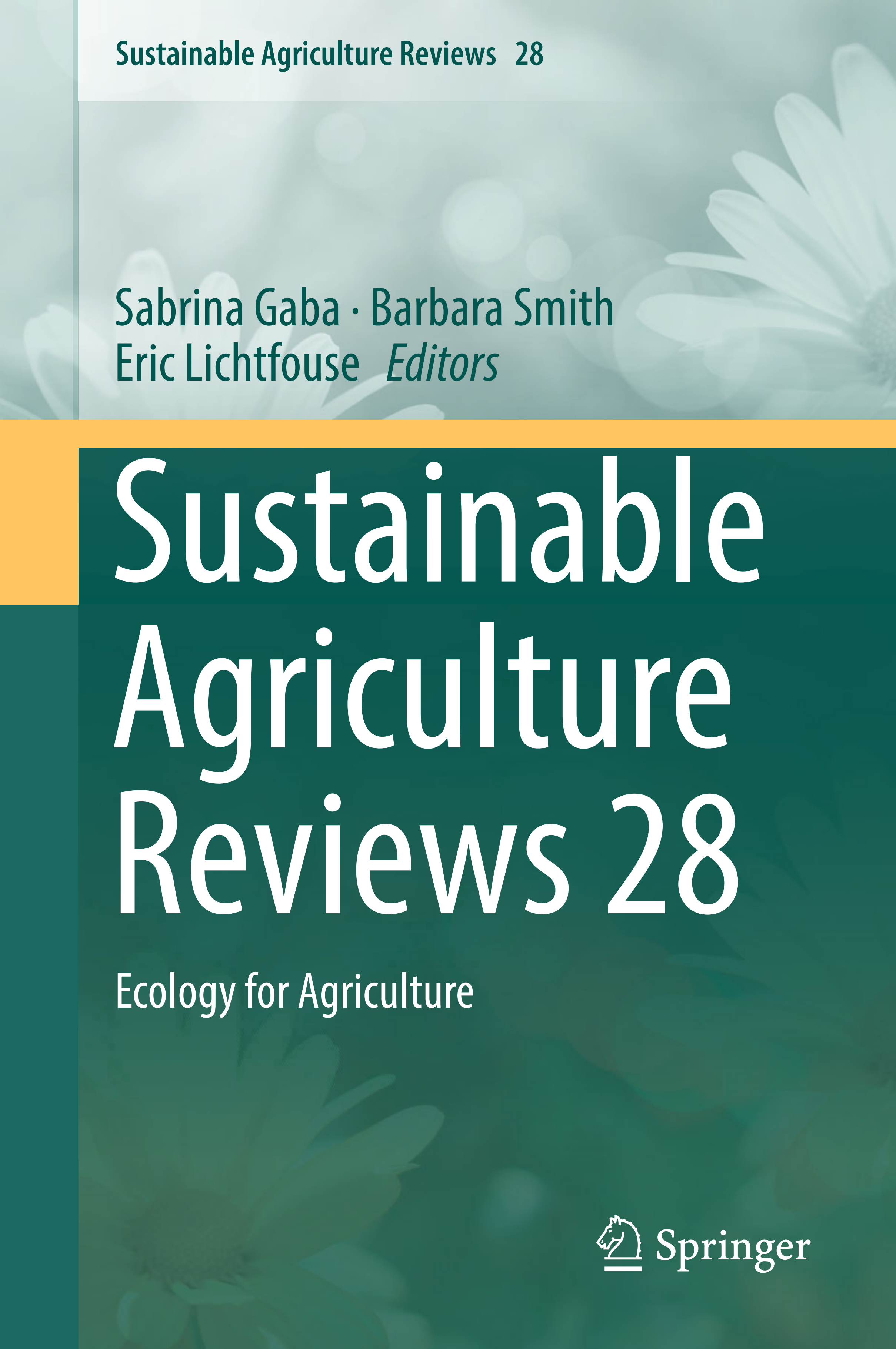

Sustainable Agriculture Reviews 28

Sabrina Gaba · Barbara Smith
Eric Lichtfouse *Editors*

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Ecology for Agriculture

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Sustainable agriculture is a rapidly growing field aiming at producing food and energy in a sustainable way for humans and their children. Sustainable agriculture is a discipline that addresses current issues such as climate change, increasing food and fuel prices, poor-nation starvation, rich-nation obesity, water pollution, soil erosion, fertility loss, pest control, and biodiversity depletion.

Novel, environmentally-friendly solutions are proposed based on integrated knowledge from sciences as diverse as agronomy, soil science, molecular biology, chemistry, toxicology, ecology, economy, and social sciences. Indeed, sustainable agriculture decipher mechanisms of processes that occur from the molecular level to the farming system to the global level at time scales ranging from seconds to centuries. For that, scientists use the system approach that involves studying components and interactions of a whole system to address scientific, economic and social issues. In that respect, sustainable agriculture is not a classical, narrow science. Instead of solving problems using the classical painkiller approach that treats only negative impacts, sustainable agriculture treats problem sources. Because most actual society issues are now intertwined, global, and fast-developing, sustainable agriculture will bring solutions to build a safer world. This book series gathers review articles that analyze current agricultural issues and knowledge, then propose alternative solutions. It will therefore help all scientists, decision-makers, professors, farmers and politicians who wish to build a safe agriculture, energy and food system for future generations.

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Preface

> The true roots of agroecology probably lie in the school of process ecology as typified by Tansley (1935), whose worldview included both biotic entities and their environment.
>
> Dalgaard, Hutchings and Porter https://doi.org/10.1016/S0167-8809(03)00152-X

Food security is and will increasingly be a major world issue in the context of ever-growing population, limitations of land resources and changing climate. Agroecology offers a promising alternative to industrial and pesticide-based crop production. However, agroecology cannot be restricted to the study of ecological processes that underlie the functioning of agroecosystems, and it engages multiple disciplines. Ecology is a science of complexity that provides a panel of theories, concepts and approaches to increase our understanding of farming systems by integrating different levels of life organization at multiple scales of time and space. This book presents reviews that analyse current challenges faced by agriculture from an ecological perspective, through the eye of several disciplines such as

Grass weeds invading maize plots (Fanazo et al., Chap. 4)

Foxglove aphid (Shah et al., Chap. 5)

eco-evolution, ecotoxicology, ecological economics and political ecology. This book is joined initiative of the Agricultural Ecology Group of the British Ecological Society and the Ecologie and Agriculture Group of the Société Française d'Ecologie.

This book presents principles and applications of ecology in agriculture. The first chapter by Gaba et al. reviews ecological concepts that are applicable for agricultural production, with emphasis on the effect of the landscape on biodiversity and ecosystem functions. The use of allelopathy, a kind of biochemical war between species, to control weeds is explained by Aurelio et al. in Chap. 2. Then, Rayl et al. teach us how to manipulate agroecosystems to favour natural pest enemies, a process known as conservation biological control, in Chap. 3. In the same vein, Fanadzo et al. provide in Chap. 4 examples of weeds and pest management using conservation agriculture practices such as cover crops. The ecology of aphids, pests that transmit viruses to tomatoes, is reviewed by Shah et al. in Chap. 5. Francaviglia et al. present the ecosystem services of soil organic carbon, with focus on carbon sequestration and irrigation, in Chap. 6. The effects of conventional and organic fertilizers on soil organic carbon and soil fungi are reviewed by Souza and Freitas in Chap. 7. Deguine et al. reveal successful agroecological control in mango production, with focus on arthropods, in Chap. 8. The last chapter by Keshavarz and Karami presents ecosystem services used to manage drought in agriculture, in the context of climate change.

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Chapter 1
Ecology for Sustainable and Multifunctional Agriculture

Sabrina Gaba, Audrey Alignier, Stéphanie Aviron, Sébastien Barot, Manuel Blouin, Mickaël Hedde, Franck Jabot, Alan Vergnes, Anne Bonis, Sébastien Bonthoux, Bérenger Bourgeois, Vincent Bretagnolle, Rui Catarino, Camille Coux, Antoine Gardarin, Brice Giffard, Antoine Le Gal, Jane Lecomte, Paul Miguet, Séverine Piutti, Adrien Rusch, Marine Zwicke and Denis Couvet

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; Tittonnel 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 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

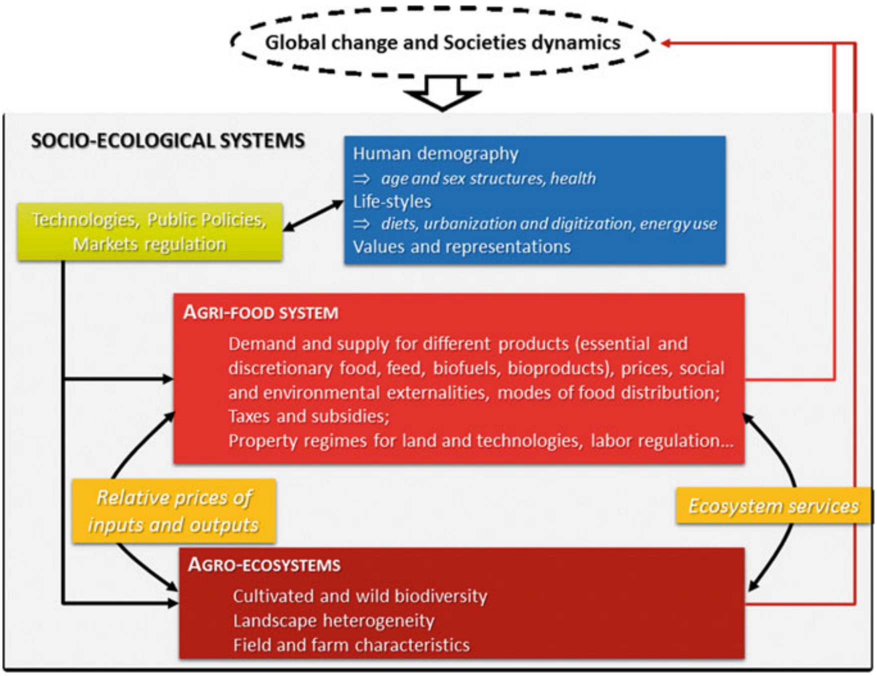

Fig. 1.2 Interaction between Agro-ecosystems, Agri-food systems and Socio-Ecosystems (adapted from Hubeau et al. 2016)

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^2 (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).

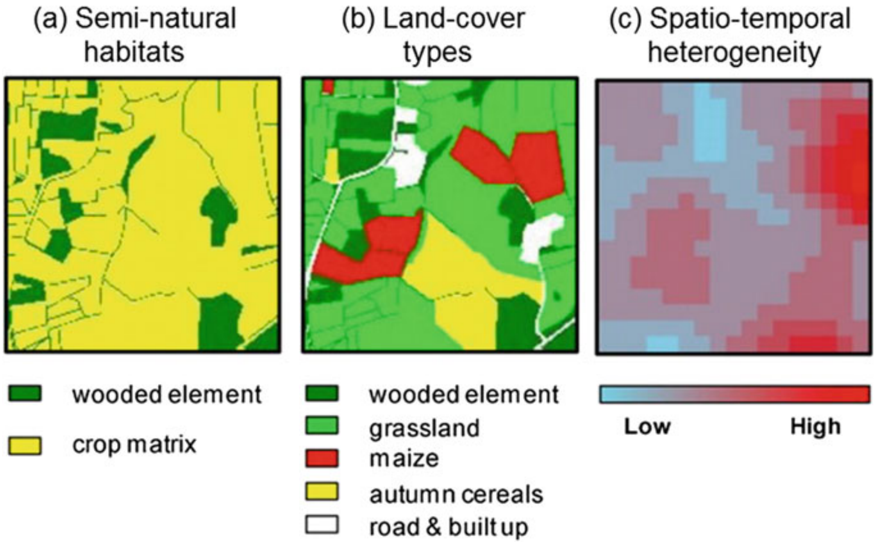

Fig. 1.3 Different representations of spatio-temporal heterogeneity, adapted from Vasseur et al. (2013): **a** spatial heterogeneity related to semi-natural habitats, **b** spatial heterogeneity related to land-cover types, and **c** spatio-temporal heterogeneity related to shift intensity in the relative 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[1] 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 (Tscharntke 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 Tscharntke 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 Duflot 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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[1] 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

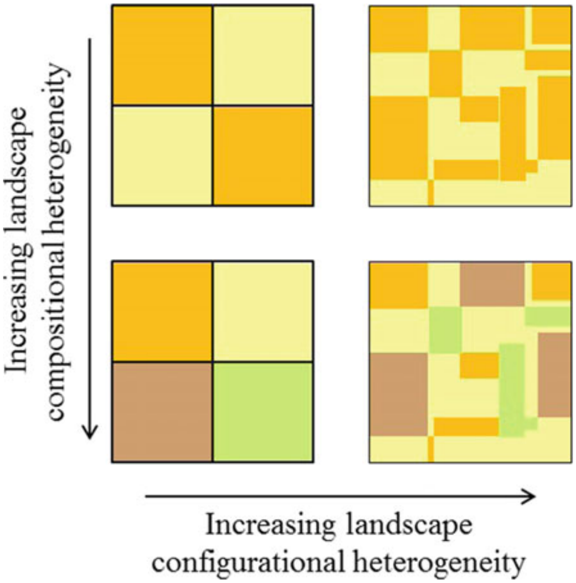

Fig. 1.4 Theoretical definition of spatial heterogeneity into its two components i.e. landscape composition and landscape configuration (adapted from Fahrig et al. 2011)

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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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

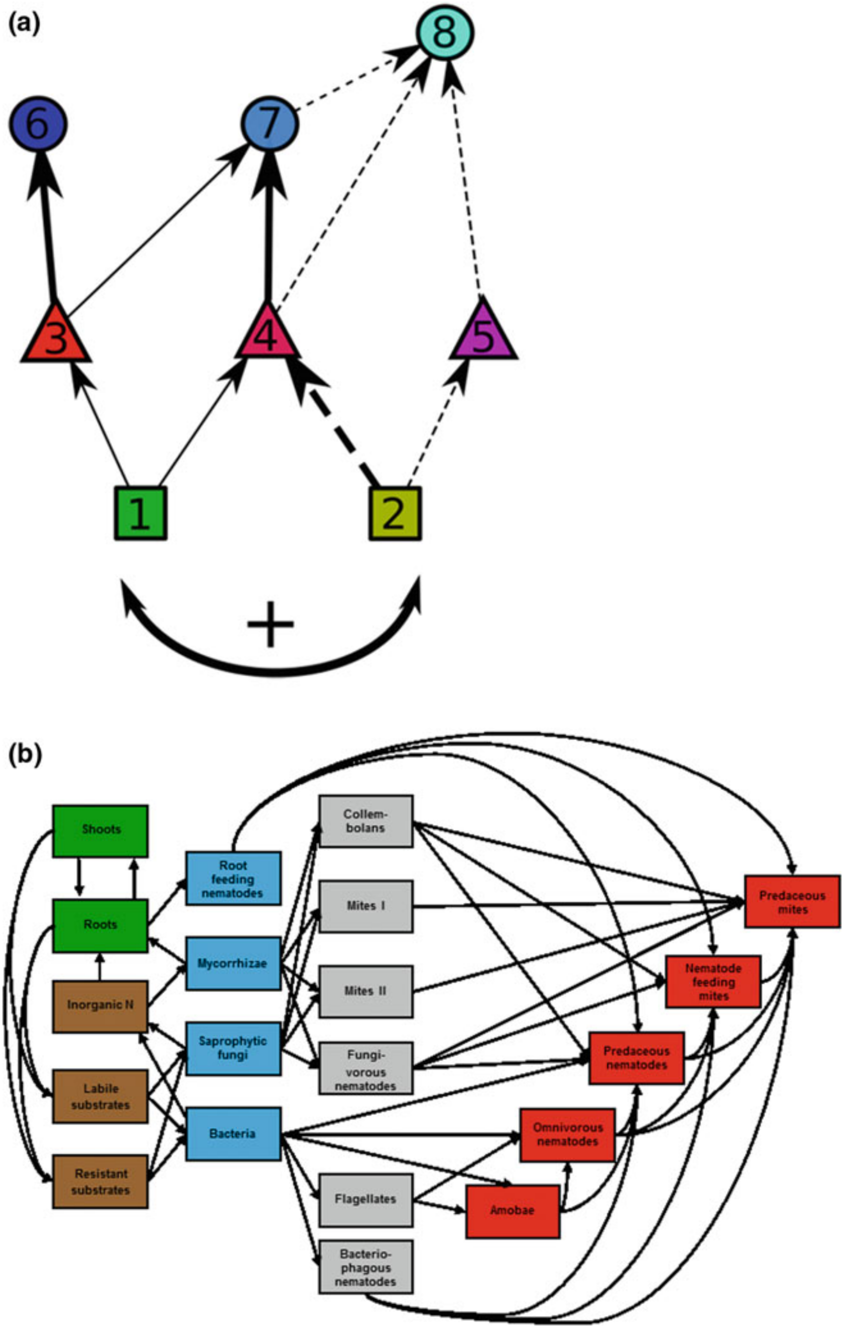
Hundreds of ecological studies have demonstrated that multispecies assemblages of plants are more productive and temporally stable than monocultures (Tilman et al. 2014). Two general mechanisms may explain these effects. First, complementarity and positive interactions between species increase production, 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_2 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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Root feeding nematodes
Mycorrhizae
Saprophytic fungi
Bacteria
Collembolans
Mites I
Mites II
Fungivorous nematodes
Flagellates
Bacteriophagous nematodes
Predaceous mites
Nematode feeding mites
Predaceous nematodes
Omnivorous nematodes
Amobae