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Landscape perspectives for agroecological weed management. A review

Sébastien Boinot¹ · Audrey Alignier^{1,2} · Jonathan Storkey³

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Abstract

Faced with the biodiversity extinction crisis and climate change, alternative approaches to food production are urgently needed. Decades of chemical-based weed control have resulted in a dramatic decline in weed diversity, with negative repercussions for agroecosystem biodiversity. The simplification of cropping systems and the evolution of herbicide resistance have led to the dominance of a small number of competitive weed species, calling for a more sustainable approach that considers not only weed abundance but also community diversity and composition. Agroecological weed management involves harnessing ecological processes to minimize the negative impacts of weeds on productivity and maximize biodiversity. However, the current research effort on agroecological weed management is largely rooted in agronomy and field-scale farming practices. In contrast, the contributions of landscape-scale interventions on agroecological weed management are largely unexplored (e.g., interventions to promote pollinators and natural enemies or carbon sequestration). Here, we review current knowledge of landscape effects on weed community properties (abundance, diversity, and composition) and seed predation (a key factor in agroecological weed management). Furthermore, we discuss the ecological processes underlying landscape effects, their interaction with in-field approaches, and the implications of landscape-scale change for agroecological weed management. Notably, we found that (1) landscape context rarely affects total weed abundance; (2) configurational more than compositional heterogeneity of landscapes is associated with higher alpha, beta, and gamma weed diversity; (3) evidence for landscape effects on weed seed predation is currently limited; and (4) plant spillover from neighboring habitats is the most common interpretation of landscape effects on weed community properties, whereas many other ecological processes are overlooked. Strikingly, the drivers of weed community properties and biological regulation at the landscape scale remain poorly understood. We recommend addressing these issues to better integrate agroecological weed management into landscape-scale management, which could inform the movement towards managing farms at wider spatiotemporal scales than single fields in a single season.

Keywords Biological control · Collective management · Environmental heterogeneity · Integrated landscape approach · Landscape diversification · Landscape heterogeneity · Plant diversity · Semi-natural habitat · Spillover · Seed predation

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1 Introduction

Through the Green Deal and the Farm to Fork Strategy, the European Union has set the ambitious goal to develop sustainable food systems and halve pesticide use by 2030 (although the pesticide reduction law is currently being negotiated). Achieving these goals requires rethinking current weed management methods. Modern crop breeding coupled with high inputs of agrochemicals currently facilitates the large-scale production of a small number of crops in increasingly homogenous landscapes. Today, around three million tons of herbicides are used each year worldwide to eliminate weed species (FAO 2021). Over-reliance on pesticides for crop protection, reduction of crop diversity, and landscape simplification have caused a dramatic loss of weed diversity and abundance (Fried et al. 2009; Kempel et al. 2020; Meyer et al. 2013; Richner et al. 2015; Storkey et al. 2012) with negative impacts on the entire food chain (Albrecht 2003; Marshall et al. 2003; Stoate et al. 2001). The intensive use of agrochemicals (herbicides and chemical fertilizers) has led to the depletion of soil seedbanks, evolution of herbicide resistance in weeds, and selection of competitive species that are increasingly difficult to control (Neve et al. 2009; Rotchés-Ribalta et al. 2020). Genetically modified crops and their unintentional hybridization with weedy or wild relatives is resulting in the emergence of “super-weeds,” with improved resistance to herbicides, insect pests, and viruses, higher tolerance to drought, or higher growth rate (Vercellino et al. 2022). In addition, the chemical-based strategy threatens human health (Baudron and Liégeois 2020; Benton and Bailey 2019; Nicolopoulou-Stamati et al. 2016) and may increase agroecosystem vulnerability to climate change (Lin et al. 2008; Storkey et al. 2021). Weed management must therefore take another path that reduces the reliance on agrochemicals. One way is to make more use of non-chemical approaches to weed control, including stale seedbeds, mechanical weeding, and intercropping, in so-called integrated weed management (IWM) systems (Riemens et al. 2022). Both chemical-based weed control and IWM are largely predicated on the aim of drastically reducing weed abundance with the assumption that this is the way to protect crop yield. However, there is also an important need to redesign cropping systems to increase their resilience to weeds (reducing the need for direct control), through ecological processes that reduce the dominance of competitive species but also increase weed diversity. This would also contribute to meeting the major challenge of biodiversity conservation given that humans use roughly half of the ice-free land area of Earth for agriculture (Fritz et al. 2015), often in the form of large and high input monocultures, with major impacts on a wide range of taxa (Etard et al. 2022; Jaureguiberry et al. 2022; Rigal et al. 2023; Sánchez-Bayo and Wyckhuys 2019).

Agroecological weed management (AWM) addresses this challenge by presenting a paradigm shift from aiming to eradicate weeds to managing agronomically and environmentally sustainable weed communities (MacLaren et al. 2020). A primary focus of AWM is manipulating abiotic and biotic interactions in the agroecosystems to manage opportunities for weed colonization, establishment, and growth in a way that reduces the negative impact on crops while maximizing biodiversity benefits by preserving weed diversity (Smith and Mortensen 2017). The focus of AWM is, therefore, less on overall abundance and more on weed community composition and diversity as important metrics of sustainable crop protection (Storkey and Neve 2018). There is indeed growing recognition that only a small proportion of dominant weed species in a field causes significant yield loss (Adeux et al. 2019; Albrecht 2003; Ferrero et al. 2017; Marshall et al. 2003; Pollnac et al. 2009; Storkey and Neve 2018), whereas many weed species support biodiversity and contribute to important ecological functions such as pollination, pest control, and soil fertility (Balfour and Ratnieks 2022; Blaix et al. 2018; Hu et al. 2023; Nicholls and Altieri 2013; Smith et al. 2020). By implication, for a constant weed abundance, a more diverse and even weed community would be expected to be less competitive and have greater environmental benefits—being agronomically and ecologically more sustainable. Recent studies have shown that weed diversity is positively associated with the overall sustainability and multifunctionality of agroecosystems (Gaba et al. 2020; Liebman et al. 2021).

Empirical studies providing the evidence base for AWM have generally focused on solutions at the field scale, for example, complex crop rotations, polycultures, cover crops, crop-livestock systems, and preservation of biological control agents (MacLaren et al. 2020). This is because it is generally assumed that weed community assembly is so strongly driven by local farming practices that processes operating at larger spatiotemporal scales are not important for modelling variation in local weed abundance and diversity (but see Alignier et al. 2013; Petit et al. 2013). Such an assumption has led agronomists and agroecologists to focus their research on small-scale processes, such as weed-crop competition, while disregarding other important processes such as weed dispersal (Ghersa and Roush 1993). This is in contrast to studies on the population dynamics of other farmland taxa, such as pollinators, natural enemies, invertebrate pests, and diseases, that are acknowledged to respond to larger scale processes, and for which our understanding of landscape effects has considerably increased in recent years (Haan et al. 2020; Jeanneret et al. 2021; Martin et al. 2019). However, as emphasized by Petit et al. (2013), the recurrent success of invasive weed species, the spread of herbicide resistance, and the turnover observed in weed communities over decades provide evidence that weed dispersal is an

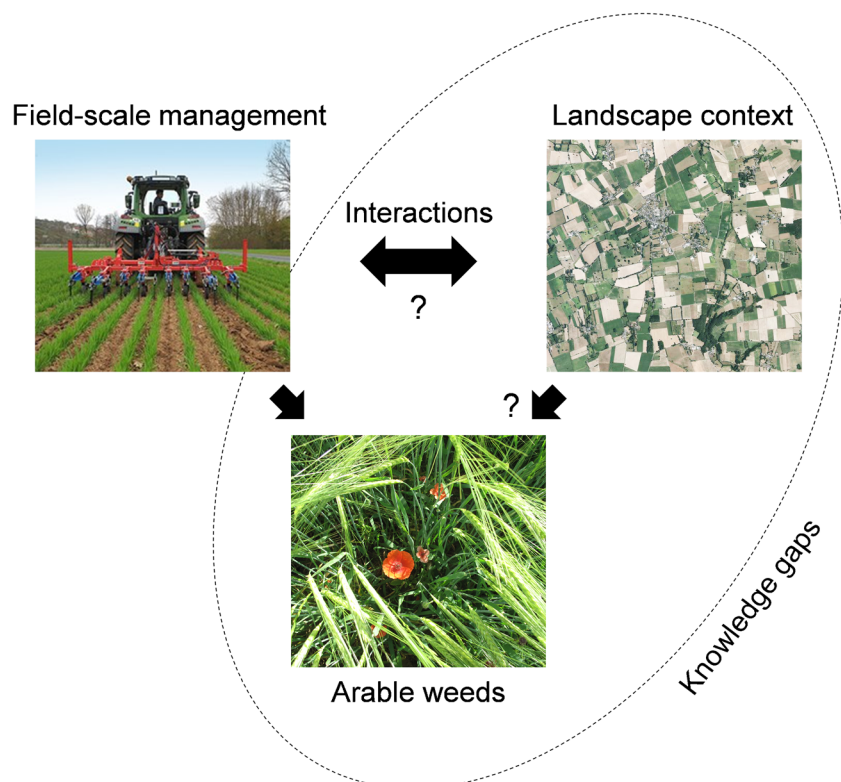
important process occurring over large spatial scales. Aside from long-distance dispersal events that may be relatively rare (but not without consequences), stepwise and secondary dispersal can also enable weeds with short dispersal ranges to move relatively large distances over time (Mayer et al. 2002; Ricci et al. 2013; Steinmann and Klingebiel 2004). The characteristics of the landscape surrounding a field (habitat diversity and configuration) are therefore expected to affect in-field weed communities through moderating the size of the regional species pool (Smart et al. 2006b) and determining the likelihood of dispersal of those species into the field.

Importantly, the population structure of weeds that may have intrinsic limited dispersal ability will also be determined by interactions with more mobile taxa such as pollinators, herbivores, seed predators, and dispersers (zoochory) that inhabit the surrounding landscape (Ehrlén and Eriksson 2003). More mobile taxa can affect the growth, reproduction, and recruitment of weeds. In particular, weed seed predation is a key regulating service for sustainable weed management (Petit et al. 2018; Sarabi 2019). For example, Davis et al. (2011) estimated that annual seed removal due to invertebrates averaged 40% of the total number of seeds produced by weeds. These authors also showed that weed seed predation can vary widely (from 8 to 70%) depending on the weed species and the agronomic context. Seed predation can not only reduce weed pressure but also impact weed community assembly and thus determine the relative abundance of

weed species farmers must deal with (Agrawal and Maron 2022; Hulme 1998). Landscape context is likely an important factor in this variation in seed predation, as invertebrate and vertebrate seed predators (e.g., carabids, ants, crickets, small rodents, and birds) need a diversity of habitats notably for overwintering, feeding, and reproduction (Barbaro et al. 2021; Fischer et al. 2018; Iuliano and Gratton 2020).

Given the potential impacts of landscape on weeds and the balance between their negative and positive functions (competition vs biodiversity support), any AWM strategy should consider the landscape-scale processes that drive weed community assembly (Fig. 1). It may be that changes to landscape context (e.g., establishment of agri-environmental schemes) are directed primarily at other outcomes than weed management, including the support of farmland birds, pollinators and natural enemies, or carbon sequestration. But, this does not negate the need to better understand the impacts of these landscape changes on weed species pools and community assembly, especially given that field-scale solutions are not always sufficient to promote weed diversity (Adeux et al. 2022). Finally, it is necessary to better understand how landscape-scale processes interact with field-scale management, either creating antagonisms or synergies for the natural regulation of the most competitive weed species and the preservation of weed diversity. Such knowledge should help propose more robust and efficient solutions to reconcile agricultural production and biodiversity conservation.

Fig. 1 Arable fields are not closed systems. Beyond management at the field scale, agroecological weed management (AWM) would benefit from considering landscape-scale effects on arable weed communities (abundance, diversity, and composition of weed species). A better understanding of the ecological processes underlying landscape effects, as well as their interactions with field-scale processes, would provide additional insights into the sustainable management of weeds.



In this review, we provide an overview of current knowledge of landscape effects on weed community properties (abundance, diversity, and composition), separating the effects of landscape compositional heterogeneity (the number and proportions of different habitat types) from those of landscape configurational heterogeneity (the spatial arrangement of habitat types) (Fahrig et al. 2011) (Section 2). We also apply this approach to the regulating ecosystem service of weed seed predation (Section 3). Then, we assess how landscape effects on weed community properties and seed predation interact with field-scale parameters, including the distance from adjacent field margin and management intensity (Section 4), and describe the spatial scales of landscape effects (Section 5). Finally, we discuss the ecological processes that likely underlie landscape effects on weed community properties (Section 6) and the potential benefits and challenges of landscape-scale change for AWM (Section 7). To meet these objectives, we gathered all the empirical studies we could find (excluding studies using landscape models and simulations) using the following search string in Web of Science last updated on August 27, 2023:

Topic: (“landscape ecology” OR “landscape effect*” OR “landscape context*” OR “landscape structure*” OR “landscape feature*” OR “landscape complexity” OR “landscape composition” OR “landscape configuration” OR “compositional heterogeneity” OR “configurational heterogeneity” OR “landscape heterogeneity” OR “landscape diversity” OR “landscape simplification” OR “landscape intensification” OR “land-use intensity” OR “landscape homogenization” OR “landscape homogenization” OR “habitat connectivity” OR “landscape connectivity” OR “habitat fragmentation” OR “landscape fragmentation” OR “habitat loss” OR “habitat amount” OR “habitat isolation” OR “land-use management” OR “landscape management” OR “land sharing” OR “land sparing” OR “land-sharing” OR “land-sparing” OR “landsharing” OR “landsparing” OR “crop mosaic” OR “edge density” OR “ecological corridor*” OR “field size” OR “landscape change*” OR “landscape history” OR “land-use history”) AND: (weed* OR “weeds” OR “plant” OR “plants” OR flora OR vegetation) AND: (“agricultural landscape*” OR “rural landscape*” OR farmland OR “crop field*” OR “arable field*” OR agroecosystem*).

Then, we scanned the resulting 2460 studies to select those assessing landscape effects on weed community properties (abundance, diversity, and composition) and weed seed predation in arable fields. We excluded studies on grasslands, which contrast with arable crops, vineyards, and orchards in terms of management type and intensity and functional attributes of spontaneous vegetation (Bourgeois et al. 2019). In total, we selected 58 studies on weed community properties and 19 studies on weed seed predation. These studies were conducted in a variety of crops, predominantly annual crops including cereals, maize, oilseed rape,

sunflower, beet, soybean, and rice ($n = 55$), but also perennial crops including vineyards and olive groves ($n = 5$). Most studies were from European countries ($n = 69$), although we found some studies in Canada ($n = 4$), South America ($n = 4$), Asia ($n = 1$), and the USA ($n = 1$).

2 Landscape effects on weed communities

To date, existing studies have assessed the effects of many landscape metrics on a variety of weed response variables: abundance, diversity, composition, or even seed rain, resource provision, and spatial distribution (Figs. 2 and 3). Most studies have focused on species alpha diversity (i.e., the number of species within weed communities at plot scale), and to a lesser extent on weed abundance (Fig. 2). Knowledge of landscape effects on weed seedbanks remains very limited compared to aboveground vegetation ($n = 7$ vs $n = 57$ studies, respectively) (Fig. 2). Functional diversity (quantifying weed communities at the level of functional traits) is also much less studied than taxonomic diversity (Fig. 2). We found that most studies assessed the effects of landscape composition as opposed to landscape configuration (Fig. 3). Because of the lack of seedbank data, we focus on aboveground weed communities hereafter.

2.1 Weed abundance

A total of 18 studies assessed weed abundance based on aboveground vegetation, generally quantified as the total number of individuals or percent cover in sampling points (most often replicates of 1 m² to 4 m² plots). Among these, very few studies found significant effects of landscape variables on weed abundance (Fig. 4a), confirming the view that weed abundance is affected more by field-scale management practices than landscape context (Petit et al. 2016). Even among studies that found significant landscape effects on weed abundance, results were contrasting. Indeed, studies found mixed effects of landscape compositional heterogeneity (estimated by total cropland cover or habitat diversity) on weed abundance, either null (Dainese et al. 2017; Ekroos et al. 2010; Flohre et al. 2011b; Lüscher et al. 2014; Uroy et al. 2022), negative (Lüscher et al. 2014; Winqvist et al. 2011), or positive (Alignier et al. 2017; Carpio et al. 2020; Hall et al. 2020). Some studies found that higher landscape configurational heterogeneity (estimated by edge density or mean field size) was associated with higher weed abundance (Carpio et al. 2020; Marshall et al. 2006). In contrast, other studies found lower weed abundance in landscapes with higher configurational heterogeneity (estimated by connectivity provided by grasslands or focal field size) (Alignier et al. 2017; Uroy et al. 2022). It is likely that specific contrasts

Fig. 2 Number of studies ($n = 58$) assessing landscape effects on a variety of weed community variables, using **a** taxonomic and **b** functional approaches, based on above-ground vegetation (in green) or weed seedbank (in brown). *Resources* gather studies assessing landscape effects on the diversity and/or abundance of weed resource provision (seeds and flowers). The *ecological group* refers to a variety of broad classifications, including, for example, growth form (grasses vs forbs), Raunkiaer’s life forms, Grime’s strategies, origin, or rarity.

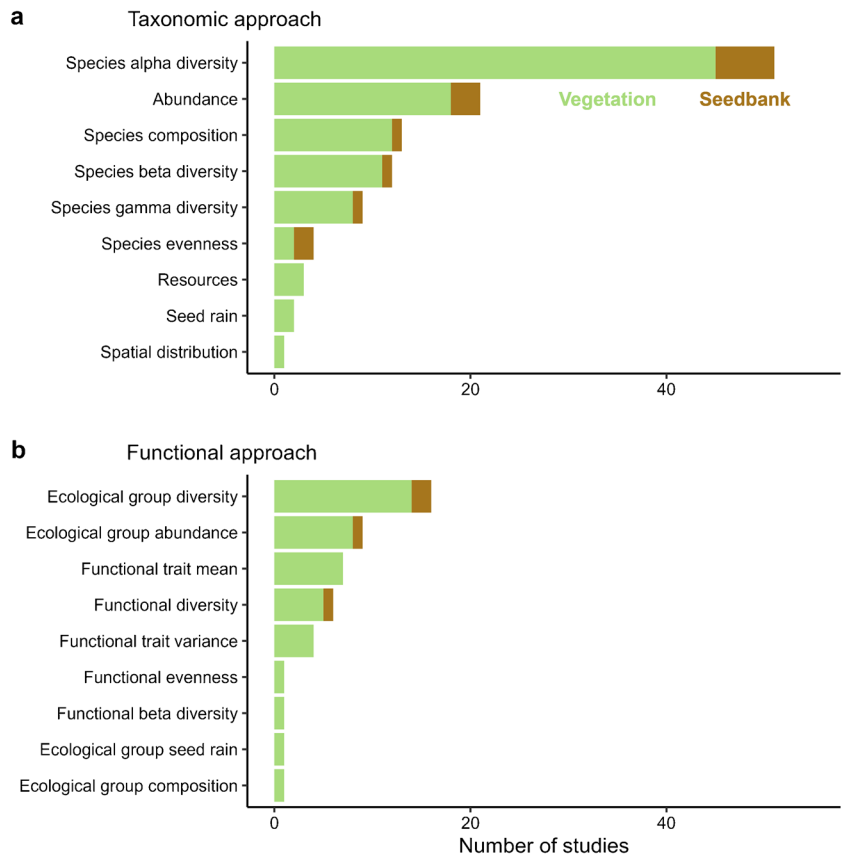
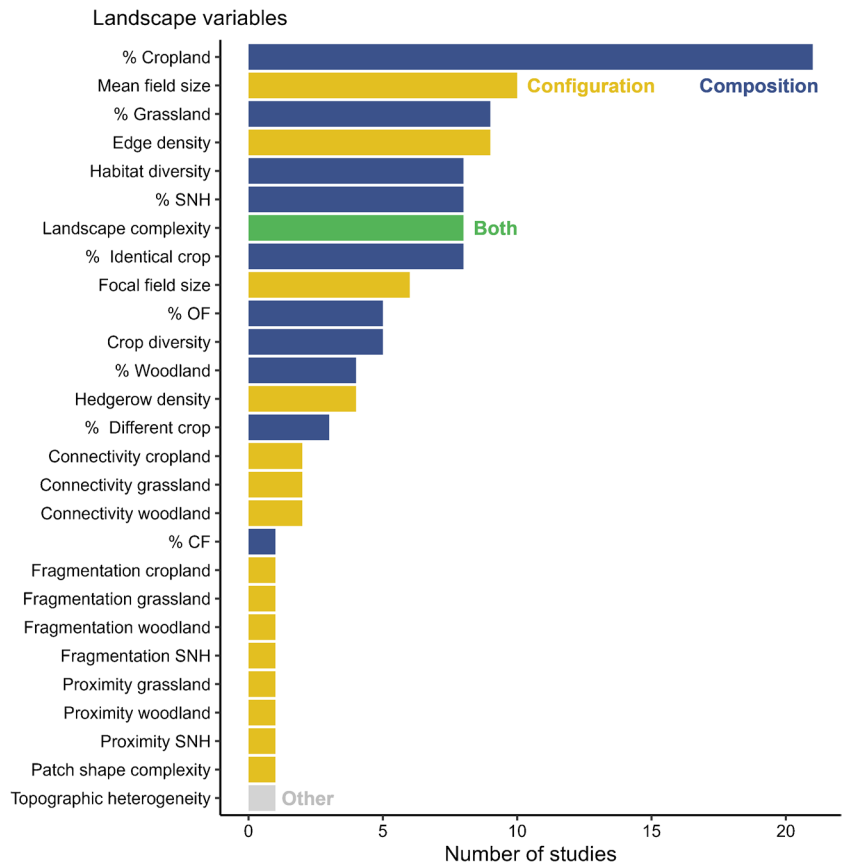


Fig. 3 Number of studies ($n = 58$) assessing landscape effects on weed community properties (abundance, diversity, and composition). For simplicity, *edge density* gathers studies assessing the effects of edges between different habitat types (e.g., overall edge density, crop/semi-natural borders, or perimeter-area ratio). *Landscape complexity* gathers studies that sampled weed communities in broad landscape contexts (simple vs complex) and studies that used principal axes of multivariate analyses based on a diversity of landscape variables (e.g., mean-field size, total cover of cropland or semi-natural habitats, and habitat diversity). % *Identical crop* refers to the total cover of arable fields cultivated with the same crop as the sampled fields. On the other hand, % *different crop* gathers studies assessing the effects of total cover of various crop types different from the sampled crops. SNH, semi-natural habitats; CF, conventional farming; OF, organic farming.



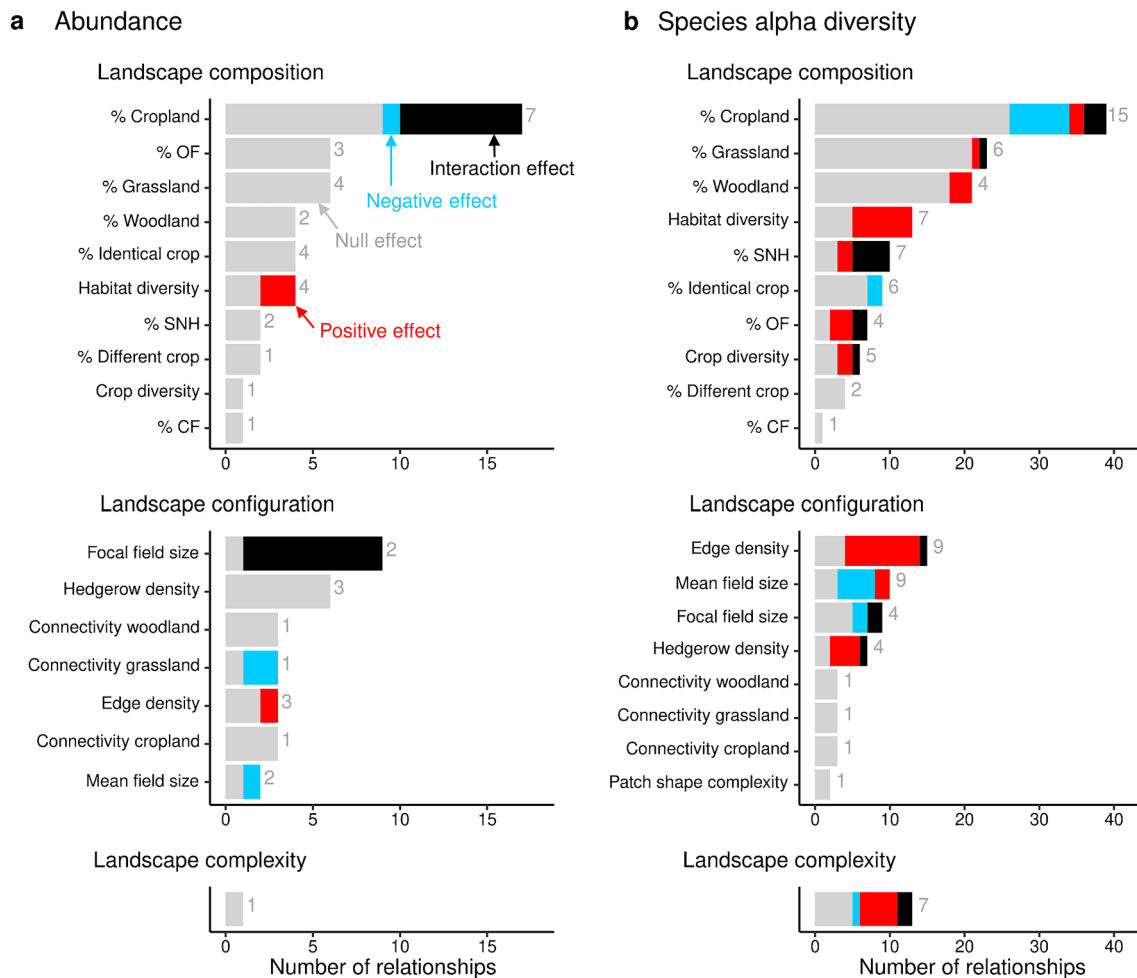


Fig. 4 Overview of landscape effects on the two most studied response variables, **a** weed abundance and **b** species alpha diversity, that is the number of species within weed communities at the plot scale. The number of studies is given to the right of the bars. For simplicity, *edge density* gathers studies assessing the effects of edges between different habitat types (e.g., overall edge density, crop/semi-natural borders, or perimeter-area ratio). *Landscape complexity* gathers studies that sampled weed communities in broad landscape contexts (simple vs complex) and studies that used principal axes of multivariate analyses based on a diversity of landscape variables (e.g., mean-field size, total cover of cropland or semi-natural habitats,

and habitat diversity). *% Identical crop* refers to the total cover of arable fields cultivated with the same crop as the sampled fields. On the other hand, *% Different crop* gathers studies assessing the effects of total cover of various crop types different from the sampled crops. SNH, semi-natural habitats; CF, conventional farming; OF, organic farming. Note that the main objective of this review is to take stock of current knowledge and identify promising avenues for research on agroecological weed management, but conclusions based on vote-counting should be interpreted with care as such method does not account for the magnitude and uncertainty of effects (Koricheva and Gurevitch 2014).

between habitats—captured by different landscape metrics in different contexts—explain the discrepancy in these results. For example, we can expect greater colonization by weedy species in crop fields adjoining other open and disturbed habitats as opposed to semi-natural grasslands or woody habitats (Metcalf et al. 2019; Ricci et al. 2018).

2.2 Weed diversity

A total of 45 studies measured the species alpha diversity of aboveground weed vegetation. In contrast to weed

abundance, many studies found significant effects of landscape variables on species alpha diversity (Fig. 4b). The fact that landscape context seems to affect weed diversity more than weed abundance is a promising result for AWM. Indeed, this result suggests that some landscape contexts can support higher weed diversity without necessarily increasing weed pressure in arable fields, although we note only 18 studies (out of 45) considered simultaneously weed abundance and diversity in their analyses. Among these 18 studies, there were more increases in weed diversity independent of weed abundance ($n = 15$ relationships) than mutual increases in

weed abundance and diversity ($n = 4$ relationships). Regarding landscape composition, many studies did not detect a significant effect of total cover of cropland or semi-natural habitats on weed diversity (Alignier et al. 2017; Armengot et al. 2011; Concepción et al. 2012b; Ekroos et al. 2010; Fahrig et al. 2015; Flohre et al. 2011b; Gabriel et al. 2006; Hall et al. 2020; Lüscher et al. 2014; Martínez et al. 2015; Pallavicini et al. 2020; Uroy et al. 2022). However, higher compositional heterogeneity did tend to promote weed diversity, but mostly in field edges, possibly through plant spillover from a diversity of neighboring habitats (Alignier et al. 2020; José-María et al. 2010; José-María and Sans 2011; Kovács-Hostyánszki et al. 2011; Solé-Senan et al. 2014). On the other hand, more extensive farming practices at the landscape scale are associated with higher weed alpha diversity. For instance, higher total cover of organic farming fields and crop diversity in the landscape are generally associated with higher weed diversity at the field scale, without affecting weed abundance (Bourgeois et al. 2020; Henckel et al. 2015; Martin et al. 2020; Petit et al. 2016; Sirami et al. 2019). There is also strong evidence that higher landscape configurational heterogeneity (estimated by hedgerow and edge density or reduced focal and mean field size) helps preserve weed diversity (Baessler and Klotz 2006; Carpio et al. 2020; Concepción et al. 2012b; Fahrig et al. 2015; Gaba et al. 2010; Gabriel et al. 2005; Guerrero et al. 2010; Hall et al. 2020; Lüscher et al. 2014; Martin et al. 2020; Petit et al. 2016; Poggio et al. 2010; Sirami et al. 2019). This result is in line with a recent global meta-analysis on a wide range of taxa (Estrada-Carmona et al. 2022), showing that landscape configuration more than the composition affects weed diversity—although this meta-analysis is based on a subset ($n = 10$) of the 45 studies we reviewed regarding alpha diversity.

Beyond alpha diversity (the number of species at the plot scale), a few studies assessed the effects of landscape on beta diversity (the change in species composition between plots, fields, or farms), and gamma diversity (the total number of species at field, farm, or region scale) (Fig. S1). It is important to consider these facets of diversity, as studies have found important differences between the drivers of alpha, beta, and gamma diversity (Boinot and Alignier 2023; Jones et al. 2022; Kessler et al. 2009; Smart et al. 2006a). Biotic homogenization (or decrease in beta diversity) that results from major anthropogenic disturbances is threatening biodiversity conservation and ecosystem functioning (Olden et al. 2004; van der Plas et al. 2016; Wang et al. 2021). From an agronomic point of view, an increase in weed beta and gamma diversity is likely indicative of more diverse environmental conditions at the landscape scale (and greater differentiation of weed ecological niches), reducing the risk of colonization by the most competitive weed species (from one field to another). Greater weed beta and gamma diversity

should also provide a higher diversity of trophic and habitat resources across space and time for biodiversity, including ecosystem service providers (pollinators, natural enemies of crop pests, and decomposers of organic matter). Different studies have found contrasting effects of landscape compositional heterogeneity (estimated by the total cover of semi-natural habitats or cropland) on weed beta diversity (Fig. S1), either null (Alignier et al. 2020; Concepción et al. 2012b; Ekroos et al. 2010; Fahrig et al. 2015; Flohre et al. 2011a), negative (Gabriel et al. 2006), or positive (Concepción et al. 2012b; Roschewitz et al. 2005). On the other hand, higher configurational heterogeneity seems to be a key driver of increasing beta diversity, either through higher edge density (Alignier et al. 2020; Concepción et al. 2012b; Poggio et al. 2010), reduced mean field size (Fahrig et al. 2015), or increased proximity of semi-natural habitats and grassland fragmentation (Dormann et al. 2007). We observe very similar results for gamma diversity (Fig. S1).

The positive association between configurational heterogeneity and weed diversity could be due to various agronomic and ecological processes. First, higher configurational heterogeneity typically results in landscapes with more fields, and probably with more diversified weed management strategies, providing a wider range of environmental conditions for weeds at landscape scale and increasing beta and gamma diversity. Second, higher configurational heterogeneity probably promotes plant spillover and in-field environmental heterogeneity resulting from neighboring arable or semi-natural habitats and increased connectivity in the landscape. We discuss the importance of plant spillover and environmental heterogeneity in determining weed community assembly in Section 6.

2.3 Weed species composition

Strikingly, few studies ($n = 12$) have assessed the effects of landscape on weed species composition, compared to weed diversity or abundance. Most studies gathered in this review focused on biodiversity conservation in agricultural landscapes, not on agronomic aspects. This reflects the current emphasis of weed control on farming practices at the field scale (e.g., crop rotation, tillage, pesticide treatment, and fertilization). Landscape effects on weed species composition, that is, how landscape composition and configuration determine the identity of weed species farmers must deal with, remain poorly understood. Yet, given only a small proportion of weed species causes significant yield loss (Adeux et al. 2019; Marshall et al. 2003), an important agronomic objective is to determine which landscape management practices (if any) effectively prevent dominance by these few highly competitive species, particularly those with evolved herbicide resistance (Dixon et al. 2021). Simulation studies concluded that controlling competitive weeds does require a landscape strategy

(Dauer et al. 2009; González-Díaz et al. 2012). Empirical studies gathered in this review show that both landscape compositional and configurational heterogeneity can significantly affect species composition (Fried et al. 2008; José-María et al. 2010; La Fuente et al. 2010; Marshall 2009; Martínez et al. 2015; Nascimbene et al. 2016; Solé-Senan et al. 2014) (Fig. S2). Functional approaches, discussed below, should help interpret the importance of such results for biodiversity conservation and agricultural production.

2.4 Functional approaches

Very few studies used a functional approach that quantifies weed community responses to the landscape at the level of functional traits, although many studies measured the abundance or diversity of ecological groups (e.g., growth form, origin, and rarity; Fig. 2). Yet, functional approaches allow a better understanding of the mechanisms driving the composition of weed communities and their impacts on agroecosystem functioning (Gaba et al. 2017; Navas 2012). When taxonomic approaches yield conflicting results, functional approaches can help elucidate more general taxa responses to landscape management practices and provide insights into the underlying mechanisms (e.g., Gámez-Virués et al. 2015; Tamburini et al. 2020). From a conservation point of view, it is also important to measure the impact of land-use intensification on functional diversity, which may be more affected than species diversity (Flynn et al. 2009).

The few studies ($n = 5$) that measured multi-trait diversity (using functional richness or Rao's quadratic entropy) revealed a positive association between landscape complexity and weed functional diversity (Carmona et al. 2020; Otto et al. 2012; Tarifa et al. 2021). Other studies found no effect of the total cover of cropland or semi-natural habitats and habitat diversity on the functional diversity of weeds in arable fields (Hall et al. 2020; Pallavicini et al. 2020), but the authors assumed that semi-natural habitats were not very diverse in the study area, or that landscape complexity gradient was too short. Focusing on individual traits included in the leaf-height-seed scheme of Westoby (1998), Boinot et al. (2022) found a higher variance of plant height, specific leaf area, and seed mass in dense and complex bocage landscapes. Tarifa et al. (2021) also found increased variance of plant height and specific leaf area, but not seed mass, in more complex landscapes. However, Guerrero et al. (2014) did not detect any effect of landscape complexity on the variance of plant height, specific leaf area, or seed mass, which was explained by an overriding effect of field-scale management intensity.

Unlike functional diversity, community-weighted means of functional traits seem less affected by landscape context. Most studies did not find significant effects of landscape

composition or configuration on the community-weighted mean of various functional traits, including, for example, plant height, specific leaf area, leaf-dry matter content, seed mass, flowering onset, and other floral traits (Boinot et al. 2022; Carmona et al. 2020; Guerrero et al. 2014; Hall et al. 2020; Pallavicini et al. 2020; Sztár et al. 2022; Uroy et al. 2022). These results suggest that landscape context has a limited impact on the abundance of the most dominant weed species established in arable fields. Nonetheless, Carmona et al. (2020) found that decreasing landscape complexity is associated with lower mean seed mass, probably because (1) species with poor dispersal abilities (high seed mass) are selected against in very intensified landscapes, and (2) species producing numerous small seeds have a persistent seedbank that helps recover from agricultural disturbances. Similarly, Uroy et al. (2022) found that higher connectivity provided by grasslands favors species producing fewer but larger seeds. Furthermore, Boinot et al. (2022) found that the mean plant height tends to decrease in denser and more complex bocage landscapes, probably because higher environmental heterogeneity promotes the coexistence of life strategies in such landscapes, thereby reducing the dominance of most competitive, taller species. Beyond the response of individual traits, it is worth noting that landscape effects on functional trait syndromes are rarely investigated.

For now, most knowledge on the functional composition of weed communities comes from studies measuring the abundance or diversity of ecological groups (Fig. 2). Most studies assessed the effects of landscape composition more than landscape configuration. Notably, there is recurring evidence that rare and declining arable weed species benefit from lower cropland cover (or higher semi-natural habitat cover), although they are generally confined to the edges of arable fields with lower management intensity (José-María et al. 2010; Kovács-Hostyánszki et al. 2011; Roschewitz et al. 2005; Rotchés-Ribalta et al. 2015; Solé-Senan et al. 2014). Dry-grassland specialists (based on reference literature) and non-nitrophilous species (based on Ellenberg's indicator value) benefit from higher semi-natural habitat cover as well (Kovács-Hostyánszki et al. 2011; Nascimbene et al. 2016). In addition to their high conservation value, the preservation of such species is very interesting for AWM as they are less competitive and potentially provide important resources for pollinators and natural enemies of crop pests (Albrecht et al. 2016; MacLaren et al. 2020).

3 Landscape effects on weed seed predation

All the studies we reviewed focused on *post-dispersal* weed seed predation, where seed predators feed on the ground after seed dispersal from the mother plant. On the

other hand, *pre-dispersal* seed predation, where insect larvae (mainly Diptera, Lepidoptera, Coleoptera, and Hymenoptera) and granivorous birds (e.g., goldfinches and greenfinches) feed on immature and mature seeds before shed from the mother plant, is largely overlooked in the literature. Pre-dispersal seed predation has been reported in some competitive weed species such as *Cirsium arvense*, *Chenopodium album*, and *Amaranthus retroflexus* and contributes—along with post-dispersal seed predation—to the natural regulation of weed populations (DeSousa et al. 2003; Forsyth and Watson 1985; Nurse et al. 2003). Most studies we reviewed measured post-dispersal weed seed predation on two occasions between May and July, during the main vegetation period but rarely in early spring or after crop harvest. The following most studied weed species were in decreasing order *Viola arvensis* ($n = 10$ studies), *Capsella bursa-pastoris* ($n = 5$), *Chenopodium album* and *Galium aparine* ($n = 4$), *Alopecurus myosuroides* and *Poa trivialis* ($n = 2$), and other species in single studies: *Amaranthus retroflexus*, *Cirsium arvense*, *Crepis biennis*, *Taraxacum officinale*, *Stellaria media*, *Galeopsis tetrahit*, *Abutilon theophrasti*, *Plantago lanceolata*, *Apera spicaventi*, *Digitaria sanguinalis*, *Poa annua*, *Poa pratensis*, and *Setaria faberii*. Of the 19 studies on weed seed predation, 11 measured total predation (invertebrates and vertebrates), eight measured predation by invertebrates only, and one measured predation by vertebrates only. Five studies have compared invertebrate and vertebrate predation rates, with some finding greater contribution from vertebrates (Fischer et al. 2011a; Tschumi et al. 2018) or invertebrates (Carbonne et al. 2023; Menalled et al. 2000) to total seed predation. Among the 11 studies that measured total predation, the mean of seed removal rates varied from 13 to 72% and averaged 41%, which highlights the potential but also the variability of post-dispersal weed seed predation (variability resulting from both ecological and methodological differences).

Like the studies on weed community properties (i.e., abundance, diversity, and composition), most studies on weed seed predation focused on the effects of landscape composition more than landscape configuration (Fig. 5), although there is strong evidence that lower field size and higher edge density promote within-field biodiversity including natural enemies of crop pests (Fahrig et al. 2015; Martin et al. 2019; Šálek et al. 2018). Surprisingly, no study found a positive effect of the total cover of semi-natural habitats on weed seed predation (Daouti et al. 2022; McHugh et al. 2020; Muneret et al. 2019; Ricci et al. 2019; Rusch et al. 2016; Tortosa et al. 2022), despite their importance in supporting natural enemies of crop pests (Chaplin-Kramer et al. 2011; Holland et al. 2016). We found contrasting effects of total cropland cover on weed seed predation, either null (Daouti et al. 2022; Trichard

Seed predation

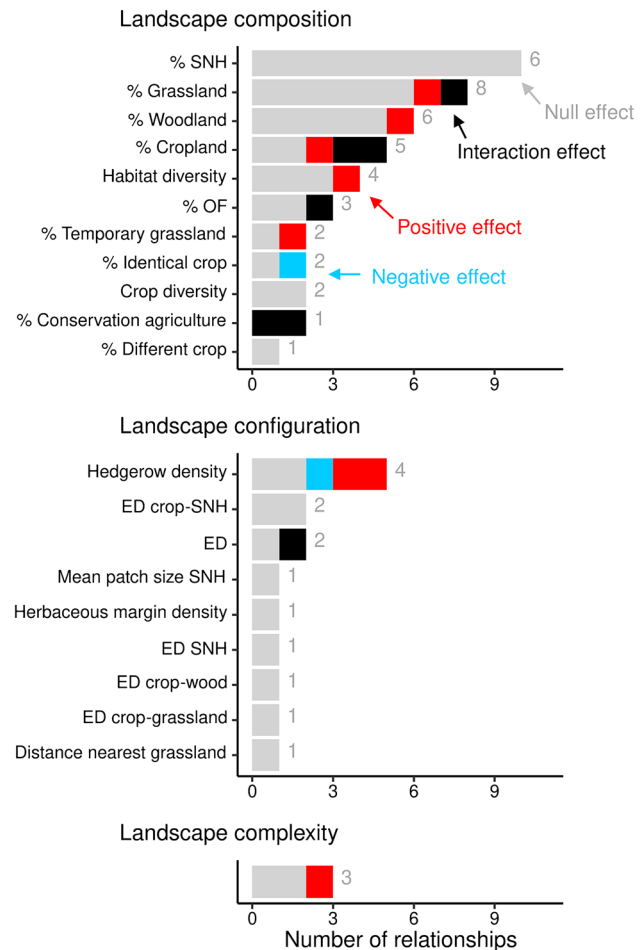


Fig. 5 Overview of landscape effects on post-dispersal weed seed predation. The number of studies is given to the right of the bars. Note that there may be more than one relationship assessed per study when a multi-scale approach was used. *Landscape complexity* gathers studies that sampled weed communities in broad landscape contexts (simple vs complex) and studies that used principal axes of multivariate analyses based on a diversity of landscape variables (e.g., mean-field size, total cover of cropland or semi-natural habitats, and habitat diversity). *% Identical crop* refers to the total cover of arable fields cultivated with the same crop as the sampled fields. On the other hand, *% different crops* gather studies assessing the effects of total cover of various crop types different from the sampled crops. ED, edge density; SNH, semi-natural habitats; CF, conventional farming; OF, organic farming.

et al. 2013), positive (Jonason et al. 2013), or depending on farming systems (Fischer et al. 2011a; Petit et al. 2017). Even when distinguishing between habitat types (grassland, woodland, hedgerows, crop types, or organic fields), evidence for landscape effects remains limited so far (Diekötter et al. 2010; McHugh et al. 2020; Ricci et al. 2019; Tortosa et al. 2022; Tortosa et al. 2023; Trichard et al. 2013; Tschumi et al. 2018, but see Badenhassner et al. 2020; Muneret et al. 2019; Perrot et al. 2021). We

list some methodological biases and ecological hypotheses that might explain the low influence of landscape or conflicting results, which require further investigation:

- Landscape gradients are not large enough, or there are non-linear relationships and threshold effects (Tscharnkte et al. 2012; van der Hoek et al. 2015)
- The spatial scale considered is not the most relevant to the underlying ecological processes (see Section 5)
- Use of overly simplistic metrics (need for a finer characterization of semi-natural habitats; e.g., Bartual et al. 2019; Tobisch et al. 2023)
- Bias due to the sentinel prey method, which involves sticking prey on a card that is then placed in the field to quantify the prey removal rate during an exposure period. Some major predators might not consume seeds stuck on cards, and a low number of weed species have been tested so far (very often *Viola arvensis*), not necessarily those that are dominant in the surveyed fields (Ali and Willenborg 2021; Saska et al. 2014; Zou et al. 2017). Using a diversity of weed species should better reflect the activity of the seed predator community. In addition, plastic roofs to protect seeds from rainfall (used in five studies in our review) can affect animal behavior and limit access to seed patches for birds (Fischer et al. 2011a; Saska et al. 2014)
- Insufficient sampling effort in space and time, given the large spatial and temporal variability of weed seed predation (as evidenced by Marino et al. 1997; Trichard et al. 2014)
- Weed seed predation service is potentially provided by a small number of common and agrobiont species that are less affected by the landscape context (Daouti et al. 2022; Muneret et al. 2019)
- Landscape effects on beneficial invertebrates are likely species-specific (Jowett et al. 2019), and the resulting feeding guilds will determine weed seed predation intensity
- No consideration of key covariates (and interaction effects) such as field-scale management intensity and resource availability, which drive predators' survival, movement, and foraging time in arable fields (Carbonne et al. 2022; Corbett and Plant 1993; Dunning et al. 1992) (see Section 4.2)
- Retention effects (i.e., semi-natural habitats are more attractive than arable fields under chemical-based agriculture) (Boinot et al. 2020)
- Diversification and dilution of resources in complex landscapes (i.e., reduced predation in focal fields but enhanced predation at landscape scale)
- Increased predation between natural enemies (intra-guild predation) in more complex landscapes due to increased

abundance and diversity of natural enemies (but see Ortiz-Martínez et al. 2020)

4 Interaction of field- and landscape-scale factors

4.1 Interaction with distance from field margins

Beneficial landscape effects on weed communities are particularly interesting for AWM when they impact a large area of crop fields, rather than being restricted to field edges. Based on available information, weed communities were sampled between 5 and 50 m from field margins across all studies (Fig. S3). In total, only 26% of studies ($n = 15$) assessed whether landscape effects vary with the distance from field margins. We can distinguish three types of landscape effects in decreasing order of importance for AWM: (1) *independent effect*: no interaction with the distance from field margins, (2) *core effect*: stronger landscape effects (negative or positive) in field cores, and (3) *edge effect*: stronger landscape effects (negative or positive) in field edges. Among studies that found significant landscape effects on species alpha diversity, there were more edge effects ($n = 5$; Alignier et al. 2020; Concepción et al. 2012b; José-María et al. 2010; Kovács-Hostyánszki et al. 2011; Solé-Senan et al. 2014) than core effects ($n = 1$; Alignier et al. 2020) and independent effects ($n = 2$; Concepción et al. 2012b; Poggio et al. 2013). The most common interpretations for edge effects are short-distance spillover from adjoining habitats and/or reduced agricultural disturbances in field edges, whereas strong filtering occurs in field cores. Conversely, Alignier et al. (2020) found a positive effect of configurational crop heterogeneity in field cores, but not in field edges. The authors assumed that the landscape effect is limited where plant diversity is already high (that is in field edges that are generally more diverse than field cores, at least under conventional farming).

Regarding weed seed predation, only 21% of studies ($n = 4$) assessed whether landscape effects vary with the distance from field margins. Among studies that found significant landscape effects, there were only independent effects ($n = 2$; Badenhauer et al. 2020; Fischer et al. 2011a), suggesting that natural enemies benefiting from higher landscape complexity or hedgerow density were efficiently colonizing arable fields—at least if spillover from semi-natural habitats is indeed the major process involved.

4.2 Interaction with field-scale management intensity

Many agroecological studies revealed that landscape effects on a wide range of taxa (and associated ecological

functions) depend on field-scale management intensity (e.g., Concepción et al. 2012a; Fusser et al. 2018; Martínez-Núñez et al. 2019; Ricci et al. 2019). We can distinguish three types of landscape effects: (1) *independent effect*: no interaction with field-scale management intensity, (2) *antagonistic effects*: local management intensity hampers the benefits of landscape heterogeneity/complexity, and (3) *compensation effects*: landscape heterogeneity/complexity has more impact on fields where biodiversity is most severely affected, and thus compensates for the negative impacts of intense local management. In this review, 77% of studies ($n = 44$) measured field-scale management intensity, defined as the intensity of agrochemical and/or tillage disturbances or comparing different farming systems (conventional vs organic). Among these, 29 studies assessed whether landscape effects vary with field-scale management intensity. Among studies that found significant landscape effects on weed species alpha diversity, there were far more independent effects ($n = 14$, Boinot et al. 2022; Carbonne et al. 2022; Carmona et al. 2020; Concepción et al. 2012b; Flohre et al. 2011a; Henckel et al. 2015; José-María et al. 2010; Kovács-Hostyánszki et al. 2011; Lüscher et al. 2014; Martin et al. 2020; Petit et al. 2016; Rey et al. 2019; Tarifa et al. 2021; Winqvist et al. 2011) than antagonistic ($n = 3$; Berquer et al. 2021; Flohre et al. 2011b; Fried et al. 2022) and compensation effects ($n = 2$; Berquer et al. 2021; Roschewitz et al. 2005). We argue that if plant spillover was the key process at play, we should expect more antagonistic effects as transient weed species adapted to semi-natural habitats will be removed at a greater rate by more intense and frequent agronomic filters (soil tillage and agrochemical inputs). These species do rely on regular dispersal from surrounding habitats to persist in intensively managed fields, where they are generally confined to field edges (Metcalfé et al. 2019). We discuss other ecological processes that might explain these results in Section 6.

Regarding weed seed predation, 63% of studies ($n = 12$) measured field-scale management intensity, and 11 studies assessed whether landscape effects vary with field-scale management intensity. Among studies that found significant landscape effects, there were more independent effects ($n = 3$; Jonason et al. 2013; Muneret et al. 2019; Ricci et al. 2019) than antagonistic effects ($n = 1$; Fischer et al. 2011a). These results show that in some cases, natural enemies benefiting from certain landscape contexts can efficiently colonize arable fields, even the most intensively managed ones. Nonetheless, in other cases, it seems both field- and landscape-scale extensification are needed to promote biological control of weeds. This most likely depends on the life strategies of weed seed predators involved (e.g., Boinot et al. 2020; Martin et al. 2019).

5 Spatial scale of landscape effects

Overall, only 25% of studies on weed community properties ($n = 14$) used a multiscale approach. Similarly, only 29% of the studies ($n = 5$) on weed seed predation used a multiscale approach. When studies are designed at a single spatial scale, landscape effects may be missed or underestimated because the chosen spatial scale is not relevant to the important biological processes at play. Across all the studies on weed community properties gathered in this review, selected buffer radii varied from 17 m to 2500 m (Fig. S4). Buffer radii most commonly used were by far 500 m ($n = 22$ studies) and 1000 m ($n = 17$) for both weed abundance and species alpha diversity. Similarly, almost all studies on weed seed predation used buffer radii of 500 m or 1000 m. It is often stated that weed communities respond to landscape context at a low buffer scale (that is less than 1000 m radius around focal fields). However, the results of the few studies ($n = 5$) that have used larger spatial scales suggest that weed diversity is also influenced by landscape context within radii of 1500 m to 2500 m (Fried et al. 2022; Gabriel et al. 2005; La Fuente et al. 2010; Rey et al. 2019; Tarifa et al. 2021). We also note that long-term weed surveys and studies on landscape history, trajectory, and temporal variability are missing in the literature, which is a common issue in landscape (agro)ecology (Marrec et al. 2022). In the following section, we explain that there might be many overlooked ecological processes underlying landscape effects on weed communities, and these processes most likely occur at different spatial and temporal scales.

6 Ecological processes explaining landscape effects

A better knowledge of ecological processes underlying landscape effects is required to (1) understand the mechanisms driving weed community assembly, (2) elucidate the contrasting associations observed between landscape and weed community properties, (3) provide relevant landscape-scale management strategies/guidelines at the appropriate spatiotemporal scales to optimize the balance between the negative and positive functions of weed communities (see Section 7).

6.1 Plant spillover and source-sink dynamics

In the articles we reviewed, plant spillover is by far the most common interpretation of landscape effects on weed communities (Fig. 6). The “plant spillover” hypothesis assumes that (1) more heterogeneous landscapes provide a diversity of habitats for ruderal plant species, and (2) plant

spillover from surrounding habitats directly increases weed abundance or diversity in arable fields (Boinot et al. 2022; Metcalfe et al. 2019; Shmida and Wilson 1985). However, plant spillover is rarely measured directly as it is very challenging to track plant dispersal in situ, especially over time.

Edge-biased distribution—the increase in weed abundance and diversity in field edges—does not necessarily provide evidence for the “plant spillover” hypothesis, as it could also be due to reduced agricultural disturbances in field edges, or increased environmental heterogeneity. Distinguishing

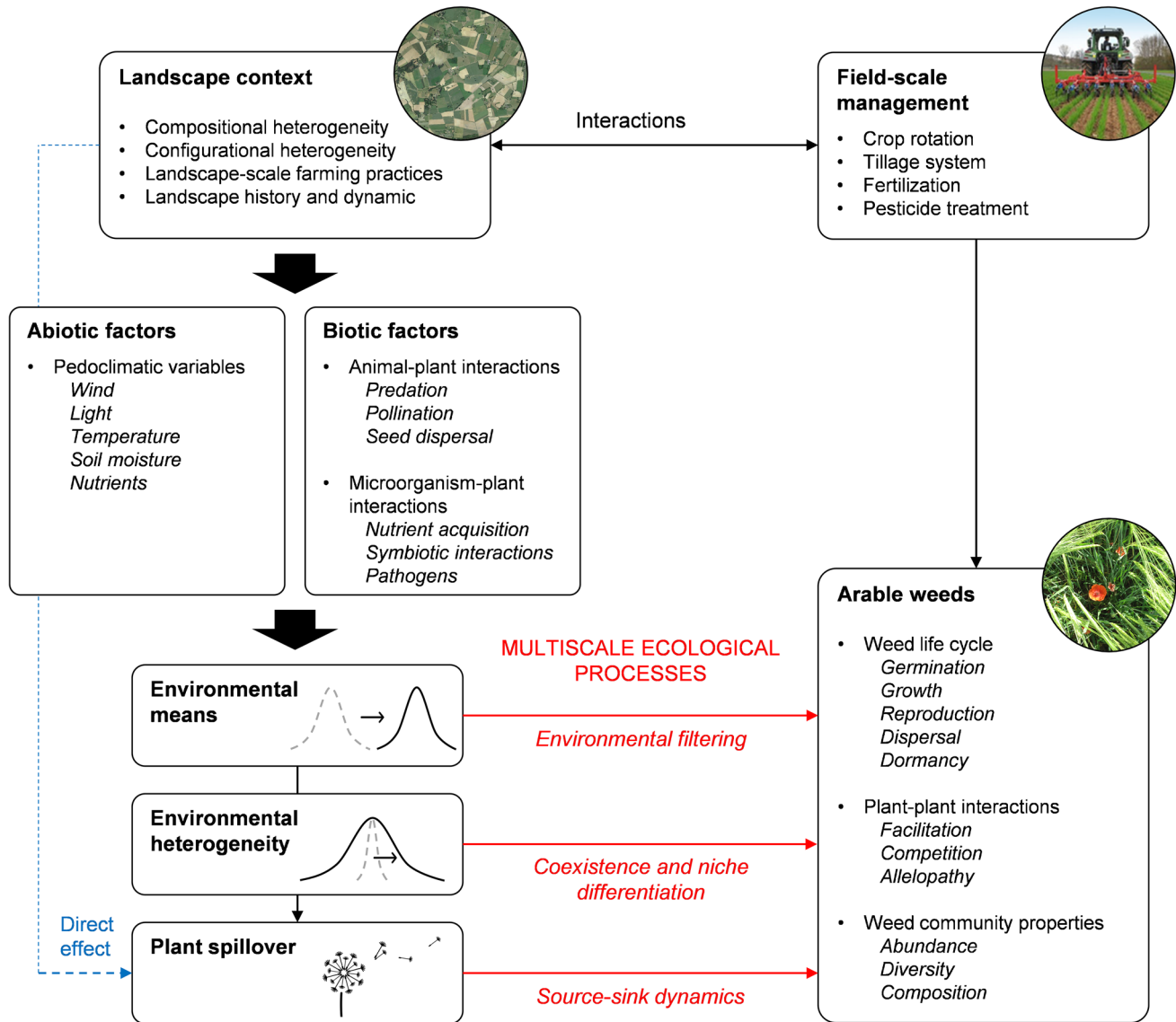


Fig. 6 A framework for future research on landscape-scale ecological processes and their contribution to AWM. Plant spillover is by far the most common interpretation of landscape effects. It is generally assumed that increased weed abundance or diversity (or changes in community composition) in arable fields is due to the dispersal of plant species from a diversity of neighboring habitats (direct effect represented by the dashed blue line). We point out that there are other overlooked ecological processes operating from local to regional scales and not necessarily related to plant spillover. Landscape context can affect both environmental means and environmental heterogeneity in crop fields and beyond. Environmental means should affect the composition more than the diversity of weeds, except at extreme values of environmental gradients where strong filtering occurs. On

the other hand, environmental heterogeneity is a key driver of diversity favoring species coexistence and niche differentiation. Environmental means and heterogeneity can affect not only plant spillover but also many other parameters that determine weed life cycles, plant-plant interactions, and weed community properties. Note that this framework is largely based on traditional community assembly theory (Booth and Swanton 2002). We did not represent feedback between weeds and their environment (modern coexistence and feedback theories: HilleRisLambers et al. 2012; Zobel et al. 2022), which can contribute to the maintenance (or loss) of weed diversity. For example, weeds can affect pollinators, natural enemies, and microorganism communities, as well as farmers’ perceptions and decisions.

“resident” species that can cope with strong agricultural disturbances and have persistent seedbank (ruderal strategy), from “transient” species that rely on regular dispersal from neighboring habitats (stress-tolerant or competitive strategies), can help assess the “plant spillover” hypothesis. Metcalfe et al. (2019) measured the fidelity of weed communities to crop habitats to quantify the relative proportion of resident and transient species. The authors showed that edge-biased distribution was associated with a decrease in fidelity to crop habitats and a higher proportion of competitive species in field edges, providing strong support for the “plant spillover” hypothesis. Beyond regular short-distance dispersal in field edges, there are probably rarer long-distance dispersal events (by wind, animals, or farming machinery) and temporal dispersal (generation-to-generation) facilitated by dormancy, which are more difficult to observe (Petit et al. 2013).

There is much evidence for plant spillover from semi-natural habitats to arable fields, and the prevailing agronomic view is that semi-natural habitats are *sources* of weeds. On the other hand, dispersal from arable fields to semi-natural habitats, and the role of semi-natural habitats as *barriers* to weed dispersal, have rarely been investigated (but see Cordreau et al. 2012; Devlaeminck et al. 2005; Ricci et al. 2018; Wilkerson 2014). Well-established perennial vegetation and litter in semi-natural habitats can act as seed traps (Bullock and Moy 2004; Doisy et al. 2014; Gabay et al. 2012; Ruprecht and Szabó 2012). Interestingly, José-María et al. (2011) found a lower abundance of wind-dispersed weed species in landscapes with a higher proportion of semi-natural habitats, including woodlands and shrublands. Wooded habitats can also reduce wind speed and affect pollen transfer (Forman and Baudry 1984; Matthias et al. 2015), which determines seed production and establishment (Auffret et al. 2017) but also the transfer of herbicide resistance genes (Loureiro et al. 2016). Furthermore, fragmentation of crop fields—interspersed with semi-natural habitats—also implies that the dispersal of weed seeds and vegetative plant fragments by agricultural operations such as tillage or harvest (Blanco-Moreno et al. 2004; Håkansson 2003; Steinmann and Klingebiel 2004) is restricted to smaller areas. This potentially prevents the expansion of weed patches in the landscape, at least if dispersal between fields by machinery is not the dominant process (Petit et al. 2013).

Whether or not landscape features promote or impede weed dispersal and population growth in crop fields will depend on the suitability of landscape habitats for ruderal plants. Later, successional semi-natural habitats generally present unfavorable or sub-optimal abiotic conditions for the growth and establishment of arable weed species, which have a high affinity for disturbed, nutrient-rich, sunny, and dry environments (Bourgeois et al. 2019). However, certain open semi-natural habitats, such as disturbed grasslands

(Munoz et al. 2020), can provide alternative habitats for ruderal plant species, supporting a wider regional species pool (Smart et al. 2006b) and promoting spillover into crop fields. Similarly, among the wide variety of field margin types, herbaceous, narrow, and disturbed margins are the most likely to provide habitat for weedy species (Aavik and Liira 2010; Boinot and Alignier 2023; Cirujeda et al. 2019; Fried et al. 2018). Resolving the uncertainties around the relative contribution of semi-natural habitats either as sources of weeds or potential barriers to dispersal (source-sink dynamics; Dunning et al. 1992) can only be addressed by a more detailed study of landscape impact on weed community composition—currently an understudied topic as discussed above. This understanding has important agronomic implications and could underpin landscape management recommendations. For example, habitats that support plant species unlikely to become highly-competitive weeds could be integrated between or within crop fields, which may make a positive contribution to ecosystem functioning by supporting seed predators (e.g., beetle banks) and other functional groups (see Section 7).

6.2 Environmental heterogeneity, coexistence, and niche differentiation

Landscape context can affect both abiotic factors (pedoclimatic variables) and biotic factors (ecological interactions) in crop fields and beyond (Cao et al. 2020; Schroeder et al. 2020) (Fig. 6). In addition, landscape effects can impact both the mean and variance of environmental conditions, referred to as environmental means and environmental heterogeneity (Stark et al. 2017). Changes in environmental means would affect the composition more than the diversity of weeds, except at extreme values of environmental gradients where strong filtering occurs. On the other hand, environmental heterogeneity is a key driver of diversity in a wide range of ecosystems (Stein et al. 2014). A diversity of environmental conditions (in space and time), and refuges from adverse environmental conditions, favors the coexistence and persistence of a diversity of species with different ecological niches. Competing species with overlapping niches can also coexist through niche differentiation and resource partitioning (Adler et al. 2013; Silvertown 2004), where plant species use the same resource in different places and at different times (e.g., through variations in root systems and phenology), or use different forms of the same resource (e.g., uptake of different chemical forms of nutrients).

Both environmental means and heterogeneity can affect plant spillover, for example, *via* the mean and variance of wind speed or the abundance and diversity of seed dispersers. Nonetheless, aside from plant spillover, we found that very few studies discussed the importance of *abiotic* environmental means and heterogeneity in weed community

assembly. Gabriel et al. (2006) found higher weed beta diversity in more complex landscapes and assumed that “local abiotic conditions within fields in complex landscapes are more variable than in simple landscapes with large, homogeneous fields, promoting heterogeneity in plant communities.” Similarly, Boinot et al. (2022) found higher weed diversity in landscapes that contain denser and more complex hedgerow networks. This increase in weed diversity was associated with an increase in community-weighted variance of Ellenberg’s values for light, temperature, and soil moisture (a proxy for environmental heterogeneity), but not with an increase in community-weighted mean of fidelity to non-crop habitats (a proxy for plant spillover). The authors concluded that environmental heterogeneity—by increasing the variability of in-field pedoclimatic conditions—was more likely the key driver of weed diversity in field cores as opposed to plant spillover.

The importance of *biotic* environmental means and heterogeneity, in terms of ecological interactions determining weed community assembly, is also generally overlooked. Agroecological studies more often investigate the effects of weeds on biodiversity than vice-versa. However, to survive in arable fields, weed species not only have to cope with strong agricultural disturbances and find suitable abiotic conditions for germination and growth but they also have to (1) survive diseases, parasitism, predation, allelopathy, and competition with other plants; (2) associate with mutualistic or symbiotic organisms; (3) reproduce; and (4) disperse. Landscape context will affect all these steps of the weed life cycle, indirectly through its impacts on living organisms interacting with weeds (Schroeder et al. 2020). First, as discussed in Section 3, landscape context can affect the communities of natural enemies of weeds (herbivores and seed predators) in arable fields (e.g., Haan et al. 2020; Martin et al. 2019). Natural enemies not only reduce weed abundance but also promote weed diversity. Indeed, natural enemy partitioning, which occurs when plant species are attacked differently by different natural enemies, can facilitate the coexistence of different plant species (Agrawal and Maron 2022; Hulme 1998). Density-dependent predation implies that weed species producing more seeds are more likely to get predated, especially if seeds are aggregated (Marino et al. 2005), potentially leaving space for less competitive weed species (unless dominant weeds are buffered by too large seedbank). Second, landscape context is a major driver of pollinator abundance and diversity in arable fields (Kennedy et al. 2013; Ragué et al. 2022), and pollination by insects has a key role in maintaining diverse weed communities (Rollin et al. 2016). Some studies gathered in our review indeed found that forb or insect-pollinated weeds are disproportionately promoted by higher habitat diversity or landscape complexity (Bohan and Haughton 2012; Gabriel

et al. 2005; Roschewitz et al. 2005; Tarifa et al. 2021). Interestingly, Petit et al. (2013) found not only higher weed diversity but also a higher proportion of insect-pollinated weeds in a preserved bocage landscape as opposed to an adjacent bocage landscape that went through a reallocation program in the early 1990s. Third, landscape context affects the presence and movement of seed dispersers such as insects, birds, and mammals in arable fields (Barbaro et al. 2021; Fischer et al. 2011b; Rey et al. 2019). Plants need to disperse in order to persist in a changing environment; to limit predation, disease, and intraspecific competition (e.g., Janzen-Connell effects); or to avoid self-fertilization and inbreeding depression (Petermann et al. 2008). Ozinga et al. (2009) provided evidence that dispersal failure contributes to the loss of plant diversity across a wide range of habitats, suggesting that restoration measures to improve local habitat quality may not always be sufficient, especially when the soil seedbank has been depleted. Fourth, there is growing evidence that landscape context can affect microorganism community assembly as well (Mony et al. 2020), in turn affecting organic matter decomposition, soil fertility, nutrient acquisition by plants, and plant health.

We contend environmental heterogeneity is more likely a key driver of weed diversity *in field cores*, as opposed to plant spillover, especially when landscape effects do not depend on field-scale management intensity (Section 4.2). Environmental heterogeneity probably helps preserve a wider range of life strategies among the subset of weed species that survive local intensive practices. Seiferling et al. (2014) revealed that an increase in environmental heterogeneity is particularly beneficial for biodiversity in highly disturbed and homogenized ecosystems, such as agroecosystems. In arable fields, higher environmental heterogeneity would increase resource opportunities in a similar way (regardless of the field-scale management intensity). Understanding the balance between the processes related to environmental heterogeneity and plant spillover along field- and landscape-scale management gradients should provide key insights for the successful implementation of AWM (see Section 7).

7 Implications of landscape-scale change for agroecological weed management

7.1 From observation of landscape gradients in space to monitoring of landscape diversification in time

Our review is based on studies that compare weed communities in contrasted landscape contexts or along continuous gradients of landscape heterogeneity. However, we are

unaware of any study that properly measured the effects of landscape *diversification* on weed communities, i.e., starting from a simplified landscape and adding heterogeneity for example by planting/restoring semi-natural habitats or diversifying farming practices. Current knowledge is thus limited by the space-for-time substitution approach (Pickett 1989), and it remains unknown whether a strategy of landscape diversification (e.g., increasing configurational heterogeneity over time) would yield equivalent results to the comparison between simple vs complex landscapes (spatial variation). Therefore, while our review provides evidence that weed diversity is often higher in landscapes with higher habitat diversity, edge density, crop diversity, organic farming cover, or lower field size, it does not guarantee that landscape-scale change will increase weed diversity, nor does it provide information on the time scale needed to induce changes. Observed effects of landscape on weed communities could theoretically be due to confounding factors such as different past land use in each landscape affecting, for example, the size and composition of the regional species pool. Pickett (1989) concluded that space-for-time substitution is irrelevant where the past has had unsuspected effects and that analysis of the influence of past environments or prior system status is needed to justify this approach. This also raises the question of the resilience of weed communities to decades of agricultural intensification; Are soil seedbanks depleted? Can landscape extensification, through natural pathways, help restore the weed flora and its ecological functions?

We identify two complementary approaches to overcome the limitations of the space-for-time substitution approach. First, studies should be designed to quantify the relative importance of the different processes underlying landscape effects (see Section 6). This would ensure that our interpretations are correct, and that observed landscape effects are not solely due to unknown confounding factors. Such knowledge should also help inform landscape-scale management strategies/guidelines at the appropriate spatiotemporal scales. Secondly, integrated landscape approaches are increasingly being promoted through science, policy, and the donor community (Reed et al. 2021). Integrated landscape approaches are promising pathways for reconciling agriculture, conservation, and other competing land uses, for example, water management or climate change mitigation (Landis 2017; Sayer et al. 2013). These approaches consist of involving all relevant stakeholders, determining realistic strategies to promote sustainable management and multifunctionality of the landscape, and resolving conflicts between the various stakeholders and inhabitants of the landscape. Importantly, these approaches facilitate the mutual exchange of knowledge between researchers and farmers and open the door to farmer-led solutions that could speed up innovation and

implementation of agroecology (Bohan et al. 2022). The implications of these integrated landscape approaches for weed management are currently unexplored but could be better understood by monitoring the response of weed communities within these initiatives implemented at the landscape scale. While it may be that the regulation of weed communities is not the primary driver of landscape-scale interventions, this new knowledge will complement examples of successful landscape-scale management of diseases, natural enemies of crop pests, or pollinators (Hannachi and Martinet 2019; Jeanneret et al. 2021; Petit et al. 2020) and allow the response of weed communities to further inform management plans.

7.2 From field-scale to collective management

As modern agriculture developed, policymakers, agronomists, and farmers focused largely on the cultivated areas of the farm and its productivity, without much regard for impacts on or from surrounding land uses. Consequently, individual fields have become the “traditional” management units, on which it is easier to implement AWM. Increasingly, however, the uncropped areas of the farm are also being managed to promote biodiversity conservation and ecosystem service provision (Jones et al. 2016). This generally involves habitat creation for the support of target taxa (for example, farmland birds or pollinators) as part of subsidized agri-environment schemes. Adapting these interventions based on an understanding of the impacts on the crop production system (including the regulation of weed communities) is currently a minor consideration when designing farm management plans. A better knowledge of the different ecological processes reviewed here would be beneficial in guiding decisions on the type and placement of habitat creation in the landscape to regulate weed communities in more natural ways (Fig. 7). For example, landscape planning and conservation efforts could pay special attention to habitats that promote abiotic and biotic environmental heterogeneity (e.g., hedgerows and woodlots) or establish open and moderately-disturbed habitats (e.g., conservation headlands) as refuges for weed populations in regions with depleted weed species pools. From an agronomic perspective, the diversification of crops and associated farming practices (tillage, sowing date, and fertilization) at the landscape scale seems promising, as it could increase biotic environmental heterogeneity, reduce the dominance of most competitive weeds, and limit the risk of weed colonization between crop fields (Dornelas et al. 2009; Mahaut et al. 2019; Sirami et al. 2019; Vasseur et al. 2013).

Importantly, several authors have argued that expanding in-field agroecological solutions at the farm or landscape scale, while a step forward, may not be sufficient to achieve expected results (sustainable agriculture,

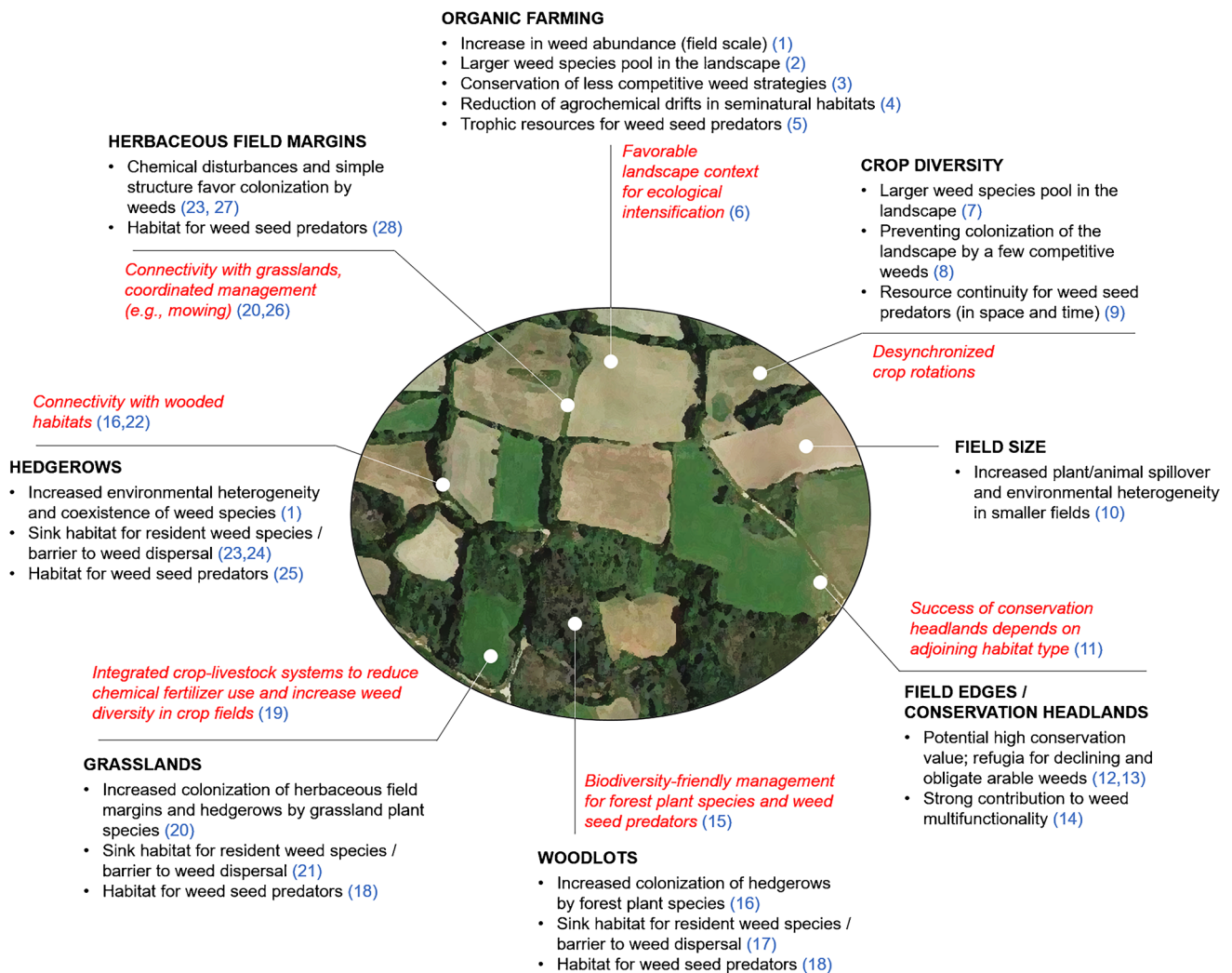


Fig. 7 An example of landscape-level thinking for agroecological weed management based on potential beneficial or detrimental functions of habitats that compose the landscape. Coordination and collaboration between farmers and other stakeholders (highlighted in red) are likely necessary because habitats are interdependent; management practices in one habitat can affect ecological functioning in another habitat. Such representation can help identify potential synergies and trade-offs between the objectives of different stakeholders (e.g., farmers, forest managers, local municipalities, and citizens). There are likely many points of congruence between agroecological weed management and other related objectives, such as biodiversity conservation or more specifically the promotion of pol-

linators and natural enemies of agricultural pests ((1) Boinot et al. 2022; (2) Henckel et al. 2015; (3) Chamorro et al. 2016; (4) Boinot and Alignier 2022; (5) Diekötter et al. 2016; (6) Fusser et al. 2018; (7) Sirami et al. 2019; (8) Dornelas et al. 2009; (9) Raderschall et al. 2022; (10) Fahrig et al. 2015; (11) Metcalfe et al. 2019; (12) Fried et al. 2009; (13) Albrecht et al. 2016; (14) Yvoz et al. 2022; (15) Hertzog et al. 2021; (16) Lenoir et al. 2021; (17) Devlaeminck et al. 2005; (18) Perrot et al. 2021; (19) MacLaren et al. 2019; (20) Smart et al. 2002; (21) Ricci et al. 2018; (22) Boinot et al. 2023; (23) Boinot and Alignier 2023; (24) Wilkerson 2014; (25) Graham et al. 2018; (26) Kirmer et al. 2018; (27) Fried et al. 2018; (28) Labruyere et al. 2016).

biodiversity conservation, and associated ecological functioning). Coordinated or even collaborative approaches across ownership boundaries are probably necessary (Cong et al. 2016; Landis 2017; Marrec et al. 2022; Prager 2015; Vialatte et al. 2019). This certainly holds for landscape-scale AWM and the potential levers highlighted in our review (based on the space-for-time substitution approach), as habitats and their functioning are interconnected (Fig. 7). For example, conversion to organic

farming could be more challenging if the field under conversion is embedded in an unfavorable landscape context that prevents the ecological intensification needed as an alternative to agrochemicals (Fusser et al. 2018). Diversifying in-field crop rotation does not guarantee that crop rotations are desynchronized at the landscape scale, which would increase both spatial and temporal crop diversity, along with weed diversity (Fahrig et al. 2015; Martin et al. 2020; Sirami et al. 2019) and resource continuity for

ecosystem-service providers (Iuliano and Gratton 2020; Raderschall et al. 2022). Finally, landscape-level thinking is required to establish/maintain connectivity between semi-natural habitats and promote their colonization by non-weedy plant species (Lenoir et al. 2021; Smart et al. 2002).

It is beyond the scope of this review to identify all barriers to the implementation of coordinated or collaborative landscape-scale management, which would have an impact on weed diversity as one component of more sustainable systems. Nonetheless, we can mention that barriers are of various kinds; political, economic, scientific, sociological, and psychological. Notably, decades of research, development, and lobbying in favor of chemical-based and intensive agriculture have led to the dominance of the agrochemical paradigm, individual field-scale management, path dependence, and lock-in (Cowan and Gunby 1996; Magrini et al. 2019; Meynard et al. 2018). Current state regulatory tools hamper the innovative capacities of the farmers. Industrial supply chains are strongly organized around standards, and there is an insufficient market for niche crops. Difficulty in identifying or understanding collective interests, unequal gains from coordination between farms, along with uncertainty, and lack of scientific knowledge and technical extension also hinder the implementation of agroecological practices and landscape-scale management (Bareille et al. 2020; Hannachi and Martinet 2019; Labarthe 2009). Improved incentives from public authorities could help farmers who share a common agroecological objective, for example, non-individual incentives conditional on achieving a collective objective to increase group coordination and eventually bring neighbors in (Villamayor-Tomas et al. 2019). Agglomeration bonus (i.e., additional payment if parcels are contiguous) could also improve territorial integrity (Kuhfuss et al. 2022). Most importantly, researchers need to work with policymakers and funding agencies to develop programs that support long-term and integrated landscape research, which is a promising approach to promote knowledge exchange between stakeholders, adaptation to specific contexts, and conflict resolution (Landis 2017; Petit et al. 2023).

8 Conclusion

As a result of agrarian individualism and the development of the agrochemical paradigm, weed management (even agroecological) largely focuses on field-scale farming practices and their effects on weed abundance and weed-crop competition. However, with the emerging view that weed diversity and composition are key drivers of the sustainability and multifunctionality of agroecosystems, consideration of the

landscape should gain importance. Our review shows that the landscape context can affect weed diversity and composition in many ways, but there is a knowledge gap about the ecological processes underlying landscape effects. Understanding the mechanisms driving weed community assembly is necessary to elucidate the contrasting associations observed between landscape and weed community properties and provide relevant landscape-scale management guidelines. Moreover, research on weed-landscape ecology is still exclusively based on the space-for-time substitution approach. Landscape-scale weed management—based on landscape diversification—remains unexplored and would require coordination between farmers and other stakeholders. In this respect, integrated landscape approaches should make it possible to test new and ambitious ways of sustainably managing weeds, complementing innovations at the field scale. To conclude, most studies we found are from Europe, which likely reflects the greater policy emphasis on agri-environment schemes. There is a need to expand research on weed-landscape ecology worldwide to facilitate the production of knowledge and the implementation of more sustainable weed management practices.

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Authors' contributions AA, JS, and SB conceived the ideas and designed the methodology. SB collected and analyzed the data and led the writing of the manuscript. AA and JS contributed to the drafts. All authors gave final approval for publication.

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Declarations

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