highly species and case study dependent, which emphasizes the need for further researches and alternative approaches.

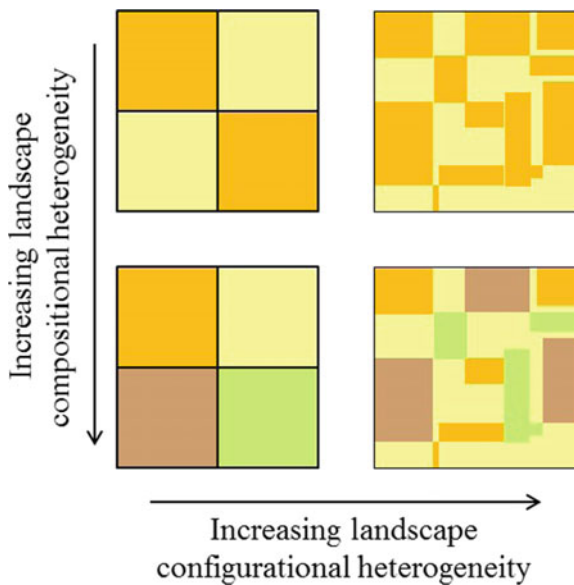
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<sup>1</sup>Landscape connectivity is defined as the ability of landscapes to facilitates or impedes the movement of organisms (Taylor et al. 1993)

**Box 2: Methodological Issues to Investigate the Effect of the Spatial and Temporal Heterogeneity of Agricultural Landscapes**

Landscape heterogeneity, defined as the composition (diversity, quality and surface of habitats) and configuration (spatial arrangement of habitats) of a landscape (Fahrig et al. 2011), is a fundamental concept in landscape ecology (Wiens 2002; Fig. 1.5a). Distinguishing the relative effects of these two components is a challenge to identify on which aspects management measures should focus. Recently, several authors have proposed a conceptual framework towards a more functional view of landscape heterogeneity for farmland biodiversity, no more based upon the amount of semi-natural habitats, but considering the agricultural mosaic as composed of cultivated habitat patches with varying quality for species (Fahrig et al. 2011). This representation of functional heterogeneity is derived from a map of cover types that are characterized according to species requirements, and not according to the perception by the human observer (or remote-sensing device). Fahrig et al. (2011) have also proposed a pseudo-experimental design to disentangle metrics of landscape compositional heterogeneity (e.g. richness or Shannon diversity of cover types) and configurational heterogeneity (e.g. mean patch size, edge density) in mosaics of crops (Fig. 1.4).

From a methodological point of view, and comparatively to spatial heterogeneity, efforts are still needed to account for landscape temporal



**Fig. 1.4** Theoretical definition of spatial heterogeneity into its two components i.e. landscape composition and landscape configuration (adapted from Fahrig et al. 2011)

heterogeneity. Bertrand et al. (2016) proposed four general metrics to account for temporal heterogeneity of cropped areas across a short period of time. However, the authors underlined that the relevance and meaning of these metrics are strongly dependent on the cropping system under evaluation and should be studied in conjunction with other landscape factors. Indeed, in a simulation work, Baudry et al. (2003) showed that landscape changes over long time were determined by changes in the farming systems and associated changes in cropping systems.

Such dynamics of agricultural landscapes may also determine temporal variability of connectivity. Usually, measures of connectivity consider only one state of the landscape that can be past (Petit and Burel 1998) or most of the time current (Tischendorf and Fahrig 2000). Studies that relate the temporal variability of connectivity with actual agricultural systems and crop rotations are rare (but see Baudry et al. 2003, Vasseur et al. 2013). Burel and Baudry (2005) also showed high variability of connectivity from year to year in a given landscape, due to the variation in area of the crops, but also on their spatial organization. Such measure of connectivity based on dynamic structural patterns of landscapes offers the possibility to more closely link biological and landscape processes and thus, to assess the ecological outcomes of various landscape scenarios.

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Wiens JA (2002) Central concepts and issues of landscape ecology. In: KJ Gutzwiller (ed) *Applying landscape ecology in biological conservation*. Springer, New York, pp 3–21.

#### ***1.4.2 Towards an Explicit Account of Agricultural Practices in the Characterization of Farmland***

The diversity of farming practices in fields such as plowing, direct seeding or different levels of pesticide use, and their landscape-level organization bring additional heterogeneity. Such “hidden heterogeneity” (Vasseur et al. 2013) may be as important, or even more relevant to consider, than the diversity of crop types, in driving biodiversity in agricultural landscapes. At a given time, the agricultural mosaic can indeed be viewed as a mosaic of cropped and ephemeral habitats of varying quality for species in terms of food resources, reproduction sites or, shelters. The quality of cropped habitats depends on crop type and phenology, and on disturbances induced by agricultural practices (Vasseur et al. 2013, Fig. 1.3). This mosaic of cropping systems is therefore likely to drive the source-sinks dynamics of species between crop fields, as demonstrated for pests (Carrière et al. 2004) or between crop fields and adjacent semi-natural habitats in the case of predatory insects (Carrière et al. 2009). In addition, the variable amount of suitable resources i.e. flowering resources in the agricultural mosaic has been shown to influence pollinators, that exhibit either concentrated or diluted patterns when flowering resources are rare, or on the contrary, when resources are largely distributed in agricultural landscapes (e.g. large areas as oilseed rape) (Holzschuh et al. 2011; Le Féon et al. 2013; Requier et al. 2015).

The agricultural mosaic is characterized by variations of resource localization and accessibility (i.e. landscape connectivity) for species (Burel et al. 2013). The connectivity of resource patches is expected to be crucial for species survival but few studies have addressed this issue and attempted to integrate it in the study of ecological processes (Baudry et al. 2003; Burel and Baudry 2005). All these studies have mainly focused on the variability in resource availability and quality related to crop type and phenology. However, the effects of landscape heterogeneity induced by agricultural practices have been less investigated. The few studies addressing this issue analyzed the effects of the amount of organic vs. conventional farming at the landscape scale. They have generally found a positive influence of large surfaces of organic farming in landscapes on the diversity of plants, butterflies, pollinators, and some groups of natural enemies and pest arthropods (Holzschuh et al.

2008; Rundlöf et al. 2008; Gabriel et al. 2010; Gosme et al. 2012; Henckel et al. 2015). Other studies have however failed to confirm the positive effect of organic farming at the landscape scale on communities of natural enemies (Puech et al. 2015). Several authors have underlined the need to go beyond the simple dichotomy “organic *versus* conventional” and to account for the diversity of farming practices at local and landscape scales (Vasseur et al. 2013; Puech et al. 2014). One of the key challenges to go further is to solve the difficulty of characterizing and mapping farming practices at the landscape scale (Vasseur et al. 2013).

### ***1.4.3 Taking into Account the Temporal Variability of Agroecosystems***

Agricultural landscapes are highly dynamic at various temporal scales. Temporal changes occurred from fine scale to long-temporal scales. Within-year variations are related to crop phenology and to the successive agricultural operations during the cropping season such as ploughing, sowing, fertilization application or pesticides sprays. Over decades, changes may intervene that affect the size and the shape of cropping areas and of semi-natural or extensively farmed areas (Baudry et al. 2003). Studies that have used diachronic data, mostly focused on long-term land use changes and their effects on various taxonomical groups such as plants (Lindborg and Eriksson 2004; Ernoult et al. 2006), vertebrates (Metzger et al. 2009) and invertebrates (Petit and Burel 1998; Hanski and Ovaskainen 2002). However, only few of these studies explicitly investigated impacts of landscape changes on populations dynamics (but see Wimberly 2006; Bommarco et al. 2014; Baselga et al. 2015), most probably because of the rarity of long-term monitoring data covering several years at the landscape scale. Similarly to space, no consensus has been found when investigating the effect of temporal dynamic of landscape on population or communities (e.g. for different results about bird communities, see Sirami et al. 2010; Wretenberg et al. 2010; Bonthoux et al. 2013). In particular, changes over short periods due to crop succession have been poorly investigated. At the field level, some studies have considered the impact of crop successions on invertebrates (e.g. for Carabidae, Marrec et al. 2015; Dunbar et al. 2016). At the landscape scale, temporal heterogeneity of the crop mosaic has mainly been assessed by changes in the proportions of specific crop types over time. For instance, high diversity in crop succession, with one year of grassland, positively affected solitary bee richness (Thies et al. 2008; Le Féon et al. 2013).

To sum up, few studies have accounted for the whole cropping system at a landscape scale and the effects of the multi-year temporal heterogeneity of crop mosaics on biodiversity are still largely unknown (but see Baudry et al. 2003; Vasseur et al. 2013; Bertrand et al. 2016, Fig. 1.3). This suggests that the effects of landscape heterogeneity should be assessed simultaneously in space and time and for several organisms rather than being extrapolated from static maps (Wimberly 2006).

## 1.5 Ecological Networks, Productivity and Biological Regulation

One pillar of agroecology is to take advantage of biotic interactions to ensure productivity and pest management instead of relying on chemical products (Shennan 2008; Médiène et al. 2011; Kremen and Miles 2012). Biotic interactions have been studied in various ecological subfields: community ecology has primarily focused on horizontal interactions between individuals of a same trophic level, while trophic ecology has primarily focused on vertical interactions between different trophic levels (Duffy et al. 2007; Fig. 1.4). An emerging line of research in network ecology focuses on interactions per se rather than through the lens of their impact on ecosystem dynamics (Tylianakis et al. 2008). The findings from these various subfields can be useful for agroecology, since they provide theoretical frameworks to interpret empirical observations (Vandermeer 1992).

### 1.5.1 Horizontal Diversity and Biotic Interactions

Hundreds of ecological studies have demonstrated that multispecies assemblages of plants are more productive and temporally stable than monocultures (Tilman et al. 2014). Two general mechanisms may explain these effects. First, complementarity and positive interactions between species increase production, and may even lead to transgressive overyielding i.e. some mixtures of species may have a higher production than the best monoculture. Second, species rich communities are more likely to contain the species that are more productive in local conditions during a given year. If these productive species compensate for the less productive species this can lead to overyielding through a sampling effect. Some study, however, suggested that such positive effect of diversity may be conditioned by soil fertility, that affects both functional traits and production ability of the most competitive species in the assemblage (Chanteloup and Bonis 2013). Some results also suggest that mixtures of cultivars, i.e. field genetically diverse crops, lead to the same types of benefice as species rich communities through the same ecological mechanisms (Barot et al. 2017).

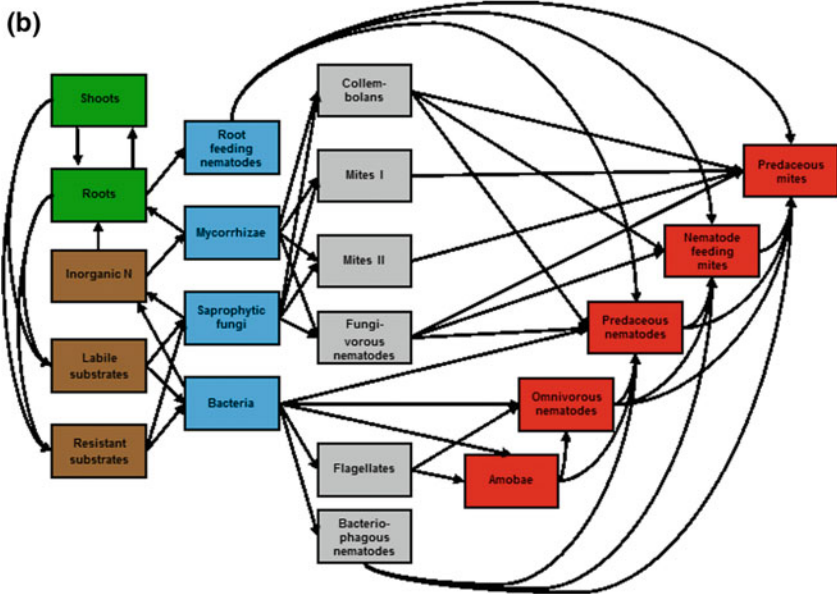
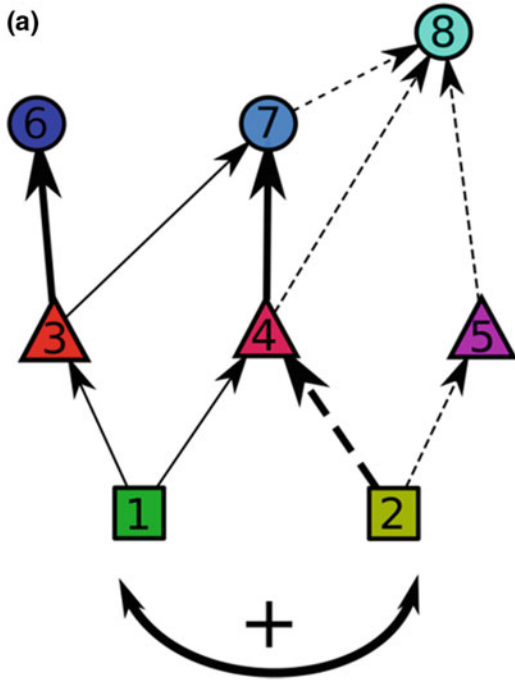
One agronomic counterpart of these sample effect is a yield benefits and the higher efficiency in resource use in intercropping systems (Vandermeer 1992). The challenge for agroecology is accordingly to design multiple cropping systems that can combine several species or cultivars simultaneously in the same area or sequentially in the crop sequence (Gaba et al. 2015), and that provide food but also others ecosystem services. For instance multiple cropping systems may generate low levels of interspecific competition between crop species, or even lead to facilitative interactions, for instance through nutrient cycling as in agroforestry systems (Auclair and Dupraz 1997) or through an increased availability of minerals (Hinsinger et al. 2011). Beyond yield, multiple cropping systems may also regulate

pests by preventing their growth, reproduction or dispersal as well as by enhancing natural enemies' efficiency. For instance, resource dilution of a host plant in the plant mixture can reduce both pest dispersal and reproduction by making the pest less efficient in locating and colonizing its host (Ratnadass et al. 2012). Push-pull strategies can also help controlling pest through the use of "push" plants which restrain pest settlement on crops and "pull" plants which attract them to neighboring plants (Cook et al. 2007). Finally, multiple cropping systems such as intercropping plants may control weeds by directly competing for resources with these wild plants (Liebman and Dyck 1993; Trenbath 1993).

Increasing horizontal diversity may also improve water and soil quality. Plant diversity is one of the most important drivers of belowground processes and increasing plant diversity in multiple cropping systems acts directly on soil fertility by increasing soil organic matter and promoting N<sub>2</sub> fixation by legumes, reducing soil erosion and the associated loss of nutrients (Dabney 1998). Indeed, multiple cropping systems influence faunal, microbial and soil organic matter dynamics through the diversity of root architecture, the quantity and quality of rhizodeposits, and the quality of plant litter. A transition from a monoculture to a diversified crop succession was shown to significantly increase microbial biomass carbon with a rapid saturation threshold due to a strong effect of cover crops (Mc Daniel et al. 2014). This overyielding of microbial biomass was observed as soon as one crop species was added in a crop sequence contrary to grasslands where the threshold is generally reached with six or eight plant species (Zak et al. 2003; Guenay et al. 2013). In addition, cereal-legume intercrops lead to a reduction of soil mineral nitrogen after harvest compared with pea sole crops (Pelzer et al. 2012), thus mitigating nitrate losses by drainage, as with cover crops and relay intercropping (Di and Cameron 2002), and hence preserving the quality of ground and drinking water.

### ***1.5.2 Vertical Diversity and Biotic Interactions***

Trophic ecology (sensu Lindeman 1942) is another body of ecological science that may be of interest for agroecology. Most of current researches focuses on pairwise trophic interactions, including the benefits brought by mutualist consumers like pollinators (Potts et al. 2010), by parasitoids (Godfray 1994; Langer and Hance 2004; Zaller et al. 2009) or by predators (Blubaugh et al. 2016; Kromp 2016; Fig. 1.6). A more recent research focus aims at understanding trophic interactions within ecological networks (Bascompte and Jordano 2007). For instance several studies investigate the potential of generalist predators for biological control (Symondson et al. 2002), the global positive relationship between natural enemy diversity and herbivore suppression (Letourneau et al. 2009; Griffin et al. 2013), or the effects of community evenness and functional diversity of natural enemy communities on biological regulation efficiency (Schmitz 2007; Crowder et al. 2010). Similarly to biotic interactions at the same trophic level (horizontal



◀**Fig. 1.5 a Example of a possible interaction network in agroecosystems.** Plant hosts are symbolised by squares; triangles represent pest species and circles could symbolize either predator or parasitoid species (but we will continue with parasitoids for clarity). All arrows represent a feeding interaction between two given species, with the arrow head pointing in the direction of the biomass flow and arrow width showing the intensity of the interaction (e.g. frequency). If we consider only the species involved in interactions represented by solid arrows, then we face a system with only one plant species in isolation (crop, square 1), which is consumed by two pest species (3 and 4). In turn, one of these pests is consumed by a specialist parasitoid (6), whereas the other parasitoid (7) consumes both pest species. If we now add a second plant species (2) in the system known to have beneficial effects on the first crop species (e.g. a nitrogen-fixing species), then the second set of interactions represented by dashed arrows could occur: this second plant species is heavily consumed by pest species 4, which could relieve the first crop from some of the pest pressure. This second plant could also have its own specialized pest (5). Another parasitoid species (8) also arrives in the system, feeding both on the specialized pest species (5) and the pest common to both plants (4). Finally, the link between parasitoids 8 and 7 demonstrates intraguild predation (or in this case, hyperparasitism), which confers species 8 a higher trophic position than the other species of its guild and which would potentially disserve the pest suppression process. Altogether, this figure illustrates an example of the possible benefits of increased biodiversity at all trophic levels for biotic control, and how these benefits may also, however, come with costs. **b Representation of detrital food web in shortgrass grassland.** Fungal-feeding mites are separated into two groups (I and II) to distinguish the slow-growing cryptosfigmatids from faster-growing taxa. Flows omitted from the figure for the sake of clarity include transfers from every organism to the substrate pools (death) and transfers from every animal to the substrate pools (defecation) and to inorganic N (ammonification) (Hunt et al. 1987)

diversity), the efficiency of functionally-rich networks in herbivore control can be due to a variety of ecological mechanisms including niche partitioning (Cardinale et al. 2003), sampling effect (Loreau et al. 2001) and facilitation (Gravel et al. 2016). However, it remains largely unknown how agricultural practices could promote such functionally-rich networks, without favouring behavioural interference and intraguild predation that can disrupt biological control (Rosenheim et al. 1995; Schmitz 2007).

Soil biota constitutes one of the main food web in agroecosystems (Fig. 1.5b), based on the consumption of plant litter and soil organic matter. This food web is very influential for many important ecosystem processes: nutrient cycling and soil organic matter dynamics, setting and conservation of soil structure, water fluxes and plant biomass production (Blouin et al. 2013; van Groenigen et al. 2014). Modelling detritivore food web thus allows predicting nutrient mineralization rates that are a major determinant of soil fertility as well as providing leverages to modify mineralization rates through direct or indirect variation in population size of the different soil taxa. Soil biota spreads over many scales of body size and is divided in microorganisms (fungi, bacteria), microfauna (e.g. amoeba, nematoda), mesoinvertebrates (e.g. collembola, enchytraeids) and macroinvertebrates (e.g. earthworms) (Lavelle et al. 2001). It also encompasses roots and vertebrates (e.g. moles, shrews). Soil biota gathers a heap of taxa, that can be translated into a diversity of shapes, stadia, ways of life or diets, that impact soil functioning from textural (arrangement of mineral particles) to structural scale (organization of aggregates, pores and horizons). The modification of nutrient availability (i.e. N or P) for plants



**Fig. 1.6** Semi-natural habitats (e.g. field margins and hedges, top left) provide shelters and trophic resources for numerous components of the biodiversity in agroecosystems (e.g. hoverflies, top right). In particular, these habitats support predators and parasitoids contributing to crop herbivore suppression (hoverfly larva and aphid mummies, bottom left). To quantify the level of biological regulation, sentinel preys can be used (bottom right, ladybird predating aphids fixed on a predation card) to estimate the potential of herbivore consumption represented by predators in field conditions

is generally reported as the major mechanism explaining the direct role of soil organisms on plant growth (for earthworms, van Groenigen et al. 2014; protists, Forde 2002; collembolans, Kaneda and Kaneko 2011; or microbes, van der Heijden et al. 2008). This mechanism can provide 10–40% of the plant requirements (Parmelee and Crossley 1988; James 1991). The soil food web contains both crop pests (e.g. wireworms, pathogenic fungi) and beneficial organisms (e.g. generalist predators, parasitoids, symbiotic fungi, plant growth promoting rhizobacteria). However the characteristics of these organisms vary with their feeding requirements as well as with agricultural practices (e.g. soil burrowing, particle relocalization).

### ***1.5.3 Integrating Trophic and Non-trophic Interactions***

Although studies on ecological interaction networks have mainly focused on trophic relationships, there is an increasing interest in co-occurrence networks analyses with no a priori on the underlying interactions. Interactions can be either

physical modifications of the environment with consequences on resource availability or signal molecule effects. Although the effects of organisms on abiotic environment have been recognized for decades, unifying concepts such as “ecosystem engineers”, or “functional domains”, are relatively recent (Fig. 1.7a). While ecosystem engineers are organisms which physically modify their environment with consequences on the availability of resources for other organisms (Jones et al. 1994), “functional domains” are defined as the sum of structures produced by a population or community of engineers (Lavelle et al. 2002). Both are particularly relevant in soil ecology where soil structure directly affects the creation, maintenance and destruction of soil organism habitats. Similarly, several soil functions such as water regulation, are deeply influenced by ecosystem engineers such as earthworms (reviewed in Blouin et al. 2013). Taking into account the effect of management practices on these organisms is thus necessary to ensure agroecosystem sustainability. Soil organisms can also interact with their environment through exchanges of information among organisms, which mainly rely on biochemical molecules. As a consequence, many soil organisms have developed the ability to detect “signal molecules”, even at very low concentration in the environment which can alter the morphology, the metabolism or the behaviour of these organisms (Zhuang et al. 2013). Signal molecules can be hormones such as auxins, cytokinins, ethylene, jasmonic acid, or salicylic acid, but also other kinds of molecules (Ping and Boland 2004). In soil networks, interactions between soil organisms and plants may therefore, not necessary, require physical contacts between the soil organism and the root. As trophic interactions, they may positively or negatively impact plant development and/or immunity (Fig. 1.7b). This ability to interact with plants, responsible for the entry of energy into soils, is a vital adaptation for soil organisms (Puga-Freitas and Blouin 2015).

#### ***1.5.4 Climate and Agricultural Practices Deeply Modify Ecological Networks***

Ecological networks are constituted of multiple interactions whose type (positive, neutral or negative) and strength are highly dependent on environmental properties (Tylianakis et al. 2008; Médiène et al. 2011). Understanding how exogenous factors such as climate or agricultural practices affect the network structure and consequences for ecosystem functioning, e.g. production, is however not straightforward, and this is even truer in heterogeneous and changing environments such as agroecosystems. For instance, Tylianakis et al. (2008) highlighted that climate change or habitat modifications “disproportionately affect” predator-prey interactions. They also showed that these responses differ between generalist and specialist predators, with specialists being more negatively affected by habitat simplification than generalists, as showed for aphids in Western Europe (Rand and Tschamtké 2007). Exogenous factors can also have differential effects depending if they are



acting alone or in combination. For example, Hoover and Newman (2004) showed that the interaction between atmospheric CO<sub>2</sub> and climate may have lower negative effect on prey-predator interactions than considered separately. Recently, Romo and Tylanakis (2013) highlighted that positive effects of temperature elevation and drought on aphid host-parasitoid interactions observed when studied separately, may “hide” deleterious effects on the efficiency of host regulation when temperature and drought are combined. The introduction of disturbances in food webs can also affect trophic network dynamics. For instance, a modelling approach revealed that manipulating low matter transfer rates had a strong influence on the trophic network dynamic, while disturbing the major path of material flow had a weak influence (Paine 1980). More recent models proposed to take into account the seasonal dynamics of trophic groups, to study the temporal coupling between mineralization by soil organisms and mineral uptake by plants. Despite increasing evidence of the effects of exogenous factors on food web structure and ecosystem functioning, we still lack of a good mechanistic understanding of the relative and interactive effects of these environmental variables.

## 1.6 Perspectives

### 1.6.1 *Novel Tools to go Further in the Understanding of Ecological Network Dynamics*

Considering trophic relationships with a whole food web perspective further enables to understand indirect effects propagating through food webs that would otherwise be overlooked through the lens of pairwise interactions. Indirect effects such as apparent competition have indeed potentially major implications for biological control (Chailleux et al. 2014) and the design of efficient nutrient cycling strategies within agroecosystems (Wardle et al. 2004). Integrated food web studies come at a cost, however, since achieving sufficient sampling effort to describe complete food webs remains challenging (Chacoff et al. 2012; Jordano et al. 2016). Excitingly, novel technologies offer great promises to tackle such challenges (detailed in Box 3). Another challenging task is to develop innovative modelling strategies to assess the functioning of complex food webs or even of coupled multi-type networks (Fontaine et al. 2011; Georgelin and Loeuille 2014). For instance, there is a strong indeterminacy of how indirect effects propagate through imperfectly documented food webs (Novak et al. 2011). Though, the field of ecological network modelling is a very active area of research (Tixier et al. 2013), such that modelling solutions to these challenges might be at reach. In particular, Bayesian propagation of uncertainties in ecological networks can be sufficient to obtain robust qualitative predictions (Jabot and Bascompte 2012). Nevertheless, one of the main challenges in ecological network studies is to move from a comprehensive description of networks to the understanding of the effect of external

factors (climate, agricultural practices, etc....) on the multiple interactions of different types (positive, neutral or negative) and strength in order to promote multifunctional landscapes.

### **Box 3: Approaches to Characterize Biological Regulation**

Agroecosystems shelter complex interaction networks both above and below ground (Fig. 1.3.). In that context, quantifying biological regulation through trophic linkages is a difficult task (Traugott et al. 2013), especially for the many small and cryptic invertebrates that composed communities (Symondson et al. 2002) and that could be effective biocontrol agents. In most studies, predation rates are estimated through the consumption of preys disposed in the field for a determined amount of time (Fig. 1.6). For host-parasitoid interactions, hosts can be conserved until the emergence of adult parasitoids, which allows a good approximation of biological regulation. Notwithstanding, cryptic interactions such as multiparasitism, hyperparasitism, or when immune host system is well adapted (e.g., encapsulation) often remain challenging (Traugott et al. 2013). In a large majority of studies, the level of biological regulation exerted by generalist predators is estimated by explaining the rates of consumption of preys/hosts by predator activity-density using correlative approaches. In such cases, no correlation is usually observed, mainly because of the high variability inherent of agroecosystems. This highlights the limits of these indirect approaches and the lack of precise knowledge on species roles in food webs (Östman 2004). Thus, other approaches have been developed to provide a more mechanistic understanding of “*who eats whom?*”.

First, the use of functional traits to inform food web structure through interaction rules offers great promises to tackle food web complexity with operational simplifications (Jordano et al. 2003; Allesina et al. 2008). Functional traits are defined here as morphological, physiological, phenological and behavioural features (sensu Pey et al. 2014) and may give more mechanistic understanding of predation, pollination or parasitism. For example Rusch et al. (2015) highlighted that functional diversity explained a greater part of variation in predation rates than taxonomic diversity or activity-density. However this approach is still correlative and mainly relies on the availability and the quality of data on processes, communities and traits.

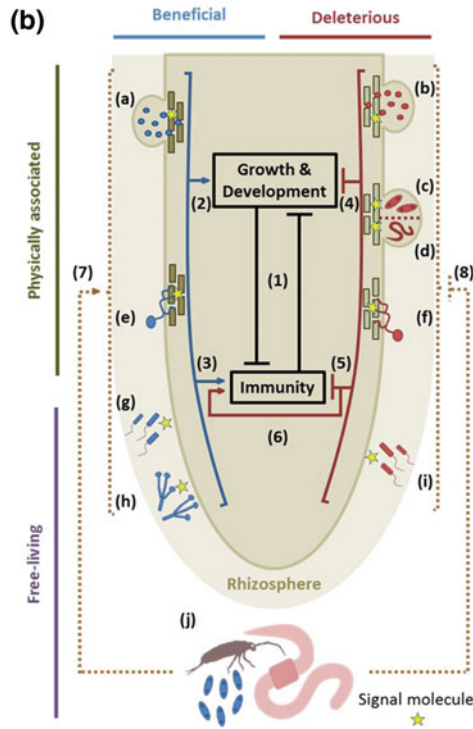
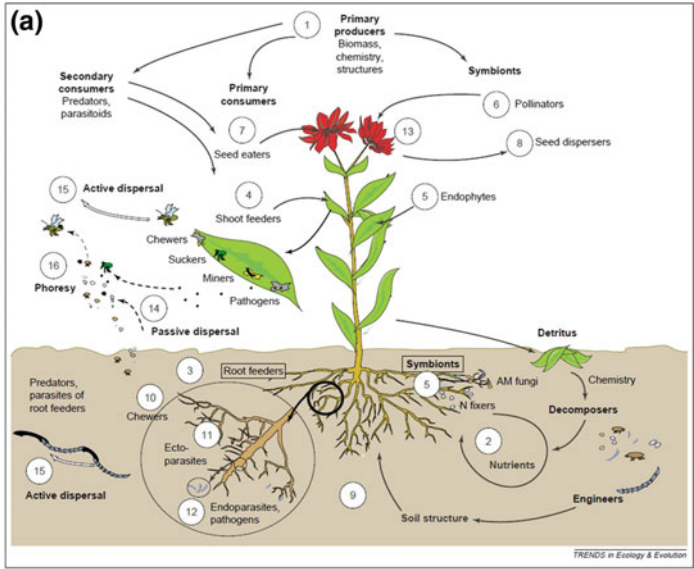
Second, the democratization of DNA-based methods such as PCR diagnostic approach or next-generation sequencing (NGS) is an opportunity to better identify trophic linkage and particularly for varied diet organisms like generalist predators (reviewed by Pompanon et al. 2012; Traugott et al. 2013; Vacher et al. 2016) and pollinators (Pornon et al. 2016). The identification of alimentary items through the molecular analysis of gut content has already given important insights such as the role of carabids in the regulation of *Ceratitis capitata* in citrus orchards (Monzó et al. 2011). It also allowed

detecting intraguild predation between generalist predators that could have major consequences on biological regulation efficiency and strategies (Gomez-Polo et al. 2015). However, this approach of molecular ecology is still facing many methodological such as building reliable database of DNA sequences with fine taxonomic resolution, going beyond the semi-quantitative approaches of trophic interactions or distinguishing between direct and secondary predation.

Third, the analysis of movements can help to determine the links within a food web. As most generalist predators actively hunt for preys, biological regulation is driven by specific movement behaviors of both predators and their prey. Movement behavior includes habitat use, paths, home range size, foraging behavior or activity patterns (Daniel Kissling et al. 2014). Passive tags (no battery) like Radio Frequency identification (RFID) have been used to precise the effects of pesticides on bees (Henry et al. 2012) but are still scarcely used for potential bioagents such as carabids or spiders. can be used on Curculionidae in banana plantations (Vinatier et al. 2010) or in strawberry crops (Pope et al. 2015). The significant decrease in both device size and cost of radio telemetry techniques in less than a decade opens tremendous opportunities to study predator movement behaviors.

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◀**Fig. 1.7 a Interdependency of aboveground and belowground biodiversity.** Aboveground plant community biomass and chemical and structural composition (1) drive the abundance and diversity of aboveground higher trophic levels, although these aboveground plant characteristics depend upon the net activity of soil functional groups, such as decomposers and symbionts (5), which make nutrients available (2), and on aboveground and belowground herbivores and pathogens (3,4), which reduce plant growth [17]. Heterotrophic organisms that interact with plants affect plant metabolism, potentially altering litter, shoot and root biomass production, distribution and chemical composition by feeding on roots (3) or shoots (4) or living symbiotically in shoots, leaves or roots (5). In the longer term, pollinators (6) as well as seed eaters (7) and seed dispersers (8) affect the persistence of the plant species and, thus, the specialist organisms associated with it. Soil organisms are constrained in their mobility and, as a result, organisms interacting with a single plant root system are subsets of the total species pool present in the direct surrounding soil (9). Depending on their size and mobility, these organisms occupy microhabitats of different sizes and might have different effects on plant growth. Although active roots have high turnover rates and are distributed throughout the soil, root herbivores and pathogens (3) can account for this ‘unstable food’ source by being relatively mobile generalist feeders (10, 11), similar to many aboveground chewing insects and free-living suckers, by adapting a specialized endoparasitic plant association (12) or by having an aboveground life phase enabling targeted active dispersal (15). Aboveground plant structures might be easier to find than are roots, and although the availability of more-specific aboveground plant tissues [e.g. buds, flowers, fruits or seeds (13)] is often brief, these can still affect the aboveground diversity of plant-associated organisms owing to the large active range sizes of aboveground organisms. Large aboveground and belowground organisms might disperse actively in a directional way (15), by flying, walking, crawling or borrowing, whereas smaller organisms (or small structures of larger organisms, such as seeds) disperse more randomly via passive dispersal (14) by air, water or via phoresy (16) (i.e. using other organisms as transport vectors). Abbreviations: AM fungi, arbuscular mycorrhizal fungi; N-fixers, nitrogen-fixing microorganisms. From de Deyn and Van der Putten (2005). **b Ecological interactions between soil organisms and plants mediated through signal molecules.** Soil organisms can be distinguished according to their physical association with plants: (a–f) root physically associated microorganisms/microfauna, (g–i) free-living microorganisms and (j) free-living micro-, meso- and macro-fauna; (a) Rhizobium, (b) Agrobacterium, (c) protozoa, (d) nematodes, (e) AM, ECM and endophytic fungi, (f) pathogenic fungi, (g) PGPR, (h) PGPF, (i) DRB and (j) micro-, meso-, macro-fauna. Arrows lines indicate a promotion, bar-headed lines an inhibition and dotted arrow lines an indirect effect of interactions mediated by signal molecules produced by soil organisms. (1) Those affecting plant growth can be detrimental to plant defence and vice et versa, due to the trade-off between these two processes. (2) Beneficial organisms promote development, induce formation of specialized organs or (3) elicit ISR. (4) Deleterious ones inhibit development, induce formation of aberrant organs, (5) hijack plant defence or (6) upon restricted infection induce SAR. We suggest that (7) free-living micro-, meso- and macro-fauna impact is mediated through the activation of beneficial microorganisms and (8) an inhibition of deleterious ones. Note that described interactions can occur within the whole root system and not exclusively at the root tip level, and induce local as well as systemic responses (Puga-Freitas and Blouin 2015)

Rusch A, Birkhofer K, Bommarco R, Smith HG, Ekbom B (2015). Predator body sizes and habitat preferences predict predation rates in an agroecosystem. *Basic Appl Ecol* **16**:250–259.

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Among others, one important challenge is the multi-functionality of soils: soils should sustain primary and secondary production, provide sustainably mineral nutrients to crops, resist erosion, and regulate water fluxes and climate. This latter ecosystem function has raised high attention with the international “4 per 1000” initiative (<http://4p1000.org>) put on the political agenda since the COP21 held in Paris in 2015. Soils through their content in organic matter contain three times more of carbon than the atmosphere (2400 Gt carbon vs 800 Gt carbon; Derrien et al. 2016). Small changes in organic matter content can act as a carbon sink or source within a decade. A decrease in atmospheric carbon by 3.5–4 Gt/year would limit the rise in temperature by +1.5/2 °C by 2100, a threshold beyond which climate change would have unpredictable (and likely disastrous) effects (IPCC 2013). One of the most credible ways to meet this goal is to increase the concentration of organic matter in soil by 0.4% (4 per 1000) per year in the 30 first centimeters of soils at the planetary scale (Balesdent and Arrouays 1999; Paustian et al. 2016). Though some strategies can already be imagined to reach this goal (Dignac et al. 2017) research is still needed. In particular, belowground trophic and non-trophic interactions should be jointly considered to increase carbon storage within agricultural soils.

### ***1.6.2 Landscape Issues for the Delivery of Multiple of Functions in Agroecosystems***

There are increasing evidences that landscape characteristics play a strong role in maintaining biodiversity and ecosystem functions (Rundlöf and Smith 2006; Henckel et al. 2015). This offers the opportunity to manage agroecosystems at a higher scale than the field, and mainly leads to the “land sparing- land sharing” debate (Green et al. 2005; Fischer et al. 2014). Land sparing strategies rely on setting aside agricultural land for wildlife whilst intensifying agricultural production on the rest of the land. By contrast, land sharing strategies focus on the reduction of production intensity throughout the land to maintain farmland biodiversity (“wildlife friendly farming”, Fig. 1.6; Green et al. 2005), whilst less amount of land is set aside for conservation in comparison with land sparing strategies. However, these two strategies are the extremes of a continuum and are not mutually exclusive

and, a combination of both natural reserves and wildlife farming practices have been shown to be efficient to conserve biodiversity (Fischer et al. 2008; Scariot 2013). While this debate has been fruitful in conservation biology, the varieties of species (with different habitat requirements, and behaviours), management strategies (from field to the territory) and agricultural landscapes, require studies devoted to the agri-environmental contexts. Current knowledge either supports land sparing or land sharing strategies, depending on the organism or the ecological process considered. For instance, semi-natural habitats in agricultural landscapes are crucial for specialist species (like forest species) as well as for flagship species (e.g. wild bees, or little bustards). Friendly farming practices such as organic farming of agri-environmental schemes, may also be useful for maintaining biodiversity in agricultural landscape throughout various ecological processes (e.g. resource complementation/ supplementation, source-sink, concentration/dilution, Fig. 1.6) (Fahrig et al. 2011; Vasseur et al. 2013). Future ecological research should focus on further assessing strategies of landscape organization to determine those who can provide multifunctional agricultural mosaic according to the socio-economic and environmental contexts.

### ***1.6.3 Towards an Eco-Evolutionary Perspective of Agroecology***

Organisms are able to adapt to rapid environmental changes and to respond to strong selection pressure. Selection is an important facet of agriculture. First, crop selection has already been applied in agriculture toward pest resistant or high-yielding cultivars (Thrall et al. 2011; Denison et al. 2013). Given that the selected genotypes (crop and livestock) interact in complex ecological networks, at different trophic levels and through different types of interactions, evolutionary processes may affect ecological dynamics in multiple ways (Loeuille et al. 2013) by altering (i) important attributes of ecological communities (such as the connectance or the number of trophic levels), (ii) the structure of interaction networks (especially those with mutualistic interactions), or (iii) ecosystem functioning such as productivity or nutrient cycling in essential ways for the agricultural activity. Second, rapid natural selection of resistance to pesticides has been very often shown in various herbivores, pathogens and weeds targeted by pesticides (Alyokhin et al. 2015). Similarly, rapid evolutionary changes related to Red Queen dynamics have been demonstrated in antagonistic interactions such as host-parasite (Decaestecker et al. 2007) or prey-parasitoid or predator relationships (Diehl et al. 2013). Ecological intensification principles put forward, the substitution of strong chemical selective pressure by biotic selective pressure. Pest adaptation to their biological control is therefore highly likely, and may have collateral effects in this extreme case (Gaba et al. 2014). Third, there is an evolutionary potential of feedbacks across soil ecosystem, particularly given likely changes in soil function such as water

regulation, and soil organisms such as earthworms (Blouin et al. 2013). Such environment and evolutionary feedbacks due to the change in selective constraints has led to the emergence of concepts such as the extended phenotype (Dawkins 1982) or the niche construction (Odling-Smee et al. 1996). Considering eco-evolutionary feedbacks and their potential counter-intuitive effects is therefore critical for the development of a more sustainable agriculture. Through experimental approaches, community evolution models could be valuable to better understand and predict the evolutionary consequences of management strategies on ecological networks over a wide range of agricultural context (Loeuille et al. 2013).

#### ***1.6.4 Is the Ecosystem Service Concept Relevant for Designing Sustainable Multifunctional Agriculture?***

The ecosystem service concept has spread rapidly these last decades even in agricultural sciences (see Sect. 1.3) and allows exploring the relationships between ES, which could be synergies or trade-offs, despite most studies still focus on a single service (generally biomass production). Considering bundles of ecosystem services is essential to reach multifunctional agricultural and may enhance organization of agricultural landscapes in order to bond a social optimum (Couvet et al. 2016). Still, ecosystem service research is facing severe challenges which could limit, in some respects, its operability (Birkhofer et al. 2015). First, as ecosystem service concept has been initially designed to deal with “natural” ecosystems, its implementation to managed ecosystems required some adaptations (Barot et al. 2017b). Second, it is often hard to evaluate the relationships between indicators or proxies of functions whereas strong uncertainties persist on ecological processes that underlie these services. Third, the lack of theoretical framework limits the exploration of the links between services (Lescouret et al. 2015). Fourth, although land use allocation is important for agricultural production, but also for emissions and greenhouse gases sequestration, open-access recreational visits, urban green space and wild species diversity (Bateman et al. 2013), land use decisions generally ignore the valuation of ecosystem services at the landscape level. Finally, most studies still focus on small spatial and temporal scales, while environmental research should address larger scales. In addition, the ecosystem service concept has been differentially embraced according to epistemic culture of scientists coming from different academic fields. For instance, the agricultural academic field elaborated on the notion of “disservices” or “negative externalities” which are now mainstreamed into the agricultural literature (Tancoigne et al. 2014). Such negative externalities include for instance land use changes which affect natural habitats, or overgrazing that result in erosion and initiates desertification. In parallel, the concept of “environmental service” has been created to address the fact that stakeholders can be responsible for the quality of an ecosystem service and might be paid



for such service (Engel et al. 2008). Debates on terminology may not only reflect the various perspectives across academic fields, but may further influence public policies. Different paradigms that are based on diverse motivations and values may also differ between stakeholders. Besides regulating and provisioning services, sociocultural services (e.g. the place attachment or the aesthetics of the landscape) or ethical considerations also contribute to human well-being. Finally, the temporal and evolutionary perspective (e.g. human-biodiversity interaction) is almost absent in the ecosystem service concept, though Faith et al. (2010) recently proposed the “evosystemic” service approach to include “the capacity for future evolutionary change and the continued discovery of useful products in the vast biodiversity storehouse that has resulted from evolution in the past”. In the same vein, Sarrazin and Lecomte (2016) advocate for “evocentric approach” in order to go beyond the ecosystem service concept and ensure evolutionary freedom. It should result in a better resilience for the organisms and systems that provide ecosystem service and for all organisms involved in their ecological networks. This approach “fosters a long term, sustainable interaction that promotes both the persistence of the nature and the well-being of humans”.

All these criticisms on the concept of ecosystem services express concerns on restrictive (one or few stakeholders) and static (both in time and space) views of the value of ecosystem services and the relationships between biodiversity and ecosystem services, respectively. However, we believe that a proper recognition of the benefits provided by biodiversity can increase the weight given to biodiversity per se and its functions in decision making for agriculture management. While agroecosystems have been mainly managed for provisioning services, we must also pay attention to possible overestimation of regulation processes that would lead to a utility perception of nature. With all these concerns in mind, ecosystem services remain a useful concept to address current challenges in agriculture mainly because they formalize the dependency of human societies on ecosystem functioning, between social-ecological and agro-ecosystem, which is key in socio-ecosystems.

## 1.7 Conclusion

In this review, we draw a picture of several relevant contributions of ecological sciences to the understanding of the spatio-temporal dynamic of biodiversity and ecosystem functions in agroecosystems. This new insights should help to design innovative farming systems at various temporal and spatial scales (from local practices during a crop cycle to the long term management of agricultural landscapes). Many insights in agroecosystem functioning have been obtained this last decade. However, we still lack a robust theoretical framework to support ecological intensification of food production systems and to translate knowledge and understanding into operational management strategies. We also need to go further in the understanding of interaction between ecological and social-economical processes and to develop approaches allowing scientist to build practices of ecological

intensification together with stakeholders and policy makers. This calls for further interdisciplinary researches to investigate the importance of social-ecological processes, at various temporal (ecological and evolutionary time scale) and spatial (from small to global) scales.

**Acknowledgements** This study is an initiative of the “Ecology and Agriculture” group of the French Ecological Society (Société Française d’Ecologie, Sfe).

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