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REVIEW ARTICLE

Potential of service plants for regulating multiple pests while limiting disservices in agroecosystems. A review

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Abstract

Service plants are primarily used in agroecosystems to provide ecosystem services that are not directly marketable. They are a promising option to promote biological pest regulation. Past studies have demonstrated their usefulness for regulating one pest category (either pathogens/parasites, herbivores or weeds). However, a multi-pest view of the role of service plants, including the potential disservices (negative impacts) that they may generate, is lacking. Such an overview is essential to meet the challenge of agroecology. This paper aims to fill this gap. Here, a trait-based approach was used to provide an overview of the potentialities of service plants, (inserted either in intercropping, in rotation with the crops, or in field edges) for regulating multiple pests, while limiting disservices. For that purpose, we first laid the foundation of a conceptual framework by synthesizing the mechanisms and service plant traits involved in the regulation of each pest category and in the mitigation of each disservice. On this basis, we analyzed (1) the compatibility in the regulation of the different pests by service plants, and (2) the compatibility between multi-pest regulation vs disservice mitigation. Our main conclusions are: (1) Despite knowledge gaps, there is good potential of service plants for multi-pest regulation; (2) The challenge lies at least as much to mitigate disservices that service plants may cause as to promote multi-pest regulation; (3) The level of incompatibility between promoting multi-pest regulation vs mitigating disservices varies with the mode of insertion of service plants, increasing with interactions with crop plants. This review shows how a trait-based approach can be used to synthesize knowledge from different disciplines and provides a tool for cross-disciplinary dialogue. It identifies priority research actions that are needed to increase synergy, genericity and adaptation of service plants to local conditions, and provides foundations for the design of service-plant based agroecosystems.

Keywords Weed · Arthropod pest · Soil-borne pest · Aerial pathogen · Disservice · Edge · Rotation · Intercropping · Companion plant · Cover crop

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1 Introduction

Pathogens, herbivores and weeds (here collectively referred to as pests) can greatly reduce crop yield and harvest quality (Oerke 2006; Savary et al. 2019; Deutsch et al. 2018). That is why synthetic pesticides generally play a key role in ensuring crop productivity in conventional cropping systems. However, reducing the use of pesticides has become necessary in view of their harmful effects for the environment and public health (Tang et al. 2021; Sabarwal et al. 2018) and pest resistance to pesticides (Ma et al. 2021; Hawkins et al. 2019). Alternatives to synthetic pesticides are needed to increase the sustainability of cropping systems. Since no alternative method is individually as efficient as pesticides, judiciously combining solutions is necessary to tackle this challenge (Liebman and Gallandt 1997), as proposed in integrated pest management and agroecological crop protection strategies (Ehler 2006; Deguine et al. 2023). The combination of solutions with partial effects on pests is particularly relevant, as pest presence at low densities does not necessarily cause crop yield losses and some of them, such as weeds, can play a positive role for beneficial insects (e.g., natural enemies and pollinators). Therefore, the goal is not to eradicate pests but rather to regulate the most harmful ones (Yvoz et al. 2021; Marshall et al. 2003; Esposito et al. 2023).

Plant diversification (Jacquet et al. 2022; MacLaren et al. 2022; Tamburini et al. 2020; Vialatte et al. 2021; Isbell et al. 2017; Bommarco 2024) and, especially, the use of service plants/crops (Garcia et al. 2018; Gardarin et al. 2022), is a promising option to promote biological pest regulation. Contrary to cash crops, service plants are primarily introduced in the agroecosystem to provide ecosystem services that are not directly marketable (i.e., differing from food, feed, fiber and fuel production), such as soil fertility, carbon sequestration, biodiversity conservation or pest regulation. Service plants/crops can be sown/planted as mono- or multi-species cultures. They can be used (1) in field edges (e.g., flower strips, hedges) or within the field, for example (2) in intercropping (e.g., legume service plants intercropped with oilseed rape or wheat crops (Verret et al. 2017); cover crops in vineyards (Garcia et al. 2018; Cabrera-Pérez et al. 2024)) or (3) in rotation with cash crops during the fallow period (Rouge et al. 2022), with diverse modalities of insertion (e.g., service plants in intercropping may be present during the full or part of the crop growth cycle) (Gardarin et al. 2022; Petit et al. 2018) (Fig. 1). Depending on the targeted ecosystem services and how they are introduced in the cropping systems, service plants have been given different names in the literature, e.g., cover plants/crops (Couedel et al. 2019), companion plants/crops (Ben-Issa et al. 2017), secondary plants/crops (Parolin et al. 2012), subsidiary plants/crops (Reimer et al. 2019), biocontrol plants (Parolin et al. 2014), trap plants/crops (Shelton and Badenes-Perez 2006) and non-crop plants (Balzan et al. 2016). Here, we have chosen to use the term 'service plants' in order to emphasize the fact that these plants provide ecosystem services (excluding production), with a particular focus on the service of pest regulation.

Service plants are generally used by farmers to provide services related to nutrient and soil management (such as reducing nitrate leaching, providing green manure and improving soil structure) (Kaspar and Singer 2011). However, there is a potential to promote pest regulation services. Indeed, many studies on the role of service plants for pest regulation have demonstrated their usefulness for regulating pests, and especially one category of pests, i.e., either pathogens (Karakas and Bolukbasi 2019), herbivores (e.g., Rhino et al. 2016) or weeds (e.g., Verret et al. 2017). However, meeting the challenge of agroecological transition definitely

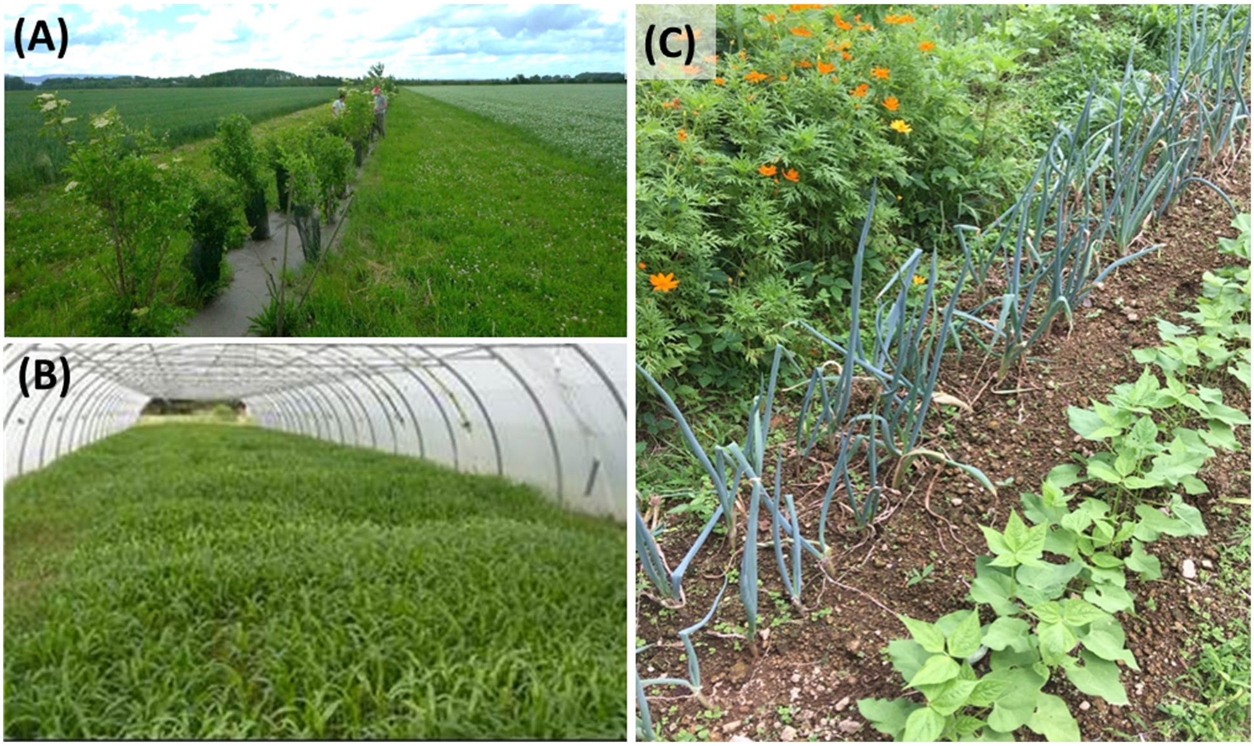
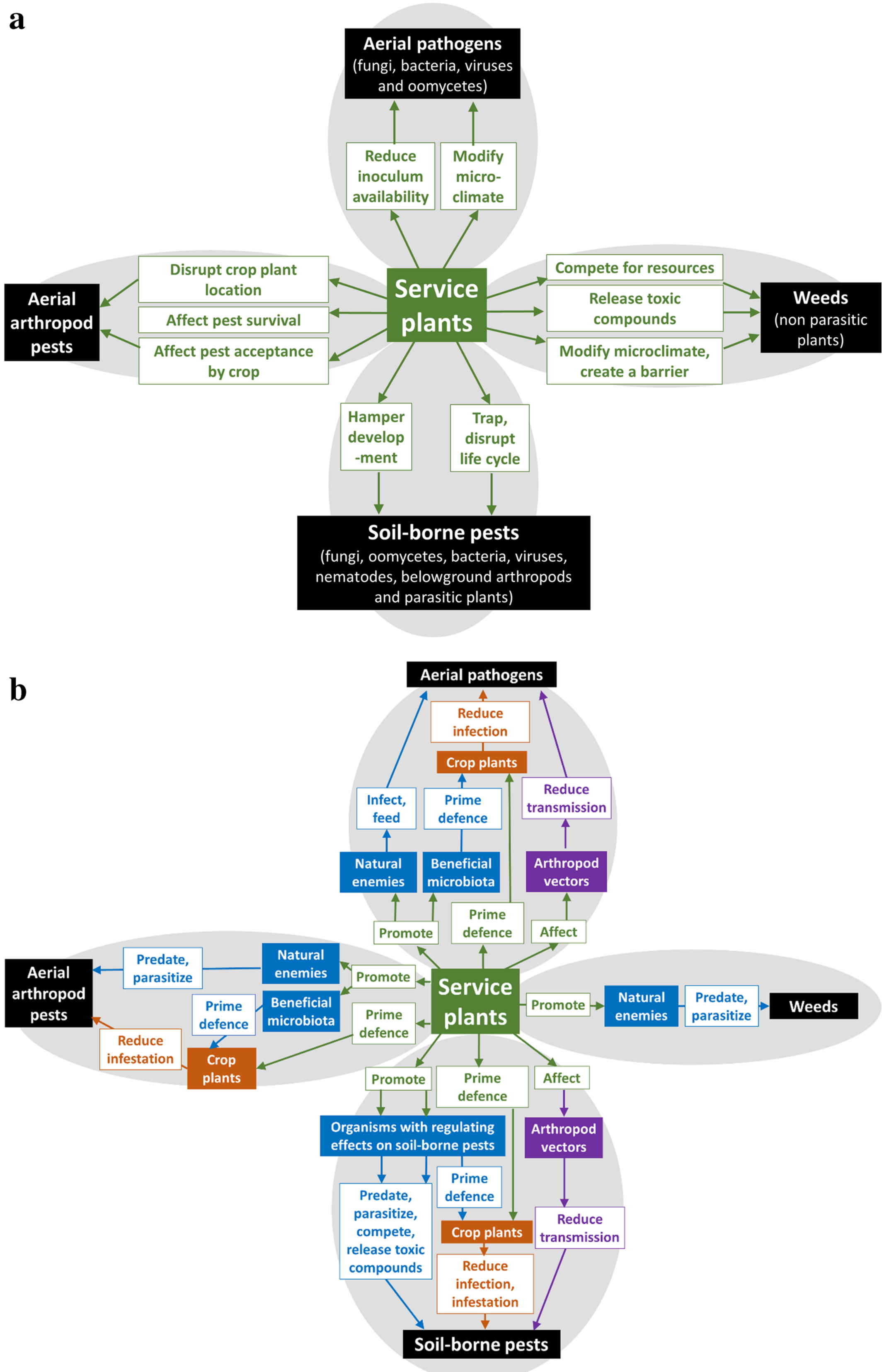


Fig. 1 Different modes of insertion of service plants in agroecosystems: **A** in field edges, or within the field **B** in rotation or **C** in intercropping with the crops. **A** Multi-species hedge recently planted at the INRAE experimental site in Bretenière (France), **B** 3-week-old forage sorghum (*Sorghum sudanense* cv. Piper) under tunnel in the South of France before burial, in rotation with the crops, to fight against root-knot nematodes and **C** Cosmos (*Cosmos sulphureus*) and chives (*Allium fistulosum*) as service plants intercropped with cucumber to control herbivores and enhance mycorrhizal networks (EARL Les Oliviers, Le Lorrain, Martinique). Photocredit: Frédéric Suffert, Claire Goillon, Marie Chave and Metty Trebeau.

requires a multi-pest view of the role of service plants in order to (1) ensure compatibility (e.g., check that the service plants that are used for regulating one pest category do not promote others) and (2) valorize complementarities (e.g., in case of multiple options when implementing service plants, choose options allowing for multi-pest regulation).

Only few original research-in-field studies have provided evidence for the simultaneous regulation of several pest categories by service plants. For example, a suppressing role of cover crop mulch was identified on both weeds and insect pests (Mangan et al. 1995; Pullaro et al. 2006). Also, marigold (genus *Tagetes*), intercropped with tomato crop, showed a multi-pest effect by regulating simultaneously nematodes (i.e., parasites), sap-feeders (i.e., insect pests) and pathogens (Zavaleta and Gómez 1995). In parallel, compiling results from different studies allows identifying plant species or botanical families with a high potential to be used as service plants for multi-pest regulation. For instance, forage sorghums used as cover crops were shown to be biofumigant plants with nematicidal, insecticidal and fungicidal actions as well as inducing crop defenses and recruiting beneficial microorganisms (Quaranta 2009). A review paper has also identified Brassicaceae (intercropped or not with Fabaceae) cover crops as having a potential to simultaneously regulate weeds, insects and pathogens (Couedel et al. 2019). While these papers illustrate potentialities of service plants for multi-pest regulation in different types of cropping systems, knowledge is still too fragmentary to provide a generic and integrative overview. Indeed, past studies have seldom considered non-parasitic weeds, herbivores and aerial and telluric pathogens/parasites simultaneously. In addition, they can be viewed as case studies as they have focused on particular (1) service plant species or botanical families (e.g., Brassicaceae in Couedel et al. 2019), or (2) modes of insertion of service plants (e.g., cover crops during the fallow period in Couedel et al. (2019) and Médiène et al. (2011) or in intercropping in Gardarin et al. (2022)) or (3) cropping systems (e.g., banana in Damour et al. (2015) or vineyards in Garcia et al. (2018)) or (4) growing conditions (e.g., tropical climate in Ratnadass et al. (2021)). Moreover, few past studies have considered the potential negative impacts (i.e. disservices in Zhang et al. 2007) that service plants may generate on crop production (e.g., competition for resources with crop plants and promotion of other pests). Finally, results from in-field studies are strongly dependent on the context (such as soil, climate, pest pressure or type of cropping system), limiting their genericity.


a
Aerial pathogens
(fungi, bacteria, viruses and oomycetes)
Reduce inoculum availability
Modify micro-climate
Service plants
Aerial arthropod pests
Disrupt crop plant location
Affect pest survival
Affect pest acceptance by crop
Compete for resources
Release toxic compounds
Modify microclimate, create a barrier
Weeds
(non parasitic plants)
Hamper develop-ment
Trap, disrupt life cycle
Soil-borne pests
(fungi, oomycetes, bacteria, viruses, nematodes, belowground arthropods and parasitic plants)
b
Aerial pathogens
Reduce infection
Crop plants
Infect, feed
Prime defence
Reduce transmission
Natural enemies
Beneficial microbiota
Arthropod vectors
Promote
Prime defence
Affect
Aerial arthropod pests
Predate, parasitize
Natural enemies
Promote
Prime defence
Beneficial microbiota
Reduce infestation
Crop plants
Prime defence
Service plants
Promote
Natural enemies
Predate, parasitize
Weeds
Promote
Prime defence
Affect
Organisms with regulating effects on soil-borne pests
Arthropod vectors
Predate, parasitize, compete, release toxic compounds
Prime defence
Crop plants
Reduce transmission
Reduce infection, infestation
Soil-borne pests

◂**Fig. 2** Mechanisms involved in the regulation of pests by service plants. **A** Direct mechanisms (i.e., directly targeting the pest) and **B** indirect mechanisms (i.e., targeting the pest through the mediation of other organisms). The action of service plants (in green), natural enemies and beneficial microbiota (in blue), vectors (in purple) and crop plants (in orange) is shown. For soil borne-pests, the generic term 'organisms with regulating effects' includes natural enemies and beneficial microbiota.

Our aim was to determine to what extent service plants can provide a relevant option to promote multi-pest regulation, while limiting potential disservices. Addressing this question is crucial for agroecological transition. Given the taxonomic and functional diversity of pests (e.g., plants, arthropods, fungi and nematodes) and regulation mechanisms involved (competition, predation and parasitism), and the diversity of the academic disciplines concerned (e.g., pathology, entomology, weed science, biology, ecology and agronomy), developing a conceptual framework appeared as a prerequisite. Trait-based approaches, originally developed in the field of comparative functional ecology, are powerful tools to provide generic knowledge (Lavorel et al. 2007). Traits (i.e., morphological, anatomical, physiological or phenological features measurable at the individual level) can be used as proxies for characterizing a large diversity of plant species regarding their functioning and effects on ecosystems (Violle et al. 2007; Wood et al. 2015). Initially used in natural ecosystem studies, trait-based approaches have been successfully applied to agroecosystems not only to understand interactions between organisms but also to provide guidelines to design pest regulation strategies (e.g., arthropod pests in Gardarin et al. (2018), or weeds in Tardy et al. (2015) and Tardy et al. (2017)). They were for example used to guide the choice of adequate plant species/varieties or the design of adequate species/variety mixtures in order to deliver single or multiple ecosystem services (Barot et al. 2017). A strength of trait-based approaches is their genericity, which makes them applicable to diverse crop types (i.e., arable crops, vegetable crops, fruit tree production, horticulture…), cropping systems and environmental conditions.

Based on such trait-based approach, we provide here an integrative and mechanistic overview of the potential of service plants for multi-pest regulation, while limiting disservices. To this end, the following research questions were addressed:

(1) Are there service plant traits involved in the regulation of several pest categories (weeds, arthropods, soil-borne pests, aerial pathogens)? Or is the regulation of each pest driven by different service plant traits (e.g., flower color is involved in the regulation of arthropods only, and plant height in the regulation of weeds only)?
(2) In case a given service plant trait is involved in the regulation of several pest categories, are there compatibilities or incompatibilities among pests? For example, in case 'plant height' is involved in the regulation of different pest categories: is the regulation of each pest promoted by a tall service plant (compatibility)? Or are some pests regulated by tall service plants while others by short ones (incompatibly)?
(3) Which combinations of service plant traits could theoretically promote multi-pest regulation? Here, we raise the question of the ideal service plant characteristics for multi-pest regulation.
(4) Are these service plant trait combinations, identified as favorable to multi-pest regulation, consistent with a limitation of the disservices by service plants?

A two-step approach was conducted. The first step laid the foundation of the conceptual framework by synthesizing, independently for each pest category, the regulation mechanisms and service plant traits affecting pest regulation. The main mechanisms and service plant traits affecting the potential disservices generated by service plants were also synthesized. The second step used the conceptual framework to address the research questions above. Based on the results of this trait-based analysis, we discuss to which extent cropping practices can be used to improve synergies while managing potential incompatibility.

2 Mechanisms and service plant traits involved in pest regulation and disservice mitigation

2.1 Pest regulation

Four categories of pests were considered hereafter. They were chosen to group together pests that can be regulated by service plants through the same mechanisms/traits. The four categories were (1) weeds (corresponding here to non-parasitic plants), (2) aerial arthropod pests, (3) soil-borne pests (including fungi, oomycetes, bacteria, protozoa, viruses, nematodes, belowground arthropods and parasitic plants) and (4) aerial pathogens (including fungi, bacteria, viruses and oomycetes).

To build our framework, we first synthesized the mechanisms involved in the regulation of each pest category by service plants (Fig. 2). Both direct (i.e., directly targeting the pest) and indirect (i.e., targeting the pest through the mediation of an intermediate organism) mechanisms were considered. For indirect mechanisms, natural enemies of pests (i.e., biological control agents), beneficial microbiota or the crop plant itself were considered as possible intermediate organisms.

We then synthesized knowledge on the main service plant traits affecting these mechanisms, considering traits related to morphology and growth, chemistry, phenology and reproductive organs. The traits are summarized in Supplementary material 1 to Supplementary material 4 for each pest category. The ideal traits of service plants for pest regulation were thought theoretically, i.e., without considering how to implement service plants in the field (e.g., which service plant species/genotypes to use, mono- or multi-species culture or which relative densities?) to reach this ideal service plant profile. The question of service plant implementation in the field is discussed in Sect. 4.

2.1.1 Weeds

Weed regulation by service plants involves both direct and indirect mechanisms (Fig. 2). Except predation that may occur also when service plants are in field edges, all the other mechanisms require service plants to be inside the field (in intercropping or in rotation with the crop). Weed regulation by competition and predation requires alive service plants, but the other mechanisms may also occur with service plant residues (e.g., mulch).

Direct mechanisms Service plant can directly regulate weeds by competing for resources, releasing toxic compounds, modifying microclimate and/or creating a barrier (Fig. 2A).

To compete for resources Competition for resources (light, nutrients, water) is the most frequently cited and studied mechanism underlying weed regulation by service plants (Colbach et al. 2023). It occurs when service and weed plants share a common resource pool, in space and time, that is insufficient to fulfil the requirements of all the plants (Zimdahl 2004). As light is unidirectional, it is generally the main limiting resource in plant canopies, and plays a key role in interactions between service plants and weeds (Wilson and Tilman 1993). However, competition for soil resources (especially water and nitrogen) may become more and more important nowadays due to (1) climate change (reduced rainfall and increased needs due to warming) and (2) transition towards cropping systems reducing the use of mineral nitrogen fertilizer.

Consequences of competition on weeds mainly include a reduction of plant growth and/or seed production (Petit et al. 2018).

The traits of service plants driving competition involve (Supplementary material 1): (1) the phenology of the service plants (relatively to that of weeds) that determines the growing period over which plants coexist (weed regulation is much stronger when service plants emerge earlier than weeds; Knezevic et al. (2017)), and (2) the dynamics in space and time of above- and belowground growth and morphology of service plants (relatively to that of weeds) that determine their capacity to access resources (Petit et al. 2018). Generally, service plants outcompete weeds when they exhibit a higher growth rate, with aboveground a more rapid soil covering (in width and height) and a large leaf area, and belowground a more rapid soil colonization (in width and depth), a higher density of fine roots (involved in resource uptake) and a stronger capacity for resource uptake (especially for resources that are crucial for weed growth). The magnitude and outcome of the competition by service plants over weeds are mitigated by the capacity of weed plants to avoid and/or tolerate resource limitation (Gommers et al. 2013).

The effect of service plant competition on weed regulation is strongly dependent on management practices applied to service plants, cropping systems and pedoclimate. This effect was attested in the field, but it was mostly assessed on the short-term, i.e., during the service plant cycle (Petit et al. 2018). Quantification on the longer term (in following crops, and at the crop succession level) remains scarce (e.g., Hodgdon et al. 2016; Rouge et al. 2023). The few studies on service plant used in the fallow period show that their effects on the weed flora are much lower than those of tillage and chemical weeding. The effects of service plants on weeds are much more visible in no-till and especially low-input situations. Crop rotation also plays a key role.

To release toxic compounds Weed regulation via the release of secondary metabolites by other plants is commonly named allelopathy. Metabolites involve a large range of molecules that can be liberated from alive plants by leaching of foliage by rain, volatilization from foliage (volatile organic compounds, i.e., VOC) or root exudation. These molecules can also be liberated from the decomposition of plant residues (Tukey 1969).

Consequences on weeds include reduction of weed seed germination, weed growth and/or seed production (Zhang et al. 2021).

Related service plant traits involve the nature of the released metabolites (including their toxicity) and the intensity of their emission. This intensity depends on the size of plant compartment emitting them (e.g., either aboveground biomass for allelopathy generated by foliage leaching, VOC emissions and plant residues, or root colonization/biomass/density in case of root exudation) (Supplementary material 1). Even if the metabolite concentration may be lower in plants with a higher biomass (no linear relationship between biomass and secondary metabolite production) and could depend of the plant phenology, it is generally assumed that the higher the biomass of a plant at a given growth stage, the greater the amount of compounds emitted (Koricheva 1999).

The effect of allelopathy by service plants also depends on the sensitivity of targeted weeds to metabolites (depending weed species and stage).

Service plant management, in interaction with soil and climate, can modulate the effect of allelopathy on weed regulation. Despite the abundant literature on the effect of crop allelopathy on weed regulation, field-based evidence is still very rare due to difficulties to disentangle allelopathy from competition effects (Mahé et al. 2022). In most in-field studies on allelopathy, the role of crop competition is disregarded or not exhaustively studied, preventing to prove whether weed regulation is due to allelopathy and/or competition (Mahé et al. 2022). Concerning the effects of allelopathy mediated by crop residues, the challenge lies in disentangling them from the effects of nitrogen immobilization generated by crop residue decomposition (Doré et al. 2004).

To modify microclimate and create a barrier effect Service plants can regulate weeds by modifying the microclimate (light, water, temperature). Indeed, the presence of service plants (either as alive plants or residues) within the field may affect soil-water availability, restrict soil-temperature fluctuation, reduce light quantity and modify light quality (red:far red ratio) at the soil surface (Cordeau et al. 2015; Kruk et al. 2006). The presence of service plants can strongly affect weed seed germination because (1) all weed species require water for germination (Guillemin et al. 2013), (2) most of them also require a light stimulus (Gardarin and Colbach 2015) and (3) the germination of some of them is sensitive to light quality (Kruk et al. 2006). When they form a mulch of residues, service plants can also regulate weeds by acting as a physical barrier affecting weed emergence (Teasdale and Mohler 2000).

For alive service plants, key traits are related to the dynamics in space and time of leaf area production (determining light interception and plant water demand) and therefore refer to plant morphology, growth and phenology (traits are similar to those involved in competition; Sect. "To compete for resources"; Supplementary material 1). Root growth and water uptake by service plants can also be influent by affecting soil water fluxes and therefore weed germination. For service plant residues, the amount of biomass produced is a key trait affecting both mulch thickness and density (Teasdale and Mohler 2000). However, these effects of service plants on weed regulation by microclimate modification and barrier effect depend on weed traits (e.g., germination date, capacity to emerge from the mulch…). These effects can also be modulated by service plant management in interaction with soil and climate. In-field studies characterizing the microclimate modifications generated by a mulch show that a mulch of residues can significantly reduce the number of emerged weed seedlings and also delay emergence (Teasdale and Mohler 2000). However, the effects of service plants through modifications of the microclimate or barrier effects may be complex to characterize in the field due to the difficulty to disentangle them from the effects of other mechanisms.

Indirect mechanisms: to promote natural enemies Service plants can promote the presence of natural enemies predating/parasitizing weeds (Fig. 2B).

Weed predation occurs mostly post-dispersal and depletes a proportion of the weed seed rain before it returns to the soil seedbank (Davis et al. 2011). Seed predation could deplete preferentially some weed species, depending on predator preferences. Stands of dense vegetation (with a large leaf area) are favorable to seed predation because they provide suitable microclimate and/or shelter to many seed-eating organisms and even alternative resources. Traits of service plants enhancing weed predation thus involve aboveground morphology and growth, as well as phenology (the key traits are similar to those involved in competition; Sect. "To compete for resources"; Supplementary material 1). Also, we hypothesize that using service plants with diverse traits related to flowers and seeds (e.g., both small and large flowers/seeds) can be useful to promote a diversity of predators that may have different requirements, and therefore to promote weed seed predation. Predation is very dependent of service plant management and cropping systems (e.g., tillage is detrimental to most seed-eating organisms, notably carabid beetles and rodents). Field-based evidence that weed seed predation is a generic and widespread process in all agroecosystems is now readily available. In contrast, evidence that this process leads to an effective regulation of weeds remains scarce (but see Bohan et al. 2011; Carbonne et al. 2020).

Service plants can also promote weed parasitism. Indeed, plant canopies modify the microclimate close to the soil surface (Sect. "To modify microclimate and create a barrier effect"), potentially enhancing microbial populations (Doran 1980; Hartwig and Ammon 2002). A few articles showed that some microbial communities associated with plant residues left on soil surface have a parasitic activity on weeds (Conklin et al. 2002; Kumar et al. 2008). However, to our knowledge, no articles have described an increased parasitic activity with living cover crops. Little is known about the specific traits of service plants promoting weed regulation by parasitism. Since the underlying mechanisms involve microclimate modification, the underlying aboveground plant traits can be assumed to be similar to those described for microclimate modification and barrier effect (Sect. "To modify microclimate and create a barrier effect") (Supplementary material 1). We hypothesize that a low root density of service plants in the top soil layers could limit drying the upper soil layers and therefore promote pathogenic micro-organisms. Service plant management in interaction with soil and climate can modulate these effects. To date, we are still lacking field-based evidences that weed regulation by service plants due to parasitism promotion is a generic and widespread process (Cook 2001).

Compatibility between regulation mechanisms To what extent canopies of service plants that are effective in promoting weed regulation by competition (the main weed regulation mechanism) can also promote other mechanisms (e.g., production of toxic compounds or predation) is still an open question. However, a rough analysis of the service plant traits involved in the different mechanisms of weed regulation rather suggests complementarities (see boxes in green in Supplementary material 1 showing no incompatibility in service plant features for most several trait categories). Indeed, service plants with a rapid growth above- and belowground are expected to promote weed regulation by competition, modification of microclimate, formation of a physical barrier, predation and parasitism. They are also expected to promote weed regulation by production of toxic compounds, provided that they produce secondary metabolites that affect the weed plants in the field.

2.1.2 Aerial phytophagous arthropod pests

Aerial arthropod pests are responsible for important crop yield losses because of their direct phytophagous action (either at the adult or the larval stage or both) on crop plants, and/or their ability to vector pathogens and other pests (Sect. 2.1.3 and 2.1.4). Service plants can thus be used both for their direct and indirect effects on arthropod pests (Fig. 2). Different modes of insertion of service plants (in intercropping, or in rotation with the crop, or in field edges) can be chosen to regulate arthropod pests, depending on the targeted mechanism. In most cases, alive service plants rather than their residues are involved in arthropod pest regulation.

Direct mechanisms Direct effect of service plants (Fig. 2A) has been nicely reviewed by Parker et al. (2013) and occurs at three steps of the pest life history: plant host location, survival and reproduction.

To disrupt crop plant location by arthropod pests The choice of a suitable host plant by phytophagous arthropods is essential for their survival and reproduction. This choice is based on different physical and chemical signals produced by the host crop plant that can be modified by service plants. Host plant choice involves different behavioral sequences taking place at different scales (ranging from the plant to the landscape). At long distance, service plants can emit VOC or present visual characteristics such as color that are more attractive than the ones of the crop plant and lure the arthropod pests away (Supplementary material 2). Such service plants are often referred to as 'pull' or 'trap' plants (if arthropod pests cannot survive on them). Service plants can also emit VOC that repel the arthropod pest or chemically mask the crop, as 'push' plants. Masking can also be achieved through physical traits affecting service plant size and aboveground architecture, leading to a visual camouflage of the crop plant. Besides masking, service plants can also be used to block arthropod pest movement and restrict access to the crop plant.

Traits of service plants disrupting crop plant location thus involve aboveground morphology and growth (e.g., leaf biomass), color of vegetative aboveground parts, and emission of constitutive or induced VOC (Supplementary material 2). Depending on whether VOC emitted by vegetative or reproductive organs are involved, timing of plant reproduction can be essential for effect on arthropod pests.

Spatial arrangement of such service plants in and around the crop plants plays a key role in their effectiveness. Service plants trapping or blocking arthropod pests are usually placed on field edges, while service plants that repel arthropods or mask crop plants are often closely intercropped with them within the field.

To reduce pest survival Phytophagy is very common in arthropods and many plants have coevolved with phytophagous arthropods and developed adaptations to alter survival of these herbivores. The production of secondary compounds that are toxic, unpalatable or sticky, or that reduce digestibility are examples of such adaptations (Supplementary material 2). Such compounds can make service plants highly attractive to female arthropods by stimulating oviposition while killing their offspring. These service plants reducing pest survival are called 'dead-end trap' plants and can be intercropped with the crop or in field edges.

To reduce crop plant acceptance and pest reproduction At the short distance (i.e., when the pest is in close vicinity to the host plant), visual or chemical characteristics of service plants can alter crop plant recognition by pest and/or reduce pest oviposition and fecundity and therefore strongly reduce infestation levels (Supplementary material 2). Service plants grown close to the crop can trigger inappropriate landing based on visual signals and cause pest departure from the field (Finch and Kienegger 1997). Fecundity reduction can also result from a disruption of feeding or oviposition behavior on the crop plant due to VOC emitted by service plants (Dardouri et al. 2021). The phenological stage (and in particular the onset of reproduction) of the service plants was shown to strongly influence this effect.

Traits of service plants reducing plant acceptance and pest reproduction involve aboveground morphology and growth (e.g., leaf biomass), color, and emission or production of secondary compounds volatile or not (Supplementary material 2). For all service plants having an action through the emission of VOC and regardless of the mechanism involved, plant chemotype can have a drastic influence on their efficiency.

All these three direct mechanisms have been successfully combined to develop a 'push-pull' strategy to control lepidopterous pests of corn crops in Africa (Khan and Pickett 2004). This strategy involves (1) service plants, planted with the crop, repelling the pest from the crop plants (i.e., push) and (2) other service plants, planted at the edge of the crop, attracting the pest (i.e., pull) but inhibiting the development of its larvae.

Indirect mechanisms Service plants might also reach and affect aerial phytophagous arthropod pests indirectly by favoring natural enemies or by priming crop plant defense (Fig. 2B).

To promote natural enemies The role of natural enemies (i.e., predators and parasitoids) for regulating arthropod pests in agroecosystems is widely recognized. Service plants favoring natural enemies are commonly called 'insectary' and/or 'banker' plants and can attract, feed, shelter and enhance reproduction of locally existing natural enemy populations. They are key players of conservation biological control strategies (Gurr et al. 2017) but can also play an important role in the efficiency of augmentative biological control by supporting the population of introduced natural enemies even when pest population is low (Messelink et al. 2014). Service plants could also favor the installation of other biological control agents such as entomopathogenic microorganisms (fungi and nematodes) but to our knowledge, this potential effect has never been tested.

Service plants promoting natural enemies may be placed inside the field plot in intercropping with the crop or in rotation before the crop, or around in field edges (e.g., floral strips or patches, beetle banks, wooden hedge).

The mechanisms underlying the effects of service plants on arthropod pests through natural enemies are two-fold and involve different service plant traits (Supplementary material 2).

On the one hand, service plants provide natural enemies of pests with alternative food (i.e., food resources other than the targeted pest) all over their lifecycle since they may feed on a range of resources (e.g., aphidophagous Syrphidae feed on nectar and pollen at the adult stage). Besides animal prey, service plants provide honeydew, fungi, floral and extra-floral nectar, pollen, fruit, plant sap and/or guttation (Lundgren 2009; Frank 2010; Huang et al. 2011). Using such alternative food sources, natural enemies can survive and reproduce for longer periods even when no pests are present, but they can also be more efficient in terms of regulation when pests are present (Gurr et al. 2017). Besides nutritive resources, service plants can also provide alternative hosts for parasitoids (Frank 2010). Regarding floral food resources, the type of inflorescence, flower morphology and color (including UV reflectance pattern) or VOC emitted by flowers are key traits guiding visits to service plants by natural enemies (Hatt et al. 2018, 2019; Zhu et al. 2020). Also, the position and number of nectaries or stamens within the flower have substantial influence on the number of species of natural enemies that are able to feed on floral resources (Lundgren 2009; Patt and Rohrig 2017; Zhu et al. 2020; He et al. 2021). Extrafloral nectary presence, accessibility, detectability along with the quality of the nectar secreted are also key traits (Patt and Rohrig 2017). Regarding service plants hosting alternative hosts or preys, quantity of VOC emission guiding natural enemies to these resources is an important trait. Sticky plants were also shown as efficient plant providing food (Krimmel and Pearse 2013).

On the other hand, service plants can provide shelter or oviposition sites to natural enemies (Gurr et al. 2017). These include appropriate spawning sites and/or habitats allowing natural enemies to reproduce and/or shelter (predation or against unfavorable climatic conditions). These refuges and reproduction sites can be helpful during the cropping period but also before and after it. It is essential that service plant morphology fits with natural enemy needs for sheltering (e.g., branched plant), moving (e.g., robust stems), favoring oviposition (e.g., big leaf blade or domatia).

Some field studies have demonstrated the efficacy of these mechanisms of action of service plants on pest regulation (Gurr et al. 2016). Combining shelter and food provision allows to sustain a reproducing population of natural enemies and to provide a control of arthropod pests all along the growing season (Huang et al. 2011; Fiedler et al. 2007; Messelink et al. 2014). For instance, the presence of leaf domatia and extrafloral nectaries are positively correlated together and with the abundance of predatory mites in *Viburnum* plants, suggesting that both traits benefit the plant bearing them (Weber et al. 2012). For augmentative biological control, the timing of natural enemy release is important (Crowder 2007) to increase or maintain their populations before the pest arrival, e.g., through extended season of floral resources with the insectary plants.

To prime crop defense Plant-plant interactions can influence the resistance of crop plants to arthropod pests (Heil and Karban 2010; Kessler et al. 2006). These interactions are mediated by signals emitted by one plant (the service plant, so called 'signal' plant) and perceived by the receiver neighboring plant (the crop plant) which gains information about their risk of herbivory and adjusts its defenses accordingly. Such interactions between plants were observed within or between species and are known as priming (Conrath 2009).

Service plant traits involved in priming include VOC (phytohormones, terpenoids or green leaf volatiles*)* or root exudates triggering resistance in receiver plants through the expression of resistance-related genes (Ninkovic et al. 2021) (Supplementary material 2). Plants showing a high emitter biomass/area (leaf biomass/area for instance) might be seen as efficient signal plants (see Sect. "To release toxic compounds" on the relationship between plant size and metabolite emission), but this hypothesis has to be confirmed.

The few examples indicate that these plant-plant signals can (1) initiate and/or reinforce the direct crop defenses such as toxic compounds (Ling et al. 2022; Sukegawa et al. 2018); (2) induce indirect defenses on crop plants such as herbivore-induced plant volatiles that attract natural enemies of the pest (Vucetic et al. 2014; Magara et al. 2015); and (3) alter the chemical profile of the crop plant, then its recognition by aerial arthropod pests at distance or upon contact (Parker et al. 2013). Low doses of VOC usually prime rather than fully induce resistance responses (Heil and Karban 2010): primed tissues do not show phenotypic changes in their resistance level but they respond faster and more strongly once attacked (Frost et al. 2008; Heil and Ton 2008).

The modification of the soil beneficial microbiota community by service plants can also trigger the priming of crop defense (soil legacy effect in Davidson-Lowe et al. 2021) (see also"To prime crop defense").

These few examples are mainly based on laboratory experiments, and field-based evidence (e.g., Sukegawa et al. 2018) is still needed.

Compatibility between regulation mechanisms Although studies remain scarce, traits of service plants may have compatible effects on the different direct and indirect regulation mechanisms (see boxes in green in Supplementary material 2). For example, high, tall and bushy service plants might work as a barrier for aerial arthropod pests and provide appropriate shelter to natural enemies as well. An extended blooming period of a service plant is useful for securing temporal availability of alternative food to natural enemies (Ribeiro and Gontijo 2017) but late flowering service plant are more efficient to disrupt plant location by pests because the signal providing by the vegetative parts might be modified after flowering (de Brito-Machado et al. 2022).

Generally, evolution seems to favor more compatibilities rather than incompatibilities. Deterrent leaf/stem exudates might be efficient against pests but also against natural enemies, particularly when their mode of action is generalist: for instance, a sticky exudate is sticky for all arthropods, including pests and natural enemies. Yet, many examples in the literature show the opposite to be true, with natural enemies taking advantage of the trapped prey by the sticky plants (Krimmel and Pearse 2013). Finally, VOC emission might be seen as antagonist too if repelling pests but also natural enemies. However, several studies have shown that this is not really the case: service plants that repel arthropod pests may also increase predator populations (Parker et al. 2013), or attract predators and parasitoids (Kasl 2004; Sobhy et al. 2022).

2.1.3 Soil-borne pests

In our analysis, soil-borne pests include microorganisms (fungi, oomycetes, bacteria, protozoa and viruses), microfauna such as nematodes and insects (e.g., arthropods during their telluric phase) as well as parasitic plants. Soil-borne pests remain in different forms of conservation in the soil (i.e., spores, cysts, eggs, larvae, seeds) before interacting with their host plant. Most of them are characterized by a low active dispersal phase, although some can also be spread from plant to plant by arthropod vectors. Chemical compounds released in the soil by the roots of the host plant enable soil-borne pests to recognize it specifically and to reach the roots on which they will develop or penetrate. This cross dialogue between roots and pests is essential in the infection process (Bais et al. 2006). Except for potential action on vectors described in Sect. 2.1.2, service plants act mainly on the phases of multiplication of soil-borne pests in the soil and on the phases of infection/infestation of the crop. Mechanisms of action are direct and indirect for both phases (Fig. 2). In most cases, both alive service plants (in intercropping or in rotation) and their residues in the soil are involved in soil-borne pest regulation.

Direct mechanisms **To hamper development before crop infection**

Service plants can reduce the size of the population of soil-borne pests before they penetrate or infect crop roots by being non-host (innate immunity, no damage, no multiplying) or bad hosts (basal defenses, low damage, low multiplication) for such pests.

Underlying service plant traits involve (Supplementary material 3) (1) the presence of lignin, suberin, silica, callose tissues in root epidermis that can act as a physical barrier (Moore and Johnson 2017); (2) the release of root exudates by non-host service plants that are repellent or even toxic to soil-borne pest. They can inhibit the germination of spores for phytopathogenic fungi or seeds for parasitic plants, hinder the multiplication of bacteria, limit the movement of zoospores for oomycetes, slow the hatching of eggs or kill juveniles in the case of nematodes (Djian-Caporalino et al. 2005, 2008; Yang et al. 2022). Some of these compounds can also stimulate egg or cyst hatching, and spore germination when the crop is not present (Scholte and Vos 2000; Drury et al. 2022); (3) a high root density and growth rate; (4) the release of VOC (such as volatile organic acids), constitutive toxic, stimulating or suicide hatch secondary compounds contained in roots and/or aerial parts from service plant residues during their decomposition in the soil (Djian-Caporalino et al. 2005, 2008, 2019); (5) a large aboveground biomass increasing the amount service plant residues to release these toxic compounds (Sect. "To release toxic compounds" on the relationship between plant size and metabolite emission). If used as mulch this biomass can also play the role of a physical barrier by significantly reducing the splash effect during heavy rains and modify the microclimate, making it less favorable for the development of soil-borne fungi (Mills et al. 2002) and (6) a late flowering with an extended vegetative period, to exude or to release more toxic compounds for some species (Karakas and Bolukbasi 2019).

Field-based evidence that these mechanisms lead to an effective regulation of soil-borne pest is available both for alive and residue usages (see references cited just above).

To trap endoparasites or disrupt their life cycle

Alive service plants in intercropping or in rotation with crop plants can trap (attract and retain) soil-borne pests and disrupt their life cycle. This mechanism concerns in most cases biotrophic endoparasites (such as root-knot or cyst nematodes that penetrate and live inside the root tissues and are dependent on the nutrient supply of the host plant to complete their life cycle). By suppressing the establishment and/or reproduction of these soil-borne pests, service plants help to decrease the infectious potential of the soil, thereby protecting the subsequent susceptible crops. They are characterized as resistant, or masculinizing plants.

Service plant traits involved in this regulation mechanism include the following (Supplementary material 3): (1) a capacity of hypersensitive reaction of the service plant, with a rapid and localized cell death in the infected plant, blocking pest migration and thereby preventing their development and reproduction (Dias et al. 2012); (2) the production of toxic secondary compounds in roots (constitutive or induced in reaction to infestation) with a biocidal effect (Fang et al. 2016); (3) a capacity to generate a masculinizing process that helps to decrease the reproduction of endoparasites which is described in varieties resistant to cyst nematodes (Djian-Caporalino et al. 2005, 2008) but not yet described for service plants. Traits related to rapid growth, root architecture and density are important, with an extensive root system penetrating to deeper soil layers able to catch more soil-borne pests that are not able to actively migrate in the soil (Scholte and Vos 2000).

Field-based evidence that these mechanisms lead to an effective regulation of soil-borne pest are available (see references cited just above). However, the use of trap plants to manage nematodes, for example, has often failed because they could also act as a reservoir for these pests (see Sect. 2.2.3); they must therefore be destroyed before the completion of the life cycle of the endoparasitic nematodes to avoid any reproduction (Djian-Caporalino et al. 2019).

Indirect mechanisms

Concerning indirect action, two main paths can be considered (Fig. 2B). One involves service plants favoring organisms with regulating effects on soil-borne pests (a generic term is used in this section as it is difficult to differentiate natural enemies and beneficial microbiota in soils). The other one involves service plants priming crop defense, either directly or via beneficial microbiota.

To promote organisms with regulating effects

Organisms with a regulating effect on soil-borne pests include endophytic or rhizospheric fungi and bacteria, predatory or parasitic nematodes of insects and of other nematodes, nematophagous fungi and fungi that are antagonistic to other plant-parasitic fungi. Alive service plants and/or their residues can attract, maintain and multiply these organisms already present in the soil or inoculated. When stimulated, these organisms can compete for resources and niches, release secondary biocidal or biostatic compounds, or predate, parasitize and infect soil-borne pests (Chave et al. 2004). Although specific mechanisms are attributed to certain organisms, it is often the microbiome considered as a whole (especially its functional diversity) that is involved in interactions between service and crop plants. In the same way, amendments of service plant residues that enhance overall microbial activity are often correlated with increased soil suppressiveness towards several pests (Mazzola 2004).

Traits of service plants that promote communities of organisms with regulating effects are related to (Supplementary material 3): (1) a dense and high-growth root system increasing the probability of early contact and establishment of a symbiotic intercropping between the service plant and beneficial organisms (Maherali 2014); (2) the production of attractive or stimulating roots exudates including VOC, and secondary compounds in roots and/or aerial parts of the service plants (Silva et al. 2018); (3) a large aboveground biomass of covering plants modifying the micro-climate to promote natural enemies by residue degradation; (4) a long vegetative period (i.e., a late flowering) to extend the period during which compounds attractive to beneficial organisms could be released(Karakas and Bolukbasi 2019); and (5) the capacity to host microorganisms regulating soil-borne pests.

While organisms with regulating effects are usually efficient in laboratory and greenhouse experiments, field results are less consistent, probably due to the poor persistence of applied organisms in the soil. Introducing service plants intercropped with crop plants was shown in some situations to maintain and multiply these beneficial organisms, whether inoculated or naturally present (Buysens et al. 2016). Moreover, long-standing suppression appears to persist after eliminating the service plants (Rodriguez-Heredia et al. 2020).

This observation supports the hypothesis that plants do not only directly interact with microorganisms, but their action as ecosystem engineers outlives them. Because of the complexity of mechanisms involved, no real field proof has yet been provided to support this hypothesis but projects are underway to better understand how it works (Vukicevich et al. 2016).

To prime crop defense

Alive service plants and/or their residues can induce or stimulate crop defense either via interactions between the service plants and the crop plants (as previously described for aerial arthropod pests in Sect. “To prime crop defense”), or through beneficial microbiota, for example plant growth promoting bacteria (which induces systemic resistance) or arbuscular mycorrhizal fungi (causing mycorrhizal induced resistance). These microorganisms, recruited by the service plant during its growth period, are used by the crop plant for its own protection (Pozo and Azcón-Aguilar 2007).

Traits of service plants that have a potential effect on crop defense (Supplementary material 3) are the following: (1) a high root density and growth rate to increase emission of exudates and to host more organisms with protective effects (alive service plants), (2) a large leaf area and biomass to increase aboveground emission of VOC (alive service plants) and secondary compounds (residues of service plants) priming crop defense and stimulating beneficial microbiota (Quaranta 2009) (see Sect."To release toxic compounds"on the relationship between plant size and metabolite emission) and (3) a late flowering to promote extended vegetative phase and therefore to attract more beneficial organisms and to stimulate more crop defense.

Induced systemic resistance and mycorrhizal induced resistance are effective against a wide range of soil-borne pests in controlled conditions and thus offer serious potential for practical applications in crop protection. This mechanism is often suggested (e.g., Ratnadass et al. 2012) but not always validated in the field as the mechanism depends on the type of pest and its infection strategy. The soil legacy effect, described in Sect."To prime crop defense"on aerial arthropod pests, also applies here for mycorrhizal cover plants sown before the crop to strengthen crop resistance to soil-borne pests.

Compatibility between regulation mechanisms

Traits of service plants may have mostly compatible effects on both direct and indirect soil-borne pests regulation mechanisms (see boxes in green in Supplementary material 3 showing no incompatibility in service plant features for several trait categories). Indeed, covering plants with a large biomass and high root density and growth rate are expected to increase the mulch of crop residues to reduce the splash effect, modify the micro-climate disrupting development of some soil-borne pests and promoting their natural enemies, increase contacts with soil-borne pests, produce more toxic compounds (VOC, root exudates or toxic compounds), even more when the plants are young (before flowering), increase the trap effect, and host higher amounts of organisms with regulating effects (e.g., highly mycotrophic plants). All these traits have already been found in forage sorghums, known (1) to reduce the harmful influence of wilts caused by *Ralstonia solanacearum*, (2) to reduce the populations of *Fusarium, Gaeumannomyces* and *Rhizoctonia* by producing biocidal compounds, and (3) to be poor hosts, trap plants and biofumigant plants releasing toxic compounds when they decompose in the ground to control root-knot nematodes (Djian-Caporalino et al. 2019; Ratnadass et al. 2012; Rodriguez-Heredia et al. 2020). For certain service plant species, however, there are uncertainties concerning the compatibility between regulation mechanisms involving chemical compounds (Aslam et al. 2017; Jabran and Farooq 2013).

2.1.4 Aerial pathogens

Service plants, acting in their living form or as residues, opens up some interesting prospects for crop protection against aerial diseases (Boudreau 2013; Stomph et al. 2020), although field-based evidence is still very limited in the literature. Regulation of aerial pathogens by service plants could involve both direct and indirect mechanisms (Fig. 2). However, these mechanisms have been mostly highlighted in crop species intercropping, or cultivar mixtures for specific pathosystems and seldom in rotation, so they were here extrapolated to service plants. Several mechanisms effective against other types of pests do not affect aerial pathogens, probably because their biology is primarily characterized by a high specificity of interaction with the host crop plant and the spatial scale involved are irrelevant. Service plants do not act as ‘traps’ for aerial pathogens and should be considered for their direct regulation action on their life cycle or indirectly for their alteration of the interaction between them and the crop. Worth noting, very few plants present in edges and margins adjoining fields are suitable for acting as service plants against aerial pathogens. Specific traits of service plants that modify the development rate of an epidemic can have a significant impact, either beneficial or detrimental, for example by modifying the microclimate.

Direct mechanisms To reduce inoculum availability: dilution and barrier effects

The barrier effect generated by service plants used as agroecological interfaces (e.g., hedges) is sometimes mentioned, but there is no evidence in the literature of the significant impact on epidemics at a large scale. The reduction of inoculum availability is rather attributed to variations in morphological traits within the field, such as variations in the width and height of the cover crops (driven by precocity, and sowing density in a lesser extent) that limit inoculum transfer between host plants by modifying wind or rain dispersal (e.g., Boudreau 2013; Vidal et al. 2018; Levionnois et al. 2023) (Supplementary material 4). Tall and wide service plants with a high biomass are thus expected to improve the barrier effect. However, in practice little is known about the specific traits of service plants promoting aerial pathogens regulation by this way, even if modelling approaches can help (e.g., Levionnois et al. 2023). The crucial point is that the service plant should be a non-host for pathogens of the crop, or, at least, should express a high level of resistance to these pathogens (Supplementary material 4). This is a necessary condition for the service plant to induce both dilution and barrier effects, which are probably the most important mechanisms of service plants on polycyclic diseases (Borg et al. 2018). However, these effects are usually not sufficiently efficient to reduce the disease intensity as certain criteria need to be met for successful epidemic control (Strauss et al. 2015). The introduction of service plants may also limit the availability of inoculum of residue-borne pathogens by improving soil biological activity leading to a faster decomposition of crop residues (Kerdraon et al. 2019).

To modify the microclimate

The introduction of service plants intercropped with a crop can modify the canopy architecture and therefore the microclimate within the field canopy by creating a microclimate environment (temperature and moisture) less suitable to the development of pathogens (Pangga et al. 2013).

The impacts of agroforestry systems on the microclimate, and ultimately on the different epidemiological components of diseases including inoculum dispersal and infection conditions, is well documented in the case of coffee fungal pathogens (reviewed in Le May and Suffert (2024)). Taller service plants (shrubs and trees) help reduce the intensity of crop contamination (auto- and allo-infections) through 'umbrella' and 'shading' effects, modifying the impact of raindrops, relative humidity and free water on leaves, as well as the impact of wind (e.g., Staver et al. 2001; Boudrot et al. 2016; Ratnadass et al. 2012) (Supplementary material 4). However, the modifications of the microclimate by service plants in these systems are strongly dependent on the production situation (Merle et al. 2022). In vineyard, in case of strong grapevine growth, intercropping service crops was shown to prevent excessive vegetative development of grapevines and to increase potential evapotranspiration, thus reducing the development of fungal pathogens (Garcia et al. 2018). However, beyond the case study mentioned above, the modification of the microclimate induced by service plants usually has antagonistic consequences that are difficult to estimate and manage. Consequently, it is practically impossible to know which specific trait of service plants are involved.

Indirect mechanisms To promote natural enemies regulating aerial pathogens

Living forms or residues of service plants can be efficient reservoirs or enhance the habitat of natural enemies, including hyperparasites of fungal pathogens (mycoparasites) (Falk et al. 1995; Sundheim 1982) and mycophagous arthropods (e.g., Bourgeois et al. 2023), which are important components of host-pathogen systems (Parratt and Laine 2016) (Supplementary material 4). This requires, in the case of hyperparasitism, that (1) a pathogen population infected by a mycoparasite pre-exists on the service plant, (2) this mycoparasite is also able to infect the pathogen of the target crop, and (3) the mycoparasite population is able to increase sufficiently rapidly to slow down the development of the pathogen on the target crop before it becomes damaging. These conditions explain why the use of service plants as a natural source of natural enemies in the field is presently a rather theoretical prospect. In French vineyards, the inoculation of *Ampelomyces quisqualis*, parasite of a wide range of powdery mildews (Kiss et al. 2004), was inconclusively tested on red clover as service plant in intercropping with the crop, in order to control *Erysiphe necator* (David Lafond, IFV Val-de-Loire, personal communication).

To be effective in field conditions, such a service plant must therefore combine a set of traits that enable it to host one or more species of mycoparasites having a broad host range within a diverse group of pathogens infecting both this service plant and the crop (Supplementary material 4). The use of such a service plant is not necessarily limited by the host specificity of the mycoparasites (Legler et al. 2016) but rather by their difficulty to persist in the long term in agroecosystems and their sensitivity to fungicides. VOC emission by aboveground service plant parts could reduce growth of airborne pathogens via the promotion of natural enemies (Rodriguez-Saona and Frost 2010; Heil and Adame-Álvarez 2010), particularly when associated with high aboveground biomass (Sect."To release toxic compounds"on the relationship between plant size and metabolite emission). While management practices can modify the efficiency of these mechanisms (Delitte et al. 2021), very little is known about the traits of service plants that enable them to express their beneficial effects on the presence of natural enemies including beneficial microorganisms because they are part of complex ecological interactions, specific of each crop species and system (Supplementary material 4).

To prime crop defense

The impact of neighboring plants on crop defense priming is now well established (Pélissier et al. 2021; Wenig et al. 2019) (Supplementary material 4). Service plants can increase the crop immunity by such effects (Sect. 2.1.2 and 2.1.3). Several studies in pre-conditioned soils showed that the modification of soil microbiota by service plants can alter the defense responses of plants towards aerial pathogens (Hu et al. 2018; Wang et al. 2019).

Underlying service plant traits could involve (Supplementary material 4): VOC production or root exudation of secondary metabolites (Kong et al. 2019) that may alter the composition of the soil microbiota with indirect consequences on pathogens (e.g., Hu et al. 2018) through induction of priming of crop defense. For instance, the impact of maize root exudates on the structuration of beneficial microbiota has been shown in the field and shows the interest of this plant species as service plant (Cadot et al. 2021). It can be assumed that these effects increase for service plants with high biomass aboveground and belowground. Moreover, since the crop nutrition is at the origin of the modification of its immunity and defense (Saijo and Loo 2020), service plants can also affect crop plant resistance, with beneficial or detrimental effects, by modifying the exploitation of resources by the crop via competition, niche complementarity and/or facilitation (Litrico and Violle 2015).

All these aspects are cutting-edge research topics still poorly investigated in field conditions and the traits of service plants that enable them to express beneficial effects on aerial pathogens of a target crop are very poorly known (Supplementary material 4).

Compatibility between regulation mechanisms

While compatibility is expected based on concordant morphological traits (see green boxes in Supplementary material 4 showing no incompatibility in service plant features for most several trait categories), there is very little known about the effect of service plants on airborne pathogens, and virtually nothing about the complementarity of chemical and host-specific traits. Potential compatibility exists in the sense that a service plant can be detrimental to the development of different pathogens through different mechanisms: for example, grass strips within vineyard plots could theoretically decrease the relative humidity that is usually favorable to fungal pathogens, increase the decomposition of grape leaves as inoculum sources, and host mycoparasites (Garcia et al. 2018). It is also essential to evaluate the effects of a service plant on the whole local aerial pathogen complex to identify potential incompatibility.

The knowledge synthesis presented in Sect. 2.1 shows that the mechanisms behind the direct effects of service plants strongly depend on the pest category, according to its trophic level and mobility. For instance, mechanisms limiting the development of a biotrophic pathogen may be ineffective against a necrotrophic pathogen (Spoel et al. 2007), and the decrease in susceptibility to a pathogen can induce an increase in susceptibility to another one. Indirect effects are more generic: 'natural enemies' are involved in the regulation of all the studied pest categories, and priming crop plant defense appears in three out of four pest categories. Globally, for a given pest category, our trait-based approach did not identify major incompatibility among regulation mechanisms. However, synthesis identified knowledge gaps for all pest categories, and especially for aerial pathogens.

2.2 Disservice mitigation

Service plants efficient for 'multi-pest' regulation may also cause disservices, i.e., negative impacts on crop productivity (in terms of quantity or quality) or on production costs (Zhang et al. 2007). Three main categories of disservices that may arise with the use of service plants were considered in our analysis. They include (1) direct repression of crop growth, (2) promotion of non-targeted crop pests and (3) persistence of service plants in subsequent crops, with service plants becoming weeds. As for pest regulation (Sect. 2.1), we synthesized knowledge on the main mechanisms and service plant traits involved in disservice mitigation (Supplementary material 5).

2.2.1 Service plants directly affect crop growth

The use of service plants in intercropping or in rotation with the crops may directly affect the growth of the intercropped or subsequent crops via four main mechanisms. (1) When service plants are intercropped with crops during the crop cycle (even partly), they can generate competition for resources (light, water and nutrients) (Gardarin et al. 2022). It is widely acknowledged that competition is the main mechanism underlying the disservices caused by service plants intercropped with crops. (2) When service plants are intercropped or in rotation with the crop, their living tissues (roots, leaves) or their residues can release toxic secondary metabolites negatively affecting the intercropped or subsequent crops (Doré et al. 2004; Jabran et al. 2015). (3) Service plant residues may physically hamper the sowing and establishment of the subsequent crop, especially when quantities of residues are high (Ryan et al. 2021). (4) Service plant residues may affect soil-mineral availability due to the immobilization of minerals by soil microbes (Wells et al. 2013), making soil-nutrients temporary less available; this phenomenon has been described for nitrogen, but may occur for other nutrients too.

All these mechanisms can negatively affect the growth of crop plants intercropped with or following service plants, with consequences on crop yield and quality. However, the individual effects of each mechanism are difficult to quantify in the field as they may occur concomitantly.

The magnitude of the adverse consequences depends on service plant traits and can be at least partly mitigated by judicious choice of the service plant species/genotypes (Supplementary material 5). For example, for service plants intercropped with crops, competition can be partly mitigated by using service plants that are smaller than the crop, with most of their leaf area located below that of the crops, and roots located in other soil layers than those colonized by the crop (Tardy et al. 2017, 2015). Similarly, plant species that are known to emit toxic secondary compounds and with a high carbon to nitrogen ratio in their tissue should be avoided to limit allelopathy and nitrogen immobilization effects, respectively.

2.2.2 Service plants become weeds in subsequent crops

Another kind of disservice caused by service plants used within the field (in intercropping or rotation with the crop) is their persistence beyond the expected growing time period, making service plants becoming weed plants (Keene et al. 2017). This may occur when (1) service plants are not completely destroyed at the end of their growing period, or (2) when they produce seeds replenishing the soil seedbank, or other storage/reproductive organs in the soil for perennial plants (source of future weed populations in subsequent crops). In such situations, service plants may become undesirable plants when the services they provide are much lower than the disservices they cause.

However, such risks of disservice can be mitigated by choosing service plant species/genotypes that are frost-sensitive (in geographical regions with cold season), easy-to-destruct (tall plants with a high water content in tissue at plant destruction and a superficial root system), palatable to mammal herbivores (although this palatability may be compromised when using service plants targeting pests through the production of defense compounds; see Coley et al. (1985)), annual (to avoid storage organs that could remain in the soil and allow vegetative reproduction) and/or sterile (Supplementary material 5).

2.2.3 Service plants promote non-targeted pests

The unintentional promotion of pests (i.e., arthropod pests, soil-borne pests, aerial pathogens or their vectors) is another disservice that may be caused by service plants intercropped or in rotation with the crops, or in field edge. This disservice was particularly described for unmanaged habitats such as natural or semi-natural areas surrounding agroecosystems viewed as potential 'reservoirs' of pests (Wisler and Norris 2005; Blitzer et al. 2012; Gillespie and Wratten 2017; Tschumi et al. 2018; Tscharntke et al. 2016), but the underlying mechanisms are applicable to service plants introduced in agroecosystems. Their unintended detrimental consequences can be (1) quantitative since the service plants (cultivated within a field or deployed around) may allow a crop pest to perpetuate over the seasons and thus influence the intensity of subsequent epidemics, and (2) qualitative as service plants can have a significant effect on the evolution of pest populations (changes in fitness/aggressiveness and combination of virulence), which constitutes a long-term risk for the agroecosystem (Burdon and Thrall 2008).

Service plants can promote pathogens (fungi, bacteria, phytoplasma and viruses) through four main types of epidemiological processes (Wisler and Norris 2005). (1) Service plants may act as reservoir alternative hosts. The concept of 'host range', which characterizes the specificity in the interaction between a pathogen and all its hosts (Dinoor 1974), is essential to assess such a risk of disservice. Several plant species botanically close to the main host crop are 'alternative hosts' in the sense that they can be facultatively colonized by fungal pathogens to which a main host crop also present in the agroecosystem is susceptible, such as fungi that infect grass spikes like *Fusarium* spp. (Duffus 1971; Mantle et al. 1977; Matelionienė et al. 2022). (2) Service plants may act as obligate alternate hosts for pathogens that require them in part of their life cycle, as for heteroecious rust fungi such as *Puccina graminis* f. sp. *tritici*, the causal agent of wheat stem rust, which can infect common barberry plants (Peterson 2018; Zambino 2010). (3) Service plants may act as reservoirs of crop pathogen vectors such as aphids and flies that disseminate many viruses (Schoeny et al. 2019). They can amplify pathogen transmission, for example through a disruption of the feeding behavior of a virus vector increasing viral transmission (Dardouri 2018).

Service plants can also promote herbivore pests and phytoparasites through three main mechanisms. (1) As for pathogens, service plants can be reservoirs for pests. For instance, trap plants, which are merely attractants with no 'dead-end' properties (i.e., not allowing pest larvae to survive), may act first as 'sinks' for pest populations but become reservoirs of pests for the same field later in the season or for neighboring fields (Djian-Caporalino et al. 2019; Hilje et al. 2001 cited by Ratnadass et al. 2012). Moreover, 'dead-end trap plants' may also end up selecting pest populations that will overcome the 'suicidal' egg-laying behavior (Thompson 1988; Thompson and Pellmyr 1991 cited by Ratnadass et al. 2012). Some 'push plants' may also divert certain pests from the crop while attracting others to it (Latheef and Ortiz 1984 cited by Ratnadass et al. 2012).

(2) Service plants may also increase the fitness and/or the abundance of herbivore pests through the provision of

additional food resources: some arthropod pest species also consume plant tissues or nectar and pollen (Kevan and Baker 1983; Romeis et al. 2005; Wäckers et al. 2007) and floral resources can increase their longevity and oviposition and their energetic state (e.g., Baggen and Gurr 1998; Winkler et al. 2009).

(3) Service plants can increase intraguild predation among natural enemies. Resources provided by service plants such as nectar, pollen, alternative food, shelters and/or oviposition sites benefit natural enemies of the pests but may also benefit higher level predators or hyperparasitoids thus increasing intraguild predation risk and reducing the efficiency of pest control (Snyder 2019; Colazza et al. 2023; Araj et al. 2008) (Sect. 2.1.3).

Such risks of disservice can be mitigated by choosing service plant species/genotypes that are non-host of pests of the target crops (including their vectors) to disrupt the cycle of pests or with a phenology not compatible with the phenology of crop pests (Supplementary material 5). Service plant morphology, flower color or ornamentations, VOC emitted, nectar and pollen should not be attractive or favorable for the aforementioned pests (including their vectors).

3 Analysis of compatibility

3.1 Which compatibility between the regulation of different pests by service plants?

Knowledge in Sect. 2.1. for each pest category was synthesized in Fig. 3, 4 and 5 to analyze compatibility for multi-pest regulation by service plants. We considered that a service plant trait attribute (e.g., tall plant) promoting regulation mechanisms for all the pest categories matched a compatibility. A plant attribute promoting a regulation mechanism for one pest category, while penalizing a regulation mechanism for another pest category, matched an incompatibility.

3.1.1 'Trait-by-trait' analysis

Most of the trait categories were involved in the regulation of several pest categories (i.e., most lines of Fig. 3, 4 and 5 involved at least two columns). This suggested potential interactions in the regulation of the different pest categories by service plants.

Focusing on individual trait categories (i.e., individual lines of Fig. 3), traits related to morphology, growth and color of vegetative parts appeared globally compatible with the regulation of several pest categories. Aboveground, tall, wide, fast-growing and covering service plants, with a large leaf area and biomass, can promote the simultaneous regulation of weeds (mainly by competing for light), soil-borne pests (by promoting toxic effects by service plant residue degradation), arthropod pests (by providing a physical barrier and enhancing emission of volatile organic compounds affecting these pests) and aerial pathogens (by providing a physical barrier). Belowground, service plants with high root development and growth can promote the regulation of weeds (by competing for water and/or nutrients if these resources are limiting), soil-borne pests (by trapping pests or hosting beneficial organisms) and aerial pathogens (by hosting more beneficial microbiota priming crop defense).

Trait categories		**Ideal service plant traits for regulating pests** (summary of Supplementary material 1 to Supplementary material 4)			
		Weeds	**Aerial arthropod pests**	**Soil-borne pests***	**Aerial pathogens***
Morphology, growth, colour of vegetative parts	**Aboveground morphology, growth and colour**	Fast growing, tall, wide and covering plant (i.e., with a large leaf area) with a high biomass	Fast growing, tall and covering plant, with a large leaf area and biomass, an attractive colour and a morphology fitting natural enemy needs	Covering plant, with a large biomass and leaf area	Tall and wide plant, with a high biomass
	Root morphology and growth	Fast growth with high root density, large volume of soil prospected in depth and width	-	Fast growth with high root density Root epidermis made up of lignin, suberin, callose	High biomass
	Soil resource uptake	High uptake rate Use of the same resource as those taken up by weeds	-	-	-
	Ornamentations and extrafloral nectaries	-	Presence of trichomes, domatias and continuous presence of nutrient-rich extrafloral nectaries favourable to natural enemies	-	-

Fig. 3 Main service plant traits related to morphology, growth and color of vegetative parts that promote the regulation of weeds, arthropod pests, soil-borne pests and aerial pathogens. '-' indicates that a given trait category has no effect on a given pest (or this effect is poorly documented). On a given line (i.e., trait category), green cells show no incompatibility in service plant features between columns (i.e., pest categories). This figure is a synthesis of Supplementary material 1 to Supplementary material 4. 'Host specificity' is not presented because it is considered as an integrative trait resulting from the combination of other traits that are (at least partly) presented in Fig. 3, 4 and 5. *Features in the 'aerial arthropod pests' column apply to 'soil-borne pests' and 'aerial pathogens' columns as arthropods can also be vectors of soil-borne pests and aerial pathogens.

Trait categories		Ideal service plant traits for regulating pests (summary of Supplementary material 1 to Supplementary material 4)			
		Weeds	**Aerial arthropod pests**	**Soil-borne pests***	**Aerial pathogens***
Phenology	**Germination-emergence period**	Earlier than that of weeds	-	-	Impact of precocity on intensity of inoculum reduction
Phenology	**Flowering period**	-	Early flowering with an extended flowering period or late flowering (depending on the targeted regulation mechanism)	A long vegetative period (i.e. a late flowering) to extend the period of emission of compounds attractive to beneficial organisms	-
Reproductive organs	**Morphology, colour and resources**	Diverse	Flower colour attracting arthropod pests (trap plants) Flower morphology, colour and resources (nectar and pollen) and fruits favourable to natural enemies of pests	-	-

Fig. 4 Main service plant traits related to phenology and reproductive organs that promote the regulation of weeds, arthropod pests, soil-borne pests and aerial pathogens. '-' indicates that a given trait category has no effect on a given pest (or this effect is poorly documented). On a given line (i.e., trait category), green cells show no incompatibility in service plant features between columns (i.e., pest categories), yellow cells show potential incompatibility, and white cells show uncertainties about compatibility or not. This figure is a synthesis of Supplementary material 1 to Supplementary material 4. 'Host specificity' is not presented because it is considered as an integrative trait resulting from the combination of other traits that are (at least partly) presented in Fig. 3, 4 and 5. *Features in the 'aerial arthropod pests' column apply to 'soil-borne pests' and 'aerial pathogens' columns as arthropods can also be vectors of soil-borne pests and aerial pathogens.

Trait categories		Ideal service plant traits for regulating pests (summary of Supplementary material 1 to Supplementary material 4)			
		Weeds	**Aerial arthropod pests**	**Soil-borne pests***	**Aerial pathogens***
Chemistry	**Emission of volatile organic compounds**	Toxic for weeds	Masking the crop plants or attracting (for trap plants) or toxic for aerial arthropod pests, or repelling aerial arthropod pests, or altering the reproduction of aerial arthropod pests Attracting natural enemies of aerial arthropod pests Priming crop defence	Toxic for soil-borne pests Attracting/promoting organisms with regulating effects Priming crop defence	Attracting natural enemies Priming crop defence
Chemistry	**Production of leaf/stem exudates**	-	Sticky plants trapping pests or prey for natural enemies Deterrent contact compounds for aerial arthropod pests Nutrient-rich leaf/stem exudates that are accessible to natural enemies of aerial arthropod pests	-	-
Chemistry	**Production of root exudates**	Toxic for weeds	Priming crop defence	Toxic for soil-borne pests Attracting/promoting organisms with regulating effects Priming crop defence	Priming crop defence
Chemistry	**Plant tissue composition**	-	Leaves producing compounds that are toxic or unpalatable or reducing digestibility for aerial arthropod pests	Toxic for soil-borne pests Capacity of hypersensitive reactions blocking the development of soil-borne pests Promoting organisms with regulating effects Priming crop defence	-
Chemistry	**Degradation products from residues**	Toxic for weeds	-	Toxic or suicide hatch for soil-borne pests Attracting/promoting organisms with regulating effects on soil-borne pests Priming crop defence	Improving soil biological activity, faster decomposition of crop residue, and living conditions for mycophagous arthropods on the ground

Fig. 5 Main service plant traits related to chemistry that promote the regulation of weeds, arthropod pests, soil-borne pests and aerial pathogens. '-' indicates that a given trait category has no effect on a given pest (or this effect is poorly documented). On a given line (i.e., trait category), green cells show no incompatibility in service plant features between columns (i.e., pest categories), and white cells show uncertainties about compatibility or not. This figure is a synthesis of Supplementary material 1 to Supplementary material 4. 'Host specificity' is not presented because it is considered as an integrative trait resulting from the combination of other traits that are (at least partly) presented in Fig. 3, 4 and 5. *Features in the 'aerial arthropod pests' column apply to 'soil-borne pests' and 'aerial pathogens' columns as arthropods can also be vectors of soil-borne pests and aerial pathogens.

Concerning traits related to phenology and reproductive organs (Fig. 4), a potential incompatibility was identified between a service plant with an extended vegetative period and therefore a late flowering (for regulating soil-borne pests) vs extended flowering period (for regulating aerial arthropod pests via indirect mechanisms). Such incompatibility has been shown for marigolds (*Tagetes* sp.): the nematicidal activity of this service plant in the soil has been detected in roots of vegetative growing plants, before flowering, but not in roots nor leaf extracts during the blooming period (Karakas and Bolukbasi 2019). Conversely, marigold flowers are necessary to directly affect aerial arthropod pests (via aphid-repellent VOC) (Dardouri et al. 2017). This potential incompatibility may be limited provided that the vegetative and the flowering stages of marigolds match with the periods when nematodes and aphids should be regulated. Otherwise, this incompatibility can be solved by management practices: marigold plants can be differently managed in a given field with, before bloom, some plants buried (on the planting row of the crop only) to promote nematode regulation, while letting the other plants blooming around for aerial arthropod pest regulation. Different varieties (i.e., chemotypes) of marigold plants may need to be combined in such case.

Compatibility related to the emission of chemical compounds by service plants was more difficult to analyze (Fig. 5). Indeed, chemicals are involved in many cases but with a large range of specificity, based on a large diversity of molecules that may be released by plants (Aslam et al. 2017; Jabran and Farooq 2013). This large diversity-large specificity brings to knowledge gaps on their direct and indirect effects on pests in different environments. However, some molecules released by plants are known to be involved in the regulation of several pest categories. For example, DIMBOA (benzoxazinoid family) can be exudated by roots of plants of the Poaceae family. This metabolite was reported to attract and kill a soil-borne pathogen (Yang et al. 2014), affect herbivorous insects (Wouters et al. 2016), regulate weeds (Jabran et al. 2015) or recruit beneficial microbiota (Cotton et al. 2019). The case of glucosinolates, contained in the vacuoles of plants of the Brassicaceae family, has been more extensively studied (Couedel et al. 2019). When plant tissues are damaged (due to plant attacks by phytophagous organisms or to plant mechanical destruction), glucosinolates can be hydrolyzed into isothiocyanates that may be either toxic to some bacteria, fungi, nematodes, insects or other plants, while being attractive for some pest natural enemies. This example points out the potential compatibility for multi-pest regulation by Brassicaceae service plants. However, further investigations are needed to test this hypothesis, particularly in field situations where pests experience mixtures of molecules.

3.1.2 'Multi-trait' analysis

Moving from a 'trait-by-trait' analysis ('line-by-line' in Fig. 3, 4 and 5) to a multi-trait analysis (cross-reading the lines of Fig. 3, 4 and 5), the consistency of the global profile of the theoretical ideal service plant features for multi-pest regulation was analyzed.

The service plant features related to morphology and growth were mostly consistent. Indeed, service plants with a high growth potential and rate aboveground (large leaf area, high aboveground biomass) also generally show a high growth potential and rate belowground (high root density and biomass), and high acquisition rates of soil resources. For example, most species from the Brassicaceae family and some of the Poaceae family can meet those criteria, even if a large within-family variability exists (Haramoto and Gallandt 2007; Tribouillois et al. 2015). Interestingly, species from these families may combine these favorable morphological and growth features, with production of toxic compounds involved in the regulation of different pest categories (Sect. 3.1.1). Despite care should be taken given the lack of knowledge on effects of molecules released by plants on pests and beneficial organisms (Sect. 3.1.1), these examples point to some potential consistency among some morphological, growth and chemical features of the theoretical ideal service plant for multi-pest regulation.

The example of *Tagetes* species points to some consistency between the floral and chemical characteristics of the theoretical ideal service plants for the regulation of multiple pests. The literature suggests that these species would combine (Njekete et al. in preparation) (1) flower features that are favorable to oviposition/colonisation for several aerial arthropod pests (trap plants), (2) leaf compounds that are repellent to aerial arthropod pests, (3) compounds inside roots or in root exudates with adverse effects on nematodes, soil-borne bacteria and weeds and (4) capacity to host for mycorrhizal fungi forming common mycorrhizal networks that support the transfer of allelochemicals to crops.

These examples illustrate the possibility to identify individual species meeting several criteria of the theoretical ideal service plant features from Fig. 3, 4 and 5. However, identifying individual species meeting all the criteria is difficult or nearly impossible in the current state of knowledge. Combining species with complementary features should make the use of service plants for multi-pest regulation possible. For example, Fabaceae species show extrafloral nectaries that promote natural enemies of arthropod pests, but a low growth potential (even if inter-species differences exist) (Tribouillois et al. 2015). They could be intercropped with fast-growing species of the Poaceae family, without extrafloral nectaries. Thus, the theoretical ideal service plant features should be more easily achieved by combining several species at the canopy level.

3.2 Which compatibility between multi-pest regulation and disservice mitigation?

To provide a more concrete overview of the potentialities of service plants for multi-pest regulation, and guide the selection criteria in a multi-pest context, compatibility was analyzed between (1) multi-pest regulation and (2) potential disservices mitigation (Fig. 6). We considered that a service plant attribute promoting pest regulation, while promoting a potential disservice, revealed an incompatibility. The analysis was performed distinctly for three modes of insertion of service plants, corresponding to different interactions between service and crop plants, and therefore different potential disservices (Supplementary material 5): in (1) field edges (service and crop plants grow in different locations at the same period), (2) rotation with the crop (service and crop plants grow in the same location but at distinct periods) and (3) intercropping (service and crop plants grow in the same location at the same period).

3.2.1 Service plants in field edges

In field edges, service and crop plants are present simultaneously but spatially disconnected since service plants are around the cropping area. With this mode of insertion, several categories of service plant traits are involved in both multi-pest regulation and disservice mitigation (Fig. 6). Potential incompatibilities (see yellow cells in the corresponding column of Fig. 6) were related to aboveground morphology and growth, ornamentation and extrafloral nectaries, chemistry, phenology and reproductive organ features. They all reflected a potential trade-off between attracting natural enemies and beneficial microbiota of targeted pests (to promote pest regulation) vs hampering non-targeted crop pests in particular aerial pathogens and arthropods (to limit disservices). This trade-off is caused by potential overlaps in the requirements of these organisms (e.g., in terms of floral

Type of traits		Service plants features to promote multi-pest regulation (summary of Fig. 3, Fig. 4 and Fig. 5)	Service plants features to mitigate disservices (summary of Supplementary material 5)		
			In field edges	In rotation	In intercropping
Morphology, growth, colour of vegetative parts	Aboveground morphology, growth and colour	Fast growing, tall and covering plant, with a large leaf area and biomass, an attractive colour and a morphology fitting with natural enemy needs	Not suitable as a shelter or refuges for crop pests		
				Tall plant at termination	
					Small, low covering plant, low biomass
	Root morphology and growth	Fast growth, high root density and biomass, large volume of soil prospected in depth and width Root epidermis made up of lignin, suberin, callose			Low biomass or roots located in layers not prospected by the crop
				Superficial root system	
	Soil-resource uptake	High uptake rate Use of the same resources as those taken up by weeds			Low uptake rate
					Use of resources different from those taken up by the crop
	Ornamentations and extrafloral nectaries	Promoting natural enemies	Not beneficial to crop pests (except for trap plants)		
Chemistry	Emission of volatile organic compounds	Hampering pests, attracting pests (for trap plants) Promoting natural enemies and beneficial microbiota and priming crop defence	Not attractive for crop pests (except for trap plants)		
					Not toxic for the crop
	Production of leaf/stem/root exudates	Hampering pests, attracting pests (for trap plants) Promoting natural enemies and beneficial microbiota and priming crop defence	Not attractive for crop pests (except for trap plants)		
				Not toxic for the crop	
	Plant tissue composition and degradation products from residues	Hampering pests Promoting natural enemies and beneficial microbiota and stimulating crop defence Improving soil biological activity and faster decomposition of crop residue	Not attractive for crop pests (except for trap plants)		
				Not toxic for the crop	
				Low carbon to nitrogen ratio Palatable for grazing High water content in tissue at plant destruction	
Phenology	Emergence, flowering	Germination/emergence earlier than weeds Compatible with the phenology of natural enemies	Not compatible with the phenology of pests (except for trap plants)		
				Annual or sterile plant Frost sensitive	
Reproductive organs	Morphology, colour and resources	Flower features attracting arthropod pests (trap plants) Flower favourable to natural enemies	Flowers not beneficial/attractive for aerial arthropod pests (except for trap plants)		

Fig. 6 Confrontation of the main service plant traits promoting multi-pest regulation and limiting potential disservices for three modes of insertion of service plants. On a given line (i.e trait category), a green cell shows no incompatibility between service plant features promoting multi-pest regulation and disservice limitation. Orange cells show incompatibility, and yellow cells indicate a potential incompatibility that is difficult to assess due to (1) specificities according to service plant and pest species and/or (2) knowledge gaps. The service plant features for multi-pest regulation are synthesized from Fig. 3. The service plant features to limit disservices are synthesized from Supplementary material 5. 'Host specificity' is not presented in this table, as it is considered as an integrative trait resulting from the combination of other traits that are (at least partly) presented in this table.

resources provided by service plants) or in their sensitivity (e.g., to chemical compounds produced by service plants), while these organisms belong to different trophic levels (e.g., pests vs natural enemies of pests) (Colazza et al. 2023). For instance, Poelman et al. (2012) demonstrated that both parasitoids and hyperparasitoids used similar chemical signals to locate their respective hosts (i.e., the herbivore for the parasitoid and the parasitoid itself for the hyperparasitoid). Overlaps in floral requirements between arthropods acting as pests vs as natural enemies were also reported. For example, Lavandero et al. (2006) showed that, for some plant species, nectar enhanced the fitness for not only natural enemies (parasitoids) but also arthropod pests. However, the nectar of other plant species enhanced the fitness of natural enemies only, suggesting that such antagonisms are not systematic. Similarly, deterrent leaf/stem exudates might be efficient against pests but also against natural enemies, particularly when their mode of action is generalist. However, in many situations natural enemies take advantage of the trapped prey by the sticky plants (Sect. 2.1.2).

3.2.2 Service plants in the field plot in rotation with crops

When service plants are grown in rotation with crops, service and crop plants grow in the same place (even if at different periods). As a consequence, additional service plant traits are involved in both multi-pest regulation and disservice mitigation, compared to the use of service plants in field edges (Sect. 3.2.1). Additional potential incompatibility in service plant traits was identified (see yellow and red cells in the corresponding column of Fig. 6). It was related to a potential trade-off between promoting multi-pest regulation vs mitigating (1) direct repression of crop growth (via residues of service plants), (2) persistence of service plants beyond the expected period, in addition to (3) non-targeted crop pest promotion.

Incompatibility was identified for service plant belowground morphology and growth, with high root growth (to promote multi-pest regulation) vs superficial root system (to ease destruction and therefore limit service plant persistence beyond the expected period).

As service and crop plants share the same soil (even if at different periods), traits related to the production of secondary compounds in soil may also generate incompatibility. Especially, secondary products (released by root exudation and/or residue decomposition of service plants) that are toxic for soil-borne pests or weeds (and therefore favorable to pest regulation) may also be:

- Toxic for the growth of the following crop (directly repressing crop growth): This is the case of residues of some Brassicaceae species that are toxic for soil-borne pests and weeds, but can reduce the germination and growth of several crop species (Haramoto and Gallandt 2007). However, this potential incompatibility is difficult to assess as the negative chemical effect on crops is hard to disentangle from a nutrient-mediated effect and would depend on the environmental conditions (Couedel et al. 2019).
- Attractive for other soil-borne pests: Fourie et al. (2016) reported both an allelopathic effect of Brassicaceous plants against several plant parasitic nematodes but also a promotion of other pests. However, the precise underlying determinants remain unclear.

3.2.3 Service plants in the field plot in intercropping with crops

When growing service plants in intercropping with the crop, service and crop plants grow at the same place and at the same time. So, trait incompatibility between multi-pest regulation and disservice mitigation was even greater, compared to the use of service plants in field edges or crop rotation (see yellow and orange cells in the corresponding column of Fig. 6). On the one hand, the trade-offs identified for the other modes of insertion of service plants also apply in the case of intercropping, and some of these trade-offs may be exacerbated. For example, the direct repression of crop growth caused by chemical compounds emitted by service plants can be mediated not only by service plant residues but also by the exudates emitted during the growth cycle of service plants (for example, a high phytotoxic activity of root exudates was reported for sorghum service plants in Głąb et al. 2017). On the other hand, an additional potential trade-off was identified between promoting multi-pest regulation vs mitigating direct repression of crop growth due to competition for resources (light, water, nutrients) by service plants.

The main trait incompatibility was between growing (1) tall and wide service plants with a high above- and below-ground biomass, a large leaf area and with high resource uptake (to promote multi-pest regulation) vs (2) small service plants with a low above- and below-ground biomass, low leaf area and with low resource uptake (to limit direct repression of crop growth). This trade-off is classical in studies on the use of service plants in intercropping with crop plants (e.g., Gardarin et al. 2022).

4 Discussion

This study based on literature review provides a comprehensive, thought-provoking overview of the potential of service plants for multi-pest regulation. In addition to integrating different pest categories (weeds, arthropods, belowground pests and aerial pathogens), the added-value of this study is the inclusion of potential disservices that service plants may cause in their different modes of insertion (field edges, or within the field in rotation or intercropping with crops). At the crossroads of disciplines (often working independently), such a knowledge synthesis provides new insights on the role of service plants for multi-pest regulation. It should be useful for guiding orientations for future research on agroecological transition.

4.1 An *a priori* good potential of service plants for multi-pest regulation

When focusing on service plant traits related to vegetative morphology and growth, phenology and reproduction, our conceptual framework identified no strong incompatibility in the regulation of the different pests. A key finding was that, globally, using tall, wide and rapidly growing service plants, with a high biomass (above- and below-ground), is inclined to promote the regulation of weeds, arthropods, soil-borne pests and aerial pathogens. This finding is linked to the key role of the spatial occupation of service plants (both above- and below-ground) in promoting the different pest regulation mechanisms. The confrontation of this finding with the literature is made difficult by the challenge to experimentally dissociate the effects of traits related to growth and morphology from other traits.

Unfortunately, the analysis could not be taken as far with regards to chemical traits. Indeed, while chemical traits were also identified as playing a role in most pest regulation mechanisms, we were not able to definitely conclude on the compatibility or not between the regulation of the different types of pests by service plants, due to (1) the large diversity of molecules that may be released by service plants, (2) the impact of biotic interactions and abiotic factors on the production and release of these molecules, (3) the absence of a synthetic database compiling all available information on the effects of these molecules on the diversity of pests and beneficial organisms, and (4) knowledge gaps. Our brief analysis of the literature focusing on a few well-studied molecules (DIMBOA and glucosinolates) identified both compatibility and incompatibility situations. To go further, a thorough analysis of the impacts of the molecules released by service plants on both the different pests and their natural enemies but also on how the production and emission of these compounds vary depending on the environment, plant genotype, physiological state or phenology is required in order to provide a comprehensive overview of the compatibility regarding the multi-pest regulation through chemical compounds.

Beyond the particular case of chemical traits, our synthesis on the mechanisms and traits involved in the regulation of each pest category identified many knowledge gaps that are mainly due to the difficulty to disentangle the effects of each trait (see above) and each regulation mechanism (as they often occur concomitantly). Identifying field-based evidence of the effects of the different regulation mechanisms and hierarchizing the role of these different mechanisms are still scientific fronts for most pest categories. Despite these gaps, the present synthesis allowed us to identify that the role of service plants to promote pest regulation differed among pest categories, with aerial pathogens being the pest category with the lower regulation potential by service plants.

4.2 A key challenge for multi-pest regulation by service plants: to mitigate disservices

Another key finding was that the strongest incompatibility was between promoting pest regulation vs mitigating potential disservices potentially caused by service plants. Our approach allowed to identify three key trade-offs underlying this incompatibility:

- The main one for service plants intercropped with crops was between promoting high service plant growth (to promote pest regulation; Sect. 4.1) vs low service plant growth (to limit direct crop growth repression). This antagonism has been frequently reported (Gardarin et al. 2022). However, its magnitude can be variable. For example, it would be lower for tall crops (e.g., banana tree) (Tardy et al. 2015), since the possibility for smaller service plants to compete for light with crops is reduced. Belowground, this antagonism could be mitigated by using service plants with a root distribution that is complementary to that of the crop plant, or by using Fabaceae service plants that can benefit from symbiotic dinitrogen fixation, thereby limiting nitrogen competition (Tardy et al. 2017).
- A potential trade-off was also identified between attracting natural enemies (to promote pest regulation) vs not attracting or hosting non-targeted pests (to limit pest promotion). Such trade-off may even occur between very different organisms (e.g., plants hosting natural enemies of insects being reservoirs for pathogens). The mitigation of such trade-off is complex and requires greater convergence between disciplines, for example entomology and plant pathology, but also between the scales at which the mechanisms potentially antagonist are addressed (from molecular/biochemical scale to landscape, as well as plant cover and plant-to-plant interactions scale).
- The last one was between releasing secondary compounds that are toxic for pests (to promote pest regulation) vs that are non-toxic for the crop (to limit direct crop growth repression).

Some elements from the literature confirmed the possibilities of such trade-offs in field conditions (Sect. 3.2). Here again (as in Sect. 4.1), a thorough analysis of the impacts of the molecules released by service plants on the different pests, their natural enemies and the crop plants is required to go further.

Interestingly, our study identified that the magnitude of these trade-offs, and therefore the level of incompatibility between promoting multi-pest regulation vs mitigating disservices, varied with the mode of insertion of service plants. Incompatibility increased with proximity in space and time between service and crop plants, from the use of service plants in field edges, to rotation and finally to intercropping with the crop

Altogether, these elements highlight the importance of reinforcing research on service plants focusing on disservice mitigation, in addition to multi-pest regulation promotion (Sect. 4.3).

4.3 How to manage antagonisms between pest regulation and disservice mitigation?

Our theoretical and systematic approach identified many potential antagonisms between multi-pest regulation and disservice limitations. They may be difficult to manage simultaneously. However, all the pests do not induce the same level of risk on a given crop in a given field. The risk of favoring some pests can be taken for pests unlikely to be present/harmful in a given situation. Management practices can be used to drive the balance between pest regulation and disservice mitigation. On this basis, a three-step strategy can be proposed to manage antagonisms. In the first step, we recommend to prioritize the pests to target, according to the most damaging pest in the production situation (according to the crop, soil, climate, expected pest pressure). Then, we recommend to prioritize the regulation mechanisms to promote, according to their efficiency and the risk of potential antagonisms with disservice mitigation. Finally, to manage the potential antagonisms in this situation, we recommend to judiciously coordinate in a systemic approach the choice of service plants, their mode of insertion and management (in articulation with crop choice, arrangement and management):

- Service plant species/variety should be chosen according to the traits described above by targeting the traits that promote the pest regulation mechanisms identified in step 1. The possibility of using service plants as mono- or as multi-species/variety should be considered (Sect. 4.4).
- The mode of insertion of service plants in both space and time should be optimized to promote pest regulation while limiting disservices. For that purpose, we recommend to reduce as much as possible direct interactions between service and crop plants. When possible, prefer using service plants in field edges > rotation > intercropping. Intermediate options can also be implemented with for example cover crops used in relay intercropping (intermediate option between rotation and association as described in Gardarin et al. 2022) or as permanent cover crops. When intercropping with the main crop is necessary (to promote the targeted pest regulation mechanisms or for other agronomical reasons), service plants can be sown by alternating rows/strips of service and crop plants, rather than in total mixture (to limit disservices). If a full mixture is required, adjusting the relative densities of service and crop plants can be used to drive the balance between pest regulation vs disservice mitigation.
- Finally, the management of service plants during their growth cycle can be adjusted to drive this balance. This point is documented in Gardarin et al. (2022) for the case of service plants intercropped with crop plants. For example, service plant mowing is an option to limit competition with crops (if service plants are intercropped with crops in alternated strips, or if they are sown before the crop). Also, the service plant destruction period should be precisely adjusted to promote pest regulation while limiting disservices. As an illustration, service plant flowering should be promoted to attract natural enemies dependent on floral resources, but destruction before seed production is required to reduce the risk of service plant persistence in the following crops. In the same vein, the service plant destruction method and traits should be judiciously coordinated, with for example the mechanical destruction of easy-to-destruct plant species, or the use of winter-kill for frost-sensitive plant species. A last example is the management of service plant residues that should also be judiciously coordinated with service plant chemical properties, with residue exported (to avoid toxicity for following crops) vs kept in the field and even shred and buried to promote the regulation of soil-borne pests and weeds that are sensitive to chemical compounds.

These few examples illustrate the diversity of management options to drive the balance between multi-pest regulation promotion and disservice mitigation. They highlight the necessity to think and manage service plants at the cropping system level, as if they were crop plants. Finally, given the large diversity of management options and the diversity in the responses of service plant species/varieties, these examples point out how increasing and synthesizing knowledge on the effect of management practices is crucial.

4.4 Limits, added value and prospects

We acknowledge that the present review was not exhaustive. For instance, it did not consider all the pests that may be regulated by service plants (e.g., mollusks or rodents), nor all the disservices that service plants may cause in agroecosystems. Moreover, this study only focused on key mechanisms and service plant traits, for which knowledge was sufficient to apply our conceptual framework. In addition, it did not consider direct interactions among pests or among beneficial organisms which are known to affect pest dynamics (Couedel et al. 2019). Another limitation lies on the fact that the trait-based approach used in the present study focuses on the traits of the service plants, but not on those of the pests to be regulated. As such, our analysis does not allow us to understand aspects of co-evolution between service plants and pests, although these mechanisms are likely to play an important role, particularly in attraction and repulsion mechanisms. These aspects of co-evolution could pose a threat if insect pests are able to adapt to the repellent molecules emitted by service plants, which would then lose their repellent power. We can also imagine opportunities if natural enemies initially repelled by these molecules manage to adapt. The extent to which these co-evolutionary phenomena represent opportunities or threats could be the subject of specific studies. Also, this study did not directly address some key issues: is it possible and how to reach ideal service plant trait combinations? Which species/varieties should be used? Do we need to mix several species/varieties? All these limitations should be addressed in future research actions (see below).

However, this work is a real step forward. First, it provides a general overview that overrides individual disciplines. It illustrates how a trait-based approach can be used to synthesize knowledge from different disciplines and to provide a tool for cross-disciplinary dialogue. In the next future, the approach developed here could be applied to additional pests and disservices. It could also include other (non-pest) services that may be delivered by service plants, such as fertility support, carbon sequestration, in order to analyze the potential of service plants for multi-service provision (Damour et al. 2015). It will be crucial to analyze whether service plants that are good for other services primarily targeted by farmers (e.g., fertility or soil structuration) are also good at regulating pests, and vice versa (Storkey et al. 2015).

Second, this work identifies mechanisms and traits with knowledge gaps, on which research should focus on. Even within a given pest category, we identified many knowledge gaps (Sect. 2.1), with generally greater gaps when multitrophic interactions are involved (e.g., indirect regulation mechanisms involving beneficial microbiota and/or crop plants). When mechanisms and traits were analyzed across pest categories or in articulation with disservice mitigation, our analysis was limited by the lack of knowledge synthesis on specific topics. As stated above (Sect. 4.1 and 4.2), a comprehensive overview of the effects of the different molecules released by service plants on the different actors (pests, beneficial organisms, crop plants) should be conducted in priority. In addition to mechanisms and traits, our work also puts forward the necessity to investigate in more detail the role of management practices on the balance between multipest regulation and disservice mitigation (Sect. 4.3). Indeed, the main difficult-to-solve trade-off between high vs low service plant growth can be at least partly solved by judiciously coordinating in a systemic approach service plant choice, mode of insertion and management as well as crop plant choice, arrangement and management. However, different contexts can produce conflicting effects. While knowledge is available, knowledge remains too fragmentary and fragmented so that we lack scientific and technical references on how to concretely coordinate these different elements according to the local production situation (soil, climate, pest pressure, field size and shape, infrastructures…). Articulating field experiments and expert knowledge, and above all, synthesizing knowledge should be among the priority research actions.

Third, this work provides food for thought regarding the choice of service plant species/varieties to be implemented according to their traits and the targeted pest regulation mechanisms. However, the question of how to achieve the ideal combinations of traits identified in this study remains open. Is it possible to identify a single species/variety that matches this ideotype? Alternatively, if different species need to be combined (Malezieux et al. 2009), should species with the same (ideal) trait values be combined? Or should contrasting species be combined in order to cover a range of trait values (e.g., combining plant species with different biomass production levels and dynamics in order to achieve a high biomass production at community level)? The approach used in this study focuses on the role of 'dominant traits' (as defined by Díaz et al. 2007) of service plants, and could refer to the concept of 'community weighted means' (corresponding, for each trait, to the mean of trait values in the community, weighted by the relative abundance of the species carrying each value). We identified the necessity of functional diversity (e.g., diversity of traits related to flowers and seeds to promote a diversity of weed seed predators; Sect. 2.1.1) for only a small number of traits and targeted pests. To broaden this approach, using the framework proposed by Díaz et al. (2007) could help to analyze the role of community weighted means, functional diversity and idiosyncratic species in achieving the ideal combinations of traits.

Moreover, the lack of knowledge on the large diversity of potential service plants species/varieties and their response to environmental conditions (that vary with pedoclimate, management practices or presence of a neighboring plants of other species in case of mixture) makes it difficult to choose the species/varieties to use. Rough information can be used: e.g., choosing species from different botanical families to limit risks by exploiting host specificity, or using Brassicaceae and Poaceae species given their high growth potential as discussed in Sect. 3.1.2, or using Fabaceae species to limit competition for nitrogen (Corre-Hellou et al. 2011). Considering plant species more broadly based on their functional groups may be a relevant option (e.g., aromatic plants or dinitrogen-fixing plants). However, this information neglects the wide inter-species diversity of trait values (even in a botanical family) both under potential conditions and in response to biotic and abiotic factors. It also neglects the role of idiosyncratic species (Díaz et al. 2007). Our work therefore highlights the necessity to investigate more precisely and to synthesize knowledge on intra- and inter-specific variability of key traits and trait response to environment, in order to infer on their effects on pest regulation and disservice mitigation. This necessity was already reported for the particular case of service plants intercropped with cash crops (Gardarin et al. 2022), but it is also valid for other modes of insertion of service plant. Conducting screening experiments (Isbell et al. 2017), including the use of high-throughput phenotyping platforms, could be highly beneficial given the large number and diversity of potential service plants (Jeudy et al. 2016; Li et al. 2022).

Weeds are among the pests that can be targeted by the use of service plants. However, as mentioned in the Introduction section, weeds can also provide services related to the regulation of other pests (e.g., by promoting natural enemies) (Laffon et al. 2024). Thus, the spontaneous flora can play a dual role, on the one hand, being harmful to crop production and therefore a target of regulation and, on the other hand, being beneficial to crop production and therefore considered as spontaneous service plants. In reality, this duality is not so clear-cut and there is a gradient between these two situations, as it is the case for non-spontaneous (i.e., sown/planted) service plants. Considering the 'service-disservice balance' is an option to go beyond the usual view that 'weeds' (i.e., spontaneous plants) only cause harmfulness and disservices, and service plants (i.e., sown/planted plants) only provide benefits and services. Thus, the concept of service plants should include spontaneous plants, which are likely to encompass a much greater variability (Roy et al. 2024).

To go beyond an approach exclusively based on service plant traits, mechanistic (i.e., process-based) models should play a key role to explicitly consider the role of management practices, in interaction with soil, (changing) climate, pest pressure and pest traits (Storkey et al. 2015). To our knowledge, such models exist per pest category (e.g., Colbach et al. 2021; Alexandridis et al. 2021; Nilusmas et al. 2020), but usually not across the pest categories studied in the present article. Developing such integrative models or connecting existing models is among the research actions to develop, in order to investigate (through simulation) the effects of service plants on multi-pest regulation and disservice mitigation in diverse contexts. We also advocate for the development of an international database to gather and share knowledge on service plant traits and performance (success and failure) in regulating different pests, while mitigating disservices, in different cropping systems and environmental conditions (BP-DB, Biocontrol Plant – Database, in preparation). All these research actions should help to provide guidelines to help farmers design service-plant based pest management strategies, according to their objective and local production situations. They should also guide breeders on the key service plant traits to focus on in order to breed more suitable varieties.

Finally, the role of service plants for multi-pest regulation in agroecosystems needs to be analyzed with regard to other agroecological pest management options (Deguine et al. 2023). Beyond all these biological/ecological/agronomic considerations, the role of service plants also needs to be analyzed from a socio-economic perspective.

5 Conclusion

This study used an original trait-based approach to provide an overview of the potential of service plants for regulating multiple and diverse pests (weeds, herbivores, above- and below-ground pathogens/parasites), while limiting disservices in different modes of insertion of service plants (intercropping or in rotation with the crop plants, or in field edges).

We found that most service plant traits were involved in the regulation of several pest categories. In general, the same plant features were favorable for the regulation of different pest categories (e.g., using tall, wide and fast-growing service plants, with a high biomass tends to promote the regulation of weeds, arthropods, soil-borne pests and aerial pathogens). Thus, although caution should be exercised due to knowledge gaps, the present study identified an *a priori* good potential of service plants for multi-pest regulation. It also identified the ideal combination of service plant traits for multi-pest regulation. However, this study highlights some incompatibility between the ideal service plant traits for multi-pest regulation and the service plant traits that limit disservices. We identified that the challenge lied at least as much in mitigating the disservices that service plants may cause (such as directly affecting crop growth, becoming weeds in subsequent crops, promoting non-targeted pests) as in promoting multi-pest regulation. The level of incompatibility between promoting multi-pest regulation vs mitigating disservices varied with the mode of insertion of service plants, according to the intensity of interaction between service and crop plants. Beyond these findings, we highlight how a trait-based approach can be used to synthesize knowledge from different disciplines and to provide a tool for cross-disciplinary dialogue. We also identified priority research actions that are needed to increase genericity and adaptation to local conditions and provide foundations for the design of service-plant based pest-regulation strategies and cropping systems. Articulating different approaches and disciplines is crucial to encompass the different scales (from molecule to agroecosystem), study objects (from pests, and service and crop plants, to farmers and stakeholders in the agricultural sector) and sources of knowledge (experiment, expert knowledge, model-based simulation). If service plants are an option among others, a diversified toolbox is needed to manage pests while minimizing the use of pesticides as much as possible. Among all available agroecological practices, service plants offer an opportunity to (re)design innovative agroecosystems by diversifying them at different scales.

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