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Multitrophic biodiversity enhances ecosystem functions, services and ecological intensification in agriculture

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Abstract

One central challenge for humanity is to mitigate and adapt to an ongoing climate and biodiversity crisis while providing resources to a growing human population. Ecological intensification (EI) aims to maximize crop productivity while minimizing impacts on the environment, especially by using biodiversity to improve ecosystem functions and services. Many EI measures are based on trophic interactions between organisms (e.g. pollination, biocontrol). Here, we investigate how research on multitrophic effects of biodiversity on ecosystem functioning could advance the application of EI measures in agriculture and forestry. We review previous studies and use qualitative analyses of the literature to test how important variables such as land-use parameters or habitat complexity affect multitrophic diversity, ecosystem functions and multitrophic biodiversity–ecosystem functioning relationships. We found that positive effects of biodiversity on ecosystem functions are prevalent in production systems, largely across ecosystem function dimensions, trophic levels, study methodologies and different ecosystem functions, however, with certain context dependencies. We also found strong impacts of land use and management on multitrophic biodiversity and ecosystem functions. We detected knowledge gaps in terms of data from underrepresented geographical areas, production systems, organism groups and functional diversity measurements. Additionally, we identified several aspects that require more attention in the future, such as trade-offs between multiple functions, temporal dynamics, effects of climate change, the spatial scale of the measures and their implementation. This information will be vital to ensure that agricultural and forest landscapes produce resources for humanity sustainably within the environmental limits of the planet.

Keywords agroecosystem BEF, food web, multifunctionality, pest control, biocontrol, pollination

多营养级的生物多样性可增强农业生态系统的功能、服务和生态集约化

摘要：人类面临的一个重要挑战是在为不断增长的人口提供资源的同时，减轻和适应持续的气候和生物多样性危机。生态集约化旨在最大限度地提高作物生产力，同时尽量减少对环境的影响，特别是通过利用生物多样性来改善生态系统功能和服务。许多生态集约化措施是基于生物营养级之间的相互作用(如授粉、生物防治)。在此，我们探讨了生物多样性对生态系统功能的多营养级效应的研究，如何能促进生

态集约化措施在农业和林业中的应用。我们综述已有研究报道，并利用文献的定性分析来检验土地利用参数或栖息地复杂性等重要变量如何影响多营养级多样性、生态系统功能以及多营养级生物多样性与生态系统功能的关系。研究结果表明，生物多样性对生态系统功能的正效应在生产系统中普遍存在，主要跨越生态系统功能维度、营养级水平、研究方法和不同的生态系统功能，但存在一定程度的环境依赖性。土地利用和管理对多营养生物多样性和生态系统功能有显著影响。我们在代表性不足的地理区域、生产系统、生物类群和功能多样性测量数据方面发现了知识差距。此外，我们还确定了未来需要更多关注的几个方面，如多种功能之间的权衡、时间动态、气候变化的影响、措施的空间尺度及其实施。这些信息对于确保农业和森林景观在地球环境有限的情况下，持续地为人类生产资源至关重要。

关键词：农业生态系统生物多样性生态系统功能,食物网，多功能，害虫防治，生物防治，传粉

INTRODUCTION AND REVIEW

One of the biggest challenges of this century is the provisioning of food to people while safeguarding biodiversity under changing global conditions. Current agricultural production often aims to maximize yield of agricultural products or their profitability. Unfortunately, in many countries, agricultural production has already reached its maximum capacity, however, drawing on extensive inputs (fertilizer, pesticides) and degrading ecosystem functions (Bommarco *et al.* 2013; Joseph *et al.* 2018). In addition, the productivity of agroecosystems has been shown to decline with agricultural intensification, and such losses do not recover even centuries after the agricultural abandonment (Isbell *et al.* 2019). Such deteriorations in ecosystem functioning are to a large extent driven by the loss of biodiversity (Hautier *et al.* 2015). So far, the sustainability of agricultural production, the stability of production systems the provisioning of other ecosystem services besides production and the maintenance of biodiversity are only rarely pursued as important aims in agricultural landscapes.

Many ecological studies have shown in experimental settings, but also in naturally assembled communities and agricultural systems (van der Plas 2019), that the relationships between biodiversity and ecosystem functions (BEF) are widespread and usually positive. Indeed, BEF relations in agroecosystems seem to be universal and robust to disturbances (Craven *et al.* 2016) and it has been suggested that BEF research may help to inform real-world ecosystem management (Manning *et al.* 2019). However, many earlier BEF studies focussed only on one trophic level, primarily the level of plants. More recently, it has been recommended to put greater emphasis on BEF relations across food webs (Eisenhauer *et al.* 2019; Hines and Gessner 2012; Thompson *et al.* 2012), as land-use effects on biodiversity and functions are often indirectly manifested through trophic cascades (Barnes *et al.* 2017; Chen *et al.* 2023; Woodcock *et al.* 2009).

Ecological intensification (EI) is an agricultural framework that aims to maximize crop productivity while minimizing synthetic inputs and cropland expansion, and that uses the promotion of biodiversity as a tool to do so (Bommarco *et al.* 2013; Garibaldi *et al.* 2019). More specifically, by enhancing coexisting biota (e.g. pollinators, natural enemies, the plant microbiome, detritivores, neighbouring plants in companion planting) and biological regulation, EI aims to improve plant water and nutrient uptake, stress tolerance, pollination and defenses against pests and diseases. Thus, this concept attempts to mimic natural systems and especially their functions (Ratnadass and Barzman 2014). Traditional agricultural systems have often, intentionally or not, also followed this approach (Malézieux 2012). EI shares certain aspects with other sustainable agriculture frameworks such as agroecology, organic agriculture, conservation agriculture and integrated pest management (Hobbs *et al.* 2008; Ratnadass and Barzman 2014).

The concept of EI encompasses the improvement of ecosystem functions and the harnessing of ecosystem services as one main approach of increasing production (Bommarco *et al.* 2013). In this regard, BEF research could help to pinpoint the measures that increase production while, or specifically through, increasing biodiversity in the agricultural landscape (Bommarco *et al.* 2013). Since some of the most important measures of EI are based on trophic interactions (e.g. pollination and pest control), results from multitrophic BEF research may contribute important information on how to

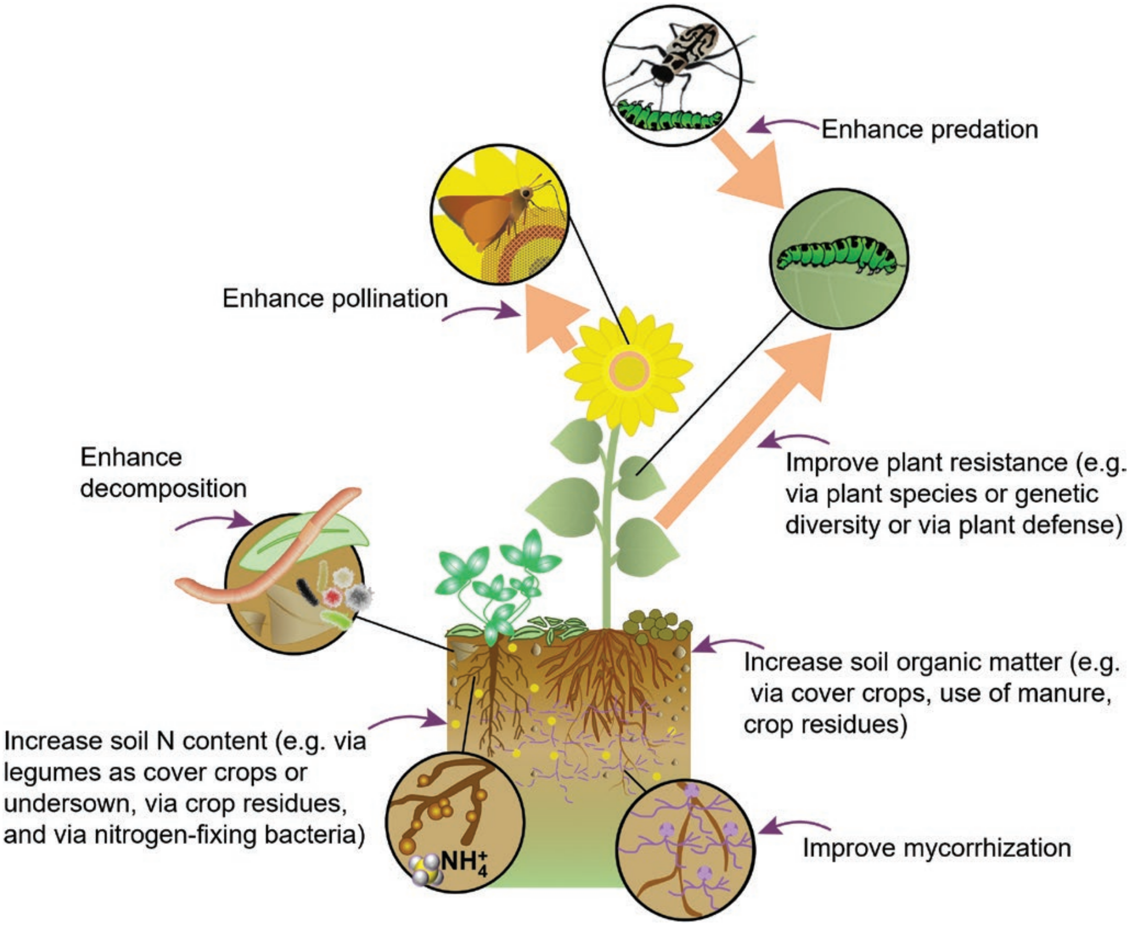

Figure 1: EI measures in a multitrophic context. Purple arrows mark those points where EI measures could enhance functions to ultimately increase crop production and stability. For details see text and Supplementary Table S9. The Images used to create the diagram are from Integration and Application Network (ian.umces.edu/media-library)

support multitrophic food webs as well as maximize multitrophic functions (Supplementary Table S9).

Trophic interactions in EI

One of the most important trophic interactions at the heart of agricultural production is the pollination of crop plants by animals (typically insects but in some cases also birds, reptiles or mammals, Fig. 1). The improvement of this ecological function in the agricultural context can be directly related to high yields. Unfortunately, in many agricultural areas, conventional intensification, pesticide use and large-scale landscape change has led to a loss in natural pollinator species richness and abundance (Burkle *et al.* 2013; Goulson *et al.* 2015; Potts *et al.* 2010; Powney *et al.* 2019) and thus often to risks of yield losses (Klein *et al.* 2007). With changing climatic conditions, further disruptions of plant–pollinator interactions may occur (Geldmann and González-Varo 2018; Memmott *et al.* 2007). BEF research on pollination has shown that a higher diversity of pollinator species typically leads to improved pollination of plants in general (Biesmeijer *et al.* 2006) but also of crop plants (Garibaldi *et al.* 2013; Kremen 2020), and also to greater yields in pollinated crops, e.g. fruits and vegetables (Kremen 2020). Specifically, studies have shown that wild bee species are often better pollinators for crop plants than honeybees (Garibaldi *et al.* 2013). One of the most common measures to improve pollination success in agriculture is the artificial and costly augmentation of the insect pollinator community through adding many individuals of a single pollinator species, often only temporarily and not without risk to the natural communities due to competition (Velthuis and Doorn 2006). In EI, other measures to increase pollination functions would be more desirable and are already used. For example, pollinators are attracted to crop fields by flower strips between fields or flowering weeds as food resources and habitat (Fig. 2; Supplementary Table S9), and this may also improve pollination of the target crops (Carvalheiro *et al.* 2011). Distance to natural and semi-natural habitat implies a concept at larger spatial scales. For example, short distances to forest edges (providing nesting or mating space) lead to higher pollinator abundance (and richness) in oilseed rape (Bailey *et al.* 2014), but this depends on bee size because of longer dispersal distances of larger bees. Overall, a change of habitat measures and habitat configuration at the landscape scale is likely the most promising measure to support pollinators and increase yield through increased pollination. A challenge, especially for smaller-scale actions remains: some measures may not only benefit pollinators but also their natural enemies, cancelling out positive effects on yield (Shackelford *et al.* 2013).

A further important trophic interaction that can be used to enhance yield under EI management is the biocontrol of harmful organisms for the target organism (Fig. 1). In agriculture this is usually the crop plant (sometimes animals, i.e. livestock), in forestry the trees. These harmful organisms can be any herbivore or pathogen species, the biocontrol species is their natural predator, parasite or pathogen. Most often in agriculture and forestry biocontrol organisms are arthropods or birds. Generally, pest control is often inefficient in conventional agriculture and especially in intensive agricultural areas. This is because of an overuse of pesticides, the resistance of pests to pesticides and the complete degradation of natural pest control due to a loss of habitats for predators (Fig. 2). In fact, predators can be more strongly affected by land use than other trophic levels in the food web (Barnes *et al.* 2014, 2017) due to their smaller population sizes and larger habitat requirements. BEF research has found that if a high diversity of predators can be maintained, this can indeed increase the predation pressure on herbivores (Rusch *et al.* 2015) and improve growing conditions for plants (Gaba *et al.* 2020). The measures that may be used in EI to improve biocontrol of crop-damaging organisms include (similar to the pollination case) the augmentation of artificially raised enemies. Many different organisms such as parasitic wasps, aphid predators and predatory nematodes or mites are readily used here (Zaitsev *et al.* 2018). As in the pollination case, this direct addition of a high number

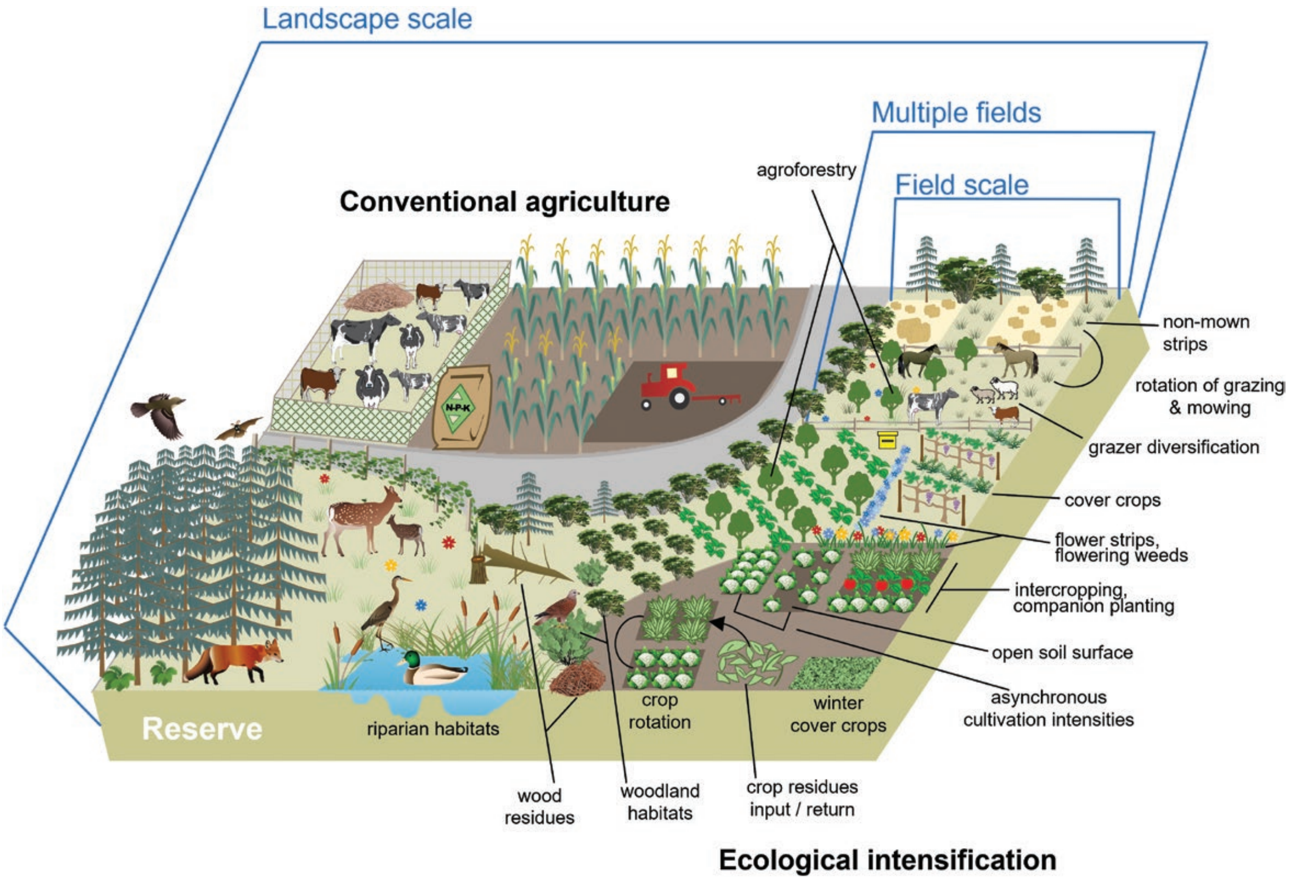

Figure 2: EI management at different spatial scales, from the field scale to the multiple-field scale to the landscape scale. See Supplementary Table S9 for details on each EI measure. The Images used to create the diagram are from Integration and Application Network (ian.umces.edu/media-library)

of individuals of one species does not fit well with the idea of enhancing biodiversity to achieve EI (Ratnadass and Barzman 2014) and bears similar risks of negatively influencing natural food webs and ecosystem functions (Hajek and Eilenberg 2018). A further measure that can be used at the field scale (Fig. 2; Supplementary Table S9) is the increase in crop diversity to benefit communities of predator species (Poeydebat *et al.* 2017; Thomine *et al.* 2022). At a larger scale—more difficult to achieve but often more effective—is the creation or maintenance of habitat for natural enemies between fields or at the landscape scale (Fig. 2; Supplementary Table S9), sometimes involving a complete agroecosystem redesign (Ratnadass and Barzman 2014). However, several challenges are involved in the possible enhancement of biological control under EI. Probably the most important and most often addressed complication is intraguild predation that can lead to predators feeding on their own guild and ultimately decreasing predation pressure on the targeted herbivores (Imboma *et al.* 2020). Additional complications may come from other food web interactions, e.g., alternative prey may affect predation (Somers *et al.* 2015). Evolution may also come in the way of EI measures, as pests and pathogens may adapt to circumvent single measures. This can lead e.g. to a resistance of pests to certain predator species, suggesting that a suit of measures needs to be put in place (Ratnadass and Barzman 2014). Thus, a more mechanistic understanding of the functional responses of predator communities to land use is required to be able to make full use of predator–prey interactions as successful measures in EI.

In addition to pollination and biocontrol, other trophic interactions and processes in a food-web context may be useful targets of EI measures (Fig. 1; Supplementary Table S9). Mycorrhizal fungi are one important group of soil organisms that can strongly enhance agricultural production (Hartmann and Six 2023). Other groups that are beneficial in EI management are nitrogen-fixing bacteria (Coniglio *et al.* 2019; Leggett *et al.* 2017), earthworms that can be used in vermicomposting and other invertebrates that aerate soil (Kremen 2020), even though this is not necessarily considered a trophic interaction. Both field and landscape-scale measures can be taken to improve decomposition and soil C and N dynamics in agroecosystems (Supplementary Table S9), for instance by adding crops in rotation to crop fields (McDaniel *et al.* 2014) and crop residues (Sereda *et al.* 2015).

In addition to the already described measures of EI that mostly work through top-down trophic interactions, EI could also be achieved by facilitating bottom-up interactions via plant resistance to pests and pathogens, e.g. through better nutrient conditions via fertilization crops and manure, less erosion, stronger individual plant defenses (Han *et al.* 2022). Including perennial crops before rotating to annual grain crop can regenerate soil health and increase crop resistance to pests (Ryan *et al.* 2018). On a different note, increased plant functional, species and genetic diversity may help to improve crop resistance to pests and herbivory (Barnes *et al.* 2020; Brooker *et al.* 2023; Kopp *et al.* 2023; Rottstock *et al.* 2014; Schöb *et al.* 2023).

Food webs and fluxes

Even intensive agroecosystems and production forests do not only contain individual interacting species pairs but more or less species-rich food webs. However, not many food-web studies have been conducted in production areas. A recent study constructed hybrid networks (combined plant–pollinator and plant–herbivore networks) and showed effects of agricultural intensification on network robustness that depended on the extinction scenario (Morrison *et al.* 2020). Quantified interaction networks which are based on empirically recorded interaction frequencies or strengths (e.g. via stomach content), in addition to presence–absence of species at a field site, are rare. A study recording quantified aphid–parasitoid–hyperparasitoid food webs showed that agricultural intensification may reduce the temporal stability of these food webs (Gagic *et al.* 2012). Less sampling-intensive co-occurrence networks have been analysed for soil microbes and have shown that agricultural intensification may reduce the complexity of soil food webs (Di Mauro *et al.* 2022).

Studies have also attempted to link food-web structure to functions such as predation. For example, more complex soil nematode food webs have been shown to have a higher potential for pest control in croplands (Sánchez-Moreno and Ferris 2007). Ecosystem energetics allow disentangling different dimensions of ecosystem functioning, such as stocks, fluxes and rates, which collectively capture the whole loop of matter transformation in an ecosystem. While stocks show the distribution of stored energy across trophic levels (e.g. standing biomass, detritus amount), fluxes link the stocks via energy transfers (e.g. production, decomposition, predation) that occur at different rates (e.g. carbon uptake efficiency, decomposition rates, predation rates). Energy or matter fluxes in food webs have rarely been considered in studies in a production context, despite the potential to better model and achieve yield increases. Early models of soil food webs and related nutrient cycling have been used to increase nutrient supply in agriculture (de Ruiter *et al.* 1994). More recently, it was shown that plant diversity in mown grasslands has strong effects on biomass storage and fluxes throughout all food-web levels (Barnes *et al.* 2020; Buzhdygan *et al.* 2020), implying that agricultural management should favour high plant diversity. Land-use transformation, e.g. from tropical forests to oil palm plantations; can lead to strong negative effects on species diversity, density and biomass and a strong reduction in energy fluxes (Barnes *et al.* 2014) and multitrophic multifunctionality (Potapov *et al.* 2019) and even a complete collapse of the food web (Malhi *et al.* 2022). Overall, a networks perspective has great potential to support sustainable agriculture, e.g. through linking multitrophic diversity to function (Potapov *et al.* 2019), identifying individual species in a food web with particular traits and designing targeted management measures (Allen *et al.* 2022).

Multiple ecosystem functions and services

Traditionally, provisioning services (such as harvests of crops, hay and wood) were considered the most important ecosystem services of productive landscapes such as agricultural areas or production forests. More recently, other ecosystem functions and services have come into the attention of the research field and of the public and these may be key to the development of EI. Examples are supporting services such as nitrification, regulating services such as pest control and cultural and aesthetic services such as human health (Gurevitch 2022; Meyer *et al.* 2018; Sacchelli *et al.* 2013; Schils *et al.* 2022; Zirbel *et al.* 2019). BEF research on multiple ecosystem functions, or more specifically on the relationship between biodiversity and ecosystem multifunctionality, has shown that multiple functions need even more species to deliver them than single functions, especially over time (Isbell *et al.* 2011; Meyer *et al.* 2016; Zavaleta *et al.* 2010), and that the link between multidiversity and multifunctionality is stronger than the link between single diversity measures and single functions (Wang *et al.* 2019). Also, the biodiversity–multifunctionality relationships strongly strengthens when at least one additional trophic level is added to the food web (Anujan *et al.* 2021). Rice–aquatic animal cocultures, e.g., increase rice yield but also improve soil organic carbon and total nitrogen while insect pests and weeds are reduced, even with lower pesticide and fertilizer amounts compared with rice monocultures (Ji *et al.* 2023). Agricultural management alters both, multidiversity and multifunctionality, and EI measures can be taken to improve them simultaneously (Potapov *et al.* 2019; Ren *et al.* 2018; Schils *et al.* 2022). For example, livestock diversification of sheep and cattle in grasslands increased ecosystem multifunctionality by increasing the multidiversity of plants, insects, soil microbes and nematodes (Wang *et al.* 2019). Relatively recently, with the rapid development of molecular methods, a large number of studies has investigated soil biodiversity–multifunctionality relationships in agricultural contexts and these studies have found, e.g., a positive effect of plant and soil biodiversity on soil- and plant-related multifunctionality (Blesh 2018; Cui *et al.* 2022) and often clear agricultural management effects on soil multifunctionality (Garland *et al.* 2021; Li *et al.* 2021; Wang *et al.* 2020; Xu *et al.* 2022; Zhang *et al.* 2021a, 2021b).

In the following, we use a systematic literature search and analysis to investigate how multitrophic BEF research may facilitate the development of EI in agriculture and forestry. Specifically, we ask if multitrophic diversity, ecosystem functions and BEF relationships depend on the environmental and biotic contexts of the study system, on the measured dimensions of ecosystem functions (i.e. rate *vs.* flux *vs.* standing stock), on trophic levels, on the methodology of the study or on different ecosystem functions considered. We also analyse effects of land-use parameters, habitat complexity and of other drivers on multitrophic diversity, ecosystem functions and BEF relationships and identify data gaps and future directions of this research in a production context.

METHODS FOR LITERATURE ANALYSIS

We performed a literature search on Web of Science on 8 November 2022. Our search encompassed papers published from 1995 to 2022, ensuring a broad range of relevant information was considered. We searched the following four terms, each involving specific search keywords (for details see Supplementary Table S1). The first term was used to identify studies that analysed those ecosystem functions that may be of interest to farmers and potentially related to profit. The second term limited the literature search to articles that assessed biodiversity in addition to ecosystem functions. The third term limited the literature review to studies conducted in agroecosystems. Finally, the fourth term ensured that our literature search was limited to articles with a focus on multitrophic interactions or multifunctionality. This literature search yielded 223 papers. We then excluded review papers and publications written in languages other than English. This process resulted in 204 search results.

We screened the titles, abstracts and keywords of these papers and retained the papers that met the following two criteria: the studies had to be conducted in agroecosystems, and the studies had to assess both biodiversity and ecosystem functions simultaneously or include estimations of biodiversity–ecosystem function (BEF) relationships. The communities in the selected studies were either assembled naturally, semi-naturally (i.e. through land use or habitat change) or manipulated directly. This screening reduced the number of papers to 83 for a further detailed read (Supplementary Data). We then extracted several parameters from these papers (for details see Supplementary Methods) to investigate the evidence in agroecosystems for biodiversity effects on ecosystem functions across different trophic levels and at the entire food-web scale. Our analysis focussed on the evidence regarding the direction of these BEF relationships, and how they are influenced by:

- the environmental and biotic context of the study systems and land use;
- whether biodiversity was directly manipulated or varied through indirect effects of land use, habitat complexity and trophic cascades;
- whether studies were observational or manipulative experiments in field and micro- and mesocosms;
- the dimensions of ecosystem functions measured (i.e. rate *vs*. flux *vs*. standing stock) and whether the target function was considered an ecosystem service or disservice.

Furthermore, we investigated evidence on the effects of land-use parameters, habitat complexity and of other drivers (Supplementary Table S2) on both biodiversity and on ecosystem functions in agroecosystems. For this we used a semi-quantitative vote-counting method, and classified the published effects extracted from the study papers into positive, neutral or negative based on the available summary statistics, such as positive or negative estimates of the tested effects and their significance levels, or the parsimony principle. Effects were considered as 'neutral' when reported *P* values were >0.05 or when statistical models without the predictor term were more parsimonious as determined by measures such as the Akaike information criterion. These categorized effects were then used to generate summary statistics necessary to address our study questions. These data analyses were performed using the statistical programming and analysis software R 4.2.1 (R Core Team 2022). We used a semi-quantitative method of vote-counting instead of a formal meta-analysis because often, the effect sizes could not be extracted from the reviewed papers. Furthermore, because the results (direction and significance of the effect) were derived from a wide variety of statistical methods used across the reviewed papers (e.g. *P* values or parsimony), it was not feasible to perform logistic meta-regressions for the differences in the extracted effects (e.g. Schmid *et al.* 2009). While it is important to acknowledge that vote-counting has its limitations compared with more quantitative meta-analysis techniques, it is still a valuable approach when data are not conducive to a meta-analysis due to wide differences in spatial scales, study designs, statistical methods and other factors among the reviewed studies (van der Plas 2019).

RESULTS FROM LITERATURE ANALYSIS

Research focus and geographical distribution

We found that BEF relationships were the research focus in only 14 out of the 83 papers that matched our search criteria. In terms of explanatory variables, the majority of studies (44) tested the effects of land-use intensification on ecosystem functions, biodiversity or on BEF relationships. The rest of the studies analysed the effects of habitat complexity (five papers), agroecosystem restoration (five papers) or ecosystem disturbances (two papers) as the drivers of BEF. Thirteen studies applied biodiversity as the management tool of the investigated agroecosystems.

The studies were primarily conducted in Asia (43%), Europe (34%) or North America (17%, Fig. 3a and b). The high number of studies from Asia was due to 29 studies carried out in China. No studies were found by our search procedure in Antarctica and Oceania. Croplands (45%) and grasslands (40%) were the most studied agroecosystem types (Fig. 3c), while around 12% of the papers studied tree plantations and forests, mostly in Asia (see Supplementary Table S3 for details on the agroecosystem types in which

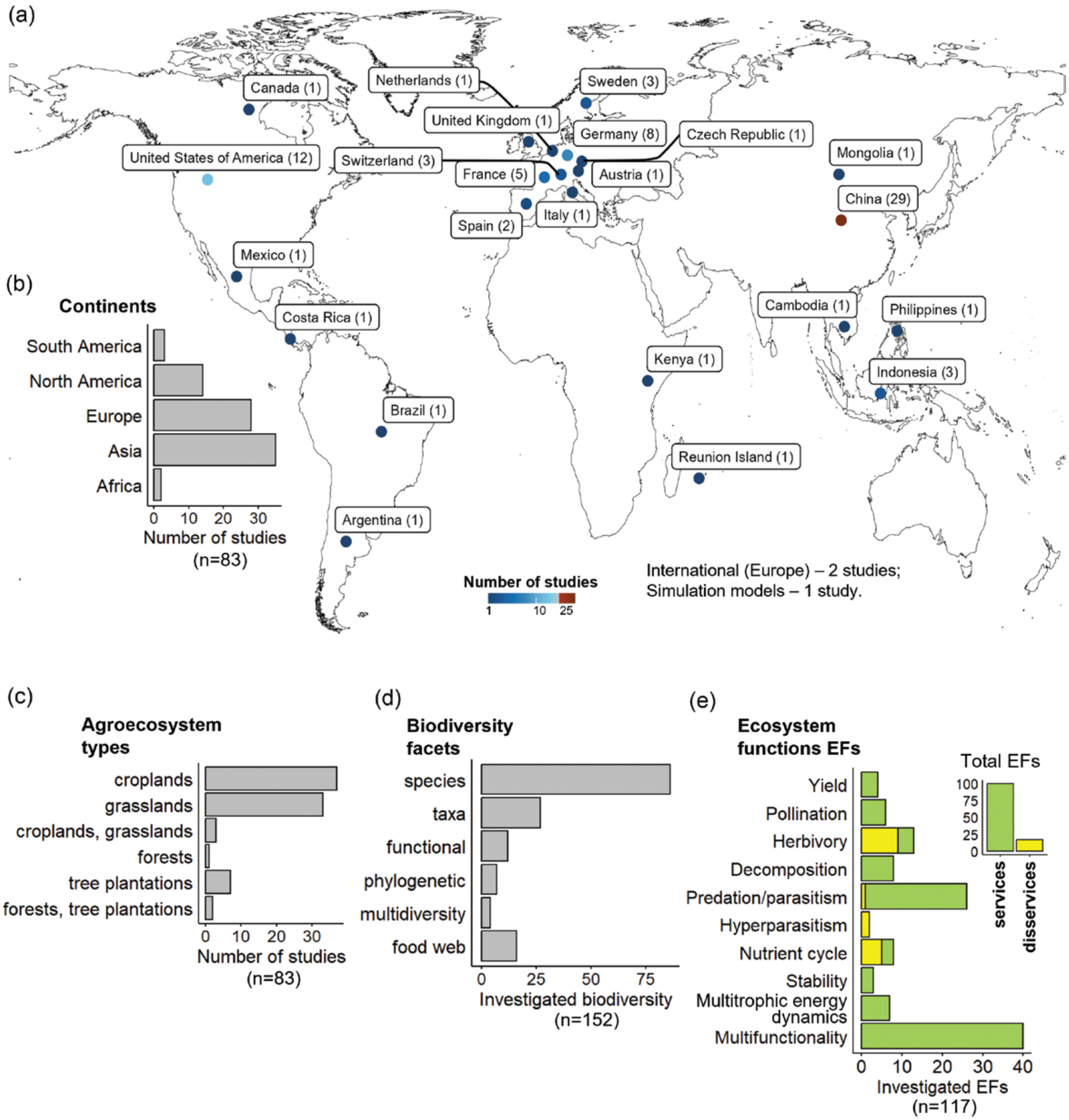

Figure 3: Country (**a**) and continental origin (**b**) of the articles analysed in the systematic literature review. The numbers in parentheses on the map indicate the number of articles per country. Agroecosystem types in which the studies were carried out (**c**). For details on agroecosystem types see Supplementary Table S3. Number of cases in which the biodiversity facets across different aspects of community organizational levels were investigated across the studies (**d**), see also Supplementary Table S5. Categories of ecosystem functions (EFs) investigated across the studies and number of cases in which ecosystem functions were considered as ecosystem services or disservices (**e**), see also Supplementary Table S6.

the studies were carried out). Field observations and collections were the most common type of data (58%, Supplementary Fig. S1), while manipulative field experiments were also performed relatively frequently across the analysed studies (37%).

Biodiversity measurements

Across the 83 selected papers we found 152 individual biodiversity measurements because the biodiversity of several different groups or taxa was considered simultaneously in some studies, and several different diversity indices were used to measure the biodiversity of the same taxa within a single study. Most studies included variation in the biodiversity of plants (38%); while about 13% of the biodiversity measurements covered the whole food-web scale (Supplementary Fig. S2a and Table S4). In 34% of the cases the studies were not confined to a specific trophic level but measured biodiversity across consumer groups of different trophic levels. Macroinvertebrates and soil microbial communities were the focus of 28% and 24% of biodiversity measurements, respectively (Supplementary Fig. S2b and Table S4). Biodiversity was typically measured on the species (57%) or taxon (18%) levels and expressed mostly by species richness or the Shannon diversity index (Fig. 3d; Supplementary Table S5). The assessment of phylogenetic diversity measures was rare in the examined papers (5%) and was predominantly used to evaluate the soil microbial community. Multidiversity metrics were also scarce, with only 4 out of the total 152 biodiversity measurements investigated.

Ecosystem functions and services

Our analysis of the 83 papers identified a total of 117 cases where ecosystem functions were measured and analysed. Some papers examined more than one ecosystem function, resulting in a total number of cases exceeding 83. Out of these 117 cases, 86% were identified as ecosystem services while 14% were categorized as disservices (Fig. 3e; Supplementary Table S6). Predation or parasitism for pest control was the most commonly studied ecosystem service (22%), while in one study the predation was considered as disservice because it was performed on prey beneficial for pest control (Tschumi *et al.* 2018). Similarly, hyperparasitism was considered as agroecosystem disservice, but was studied rarely. Herbivory was tested more often and in 70% of the cases it was expressed as a disservice, while in the rest of studies it was considered an ecosystem service targeting weed control. Functions related to nutrient cycling were often considered as disservices, specifically CH_4 emission, dissolved organic carbon leaching, soil N leaching and N_2O emission (Supplementary Table S6). Pollination, decomposition and yield functions appeared rarely across the studied papers because given our search criteria we focussed rather on multitrophic interactions than on individual functions performed by lower trophic levels (Supplementary Table S1).

In terms of measurement methods, most of the studied ecosystem functions were measured as rates (in 30% of the cases), fewer as stocks (21%) and much less as fluxes (13%) (Supplementary Fig. S2c). Of the 117 ecosystem services reported by the papers, 53 were measured aboveground in the herb layer (66%) and at the soil surface (15%), 29% were measured belowground and 25% were measured both above- and belowground (Supplementary Fig. S2d and Table S7). Multifunctionality metrics dominated the tested functions, accounting for 34% of the cases, and mainly included soil properties (12%) or combinations of soil properties together with rates, stocks and fluxes (65%, Supplementary Fig. S3a and Table S6). In 15% of the cases, biodiversity was integrated into the multifunctionality measure. Averaging across ecosystem functions was the most common method for multifunctionality calculations (in 65% of the cases), followed by multiple-threshold (in 20%) and single-threshold approaches (in 3%) and the combinations of these methods (Supplementary Fig. S3b).

BEF relationships

We found at total of 187 cases where both, ecosystem functions and biodiversity metrics were studied simultaneously. This count also includes situations where within the same study a single ecosystem function was studied in relation to different biodiversity measures or where a single biodiversity measure was studied in relation to different ecosystem functions. Out of these 187 cases, only 140 tested BEF relationships. The BEF tests showed that 62% of relationships were positive, 27% were negative and 11% were neutral ones (Fig. 4). Of our five broad trophic-level categories, plant diversity effects on ecosystem functions were most often tested (in 45% of the cases) with positive BEF relationships (71%) strongly outnumbering negative and neutral ones. Biodiversity effects of consumers combined across different trophic levels were also widely studied (32% of the cases), with 62% of studies reporting positive BEF relationships. Tests of the biodiversity effects measured on the whole food-web scale were less common (16% of the cases) and showed the highest proportion of neutral BEF relationships (46%), although positive biodiversity effects still strongly outnumbered the negative ones. Diversity effects of secondary consumers (i.e. predators and parasitoids) were rarely tested and depended strongly on the ecosystem function considered. Thus, positive effects were found for plant yield and decomposition rates, negative effects for herbivory damage and predominantly neutral effects for predation/parasitism levels.

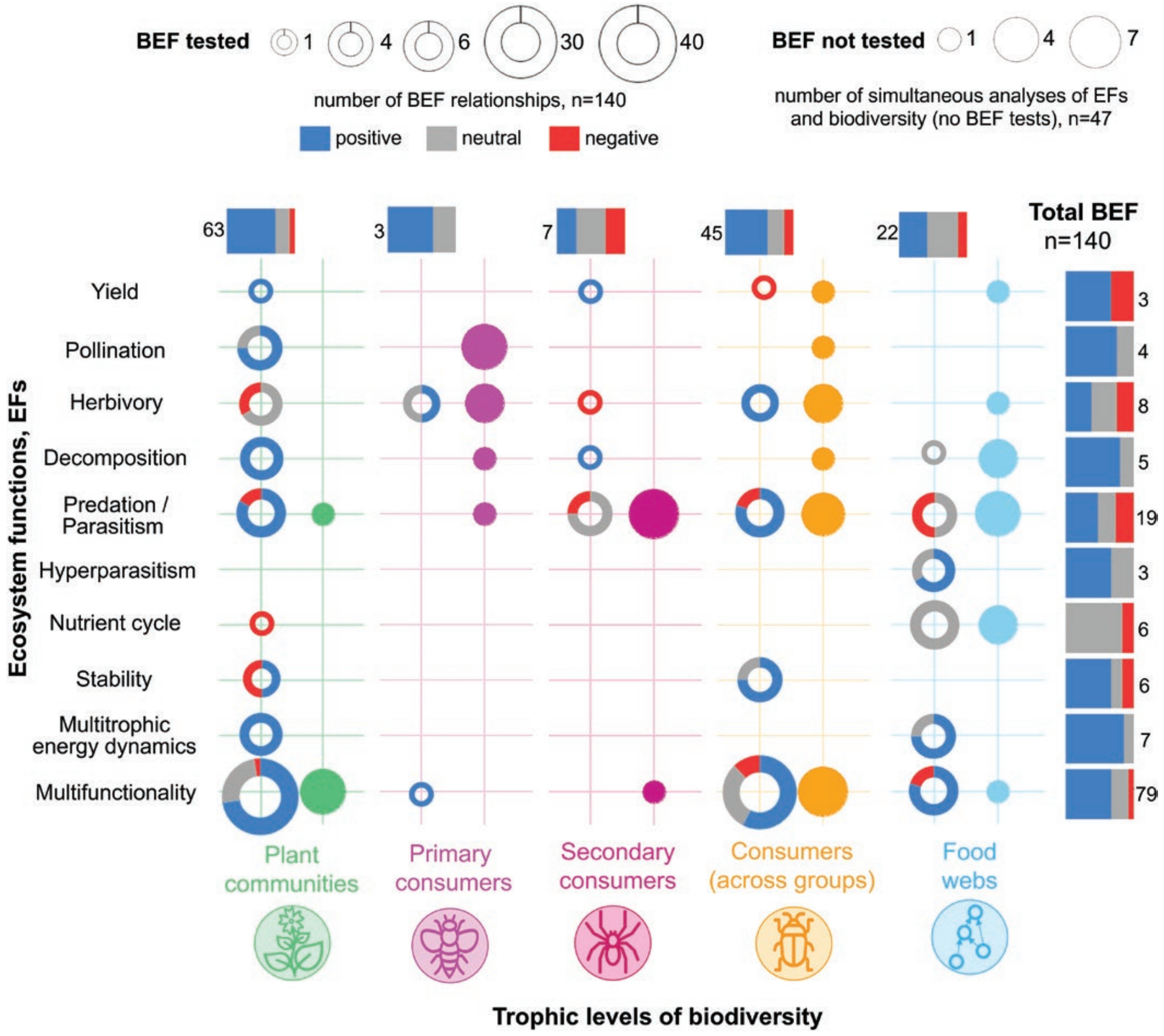

Figure 4: Number of BEF relationships (shown by open circles) tested for each category of ecosystem functions and each trophic level of investigated biodiversity (marked by different colours), and the proportions of positive, neutral and negative BEF relationships. Stacked bars and the numbers near each bar show the proportions and numbers of total BEF relationships investigated for each ecosystem function (right panel) and for each trophic level (upper panel). Filled circles show the number of cases where ecosystem functions and biodiversity were simultaneously investigated but no BEF tests were performed. The circle colours show the trophic level of the biodiversity investigated. For details on trophic groups, trophic levels and the categories of taxa for which biodiversity was investigated see Supplementary Table S4. For details on ecosystem functions investigated see Supplementary Table S6.

In terms of ecosystem functions, most BEF relationships were tested for ecosystem multifunctionality (79 cases out of 140 in total), with biodiversity measured predominantly for plant communities and for the biodiversity of combined consumers, regardless of their trophic group (42% of the cases, mostly for soil microbial communities). In 67% of these studies, positive BEF relationships were reported, while negative relationships were reported only in 8% of cases. Biodiversity effects on multitrophic energy dynamics (i.e. stocks and fluxes of energy and biomass across the entire food web) were tested only in 5% out of the total of 140 BEF cases. Of these studies, the majority examined the effects of plant diversity (43%) and whole food-web diversity (57%). Positive effects were reported in 86% of these studies and negative effects in none of the studies. BEF relationships for stability of ecosystem functions were rarely tested, but out of the few cases where it was done, 67% of BEF relationships were positive. The biodiversity effects on predation or parasitism were the second-most frequently tested (in 19 out of total 140 BEF cases) and 47% of the investigated BEF relationships investigated were positive, while 26% were negative and 26% neutral. Hyperparasitism was uncommon in the BEF studies

(2%) and tested only for the effects of food-web scale biodiversity. BEF for herbivory was tested across all the study trophic levels but not for the whole food-web scale, out of which 37% were positive, nearly 37% were neutral and 25% were negative. Most of the negative effects were reported for biodiversity of secondary consumers (i.e. predators and parasitoids, Supplementary Table S4). The responses of plant yield, pollination and decomposition to biodiversity variations were tested rarely across the multitrophic studies that we found using our literature search criteria.

In 38 cases of the investigated 140 BEF relationships (i.e. in 27%) the biodiversity variations were experimentally manipulated, while in the rest of cases biodiversity variations were created indirectly through land-use intensification (in 62% of BEF tested), via habitat complexity (in 7%) or via trophic cascades (in 10%; predominantly bottom-up cascading effects, Fig. 5a). Experimental studies with direct diversity manipulations reported 82% positive, 13% negative and 5% non-significant (i.e. neutral) BEF relationships. In contrast, the biodiversity changes caused by trophic cascades showed less positive biodiversity effects on ecosystem functions (40%) and a higher fraction of non-significant effects (30%). Overall, the studies with direct biodiversity manipulations reported seven times more significant BEF relationships and ~30% of more positive effects compared with studies using indirect biodiversity changes. We found that 58 out of 140 reported BEF relationships were tested in experimentally controlled studies. The majority of these were performed under field conditions (Fig. 5b). In experimental studies, positive biodiversity effects (71%) outnumbered negative effects (12%). In observational studies, we also found a predominance of positive effects (54%), but relatively less than in experimental studies. The observational studies reported twice as many neutral BEF relationships than experimental studies (35% and 17% of BEF, respectively). Furthermore, we investigated if the BEF relationships depended on the dimensions of ecosystem functioning, i.e. whether the function was measured as a rate, stock or flux (Fig. 5c; Supplementary Table S6). We found that positive biodiversity effects outnumbered negative effects for all ecosystem function dimensions. However, 50% of the tested BEF relationships for the fluxes were non-significant, for rates 24% and for stocks 13%. BEF relationships were tested predominantly for ecosystem services (in 123 cases out of 140 BEF investigations, Fig. 5d; Supplementary Table S6); 64% of those were positive and only 10% were negative. By comparison, for the disservices we found a lower fraction of positive (31%) and a much higher fractions of negative (23%) and of non-significant (46%) BEF relationships. In 62 cases out of the 140 investigated BEF relationships, the studies reported a context dependency of the relationships (Supplementary Table S8 and Fig. S4, for details see Supplementary Results).

Effects of land-use drivers

We also assessed the effects of drivers other than biodiversity on ecosystem functions, as well as their effects on biodiversity (Fig. 6). Most of the studies across our literature search tested the influences of land-use-related variables on BEF and showed predominantly negative effects on both (55% and 66%, respectively), specifically grazing intensity, general management intensity and fertilization (Fig. 7; Supplementary Table S2). In only 16% of the cases the land-use effects on biodiversity were positive (Fig. 6). Similarly, we found few positive effects of land-use drivers on ecosystem functions (in 7% of the cases, Figs 6 and 7; Supplementary Table S2, for details on other drivers see Supplementary Results). We also found that land-use intensity reduced ecosystem multifunctionality (Supplementary Fig. S3c).

DISCUSSION

We investigated the extent of evidence in agriculture and forestry of effects of biodiversity on ecosystem functions across different trophic levels and at the whole food-web scale and how these BEF relationships depend on land use, environmental variables, specific properties of the study system and on food-web contexts. Here, we discuss how these results may support EI in agriculture and forestry, highlight critical data gaps and limitations for the implementation of existing results and identify future directions to overcome these limitations.

Prevalent positive BEF relationships across dimensions, trophic levels, methodologies and ecosystem functions

Our results show that positive BEF relationships dominate in agroecosystems. We found these positive BEF results consistently across the different dimensions of ecosystem functions, such as stocks, rates or fluxes. Because we used a ‘vote-counting’ approach in our systematic literature review and

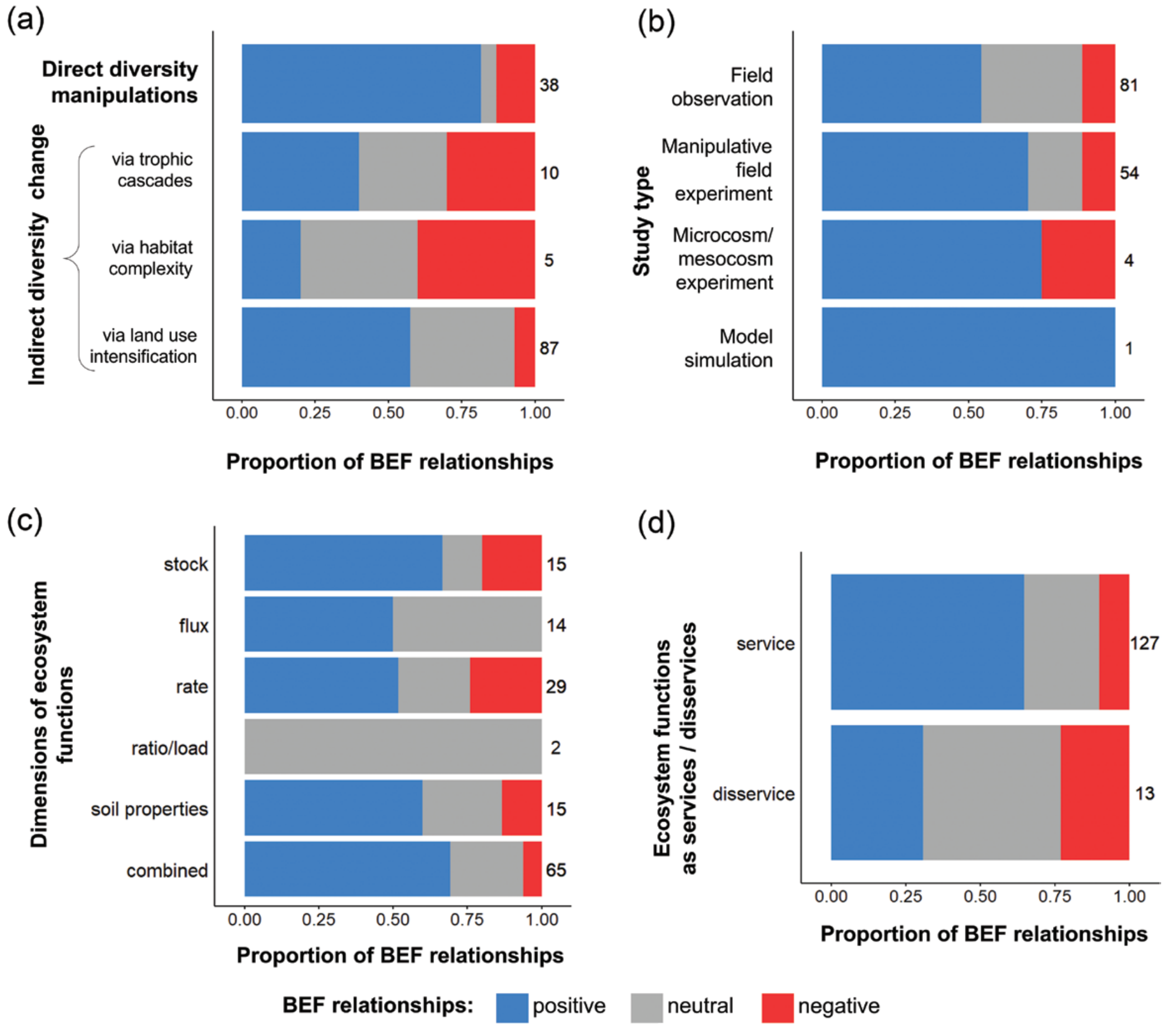

Figure 5: The proportion of positive, neutral and negative BEF relationships among studies with direct diversity manipulations *vs*. indirect diversity change through trophic cascades, increased habitat complexity and land use (**a**); among observational studies compared with manipulative experiments in field and micro- and mesocosms (**b**); depending on the dimensions of ecosystem functions (**c**) and ecosystem services and disservices (**d**), see Supplementary Table S6 for details. Numbers near bars show the number of assessed BEF relationships (*n* = 140).

analysis, we could not assess publication bias and therefore our result must be interpreted with caution. Positive BEF relationships were also prevalent across trophic levels, with the strongest biodiversity effects observed when plant diversity varied. These plant-level biodiversity effects can cascade through the food web (Barnes *et al.* 2014; Buzhdygan *et al.* 2020). Still, most of the investigated literature focussed on plants, while BEF tests on the food-web scale were rare in our analysed set of studies (but see e.g. Potapov *et al.* 2019). The few existing food-web scale studies showed a higher number of neutral BEF relationships compared with studies where diversity at a single trophic level was considered. Previous studies indeed indicated that biodiversity effects may attenuate across the food web. For example, the effects of plant community diversification in grasslands on biodiversity, trophic interactions and energy stocks and fluxes of different trophic groups decreased with their trophic level, i.e. they were the most pronounced in the trophic level adjacent to plants (Buzhdygan *et al.* 2020; Rzanny and Voigt 2012; Scherber *et al.* 2010). In our study, we also found that the BEF relationships were weaker in studies where biodiversity changes occurred indirectly via trophic cascades, compared with those where

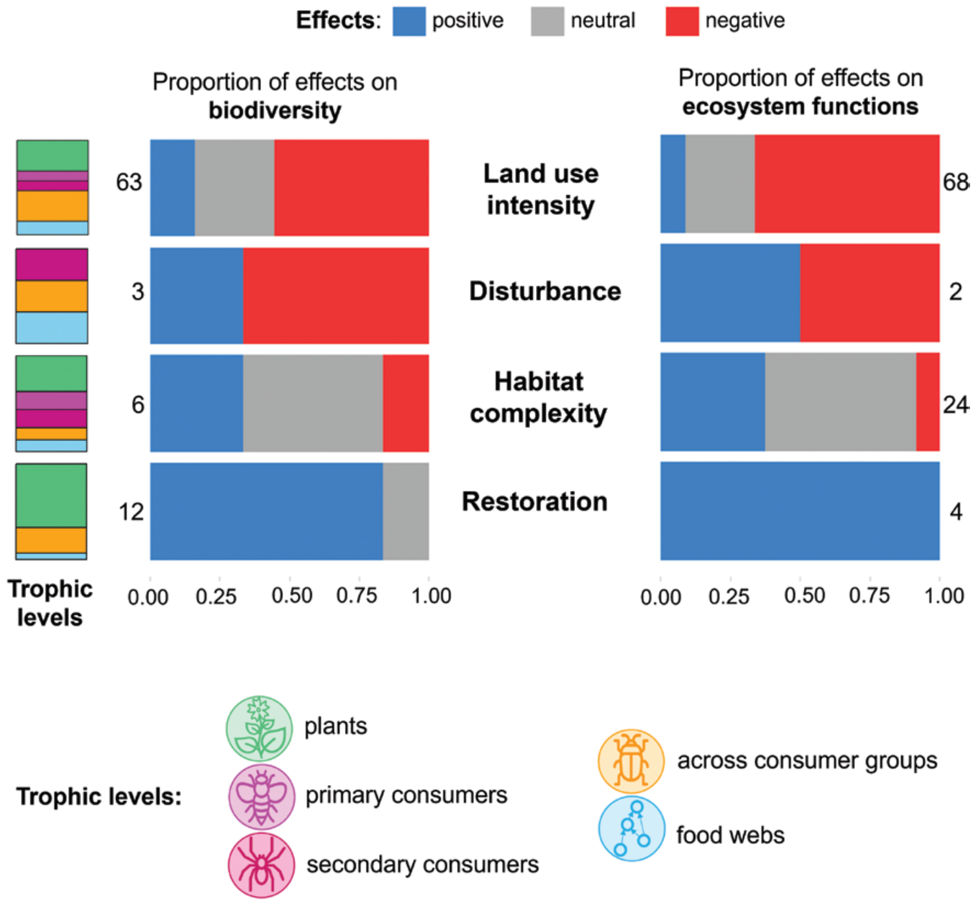

Figure 6: The proportion of positive, neutral and negative effects of land-use intensity, disturbance, habitat complexity and restoration as drivers of biodiversity (left panel) and ecosystem functions (right panel). Numbers near bars show the number of the investigated effects of each driver. The stacked bars (left panel) show for each driver the percent of trophic levels for which biodiversity was measured. For details on the investigated drivers included in each category see Supplementary Table S2.

biodiversity was directly manipulated. However, at higher trophic levels and at the food-web level the positive biodiversity effects still outnumbered the negative ones. Thus, it is crucial to conduct studies that directly manipulate biodiversity across trophic levels to investigate the consequences for ecosystem functions (e.g. Kohli *et al.* 2019), as emphasized by previous studies (Eisenhauer *et al.* 2019; Hines *et al.* 2015; Thompson *et al.* 2012).

Our results showed that BEF effects were also consistently positive across study methodologies. However, experimental studies reported a higher fraction of statistically significant BEF relations and more positive biodiversity effects than observational studies. The weaker BEF results in observational studies are likely caused by lower statistical power, higher variability of ecosystem function drivers and the existence of potential confounding variables (van der Plas 2019). When expressed as disservices, the ecosystem functions responded positively to biodiversity in only half the cases compared with services and showed a much larger fraction of non-significant BEF relationships. However, the positive biodiversity effects outweighed the negative effects in both services and disservices, thus reinforcing the need to explicitly consider the socioeconomic value of ecosystem functions when applying BEF results to agroecosystem management and restoration (see also *Implementation* below). Because there are certain trade-offs and caveats attached to the multifunctionality concept (see Supplementary Discussion), and some of these also emerged from our study (e.g. trade-offs between functions and services *vs.* disservices, problems with the scale of the multifunctionality measurements or methodological aspects of the index calculation), the overall positive BEF effects for multifunctionality are even more notable. Despite prevalent BEF effects across dimensions of ecosystem functions, trophic levels, different methodological types of studies and

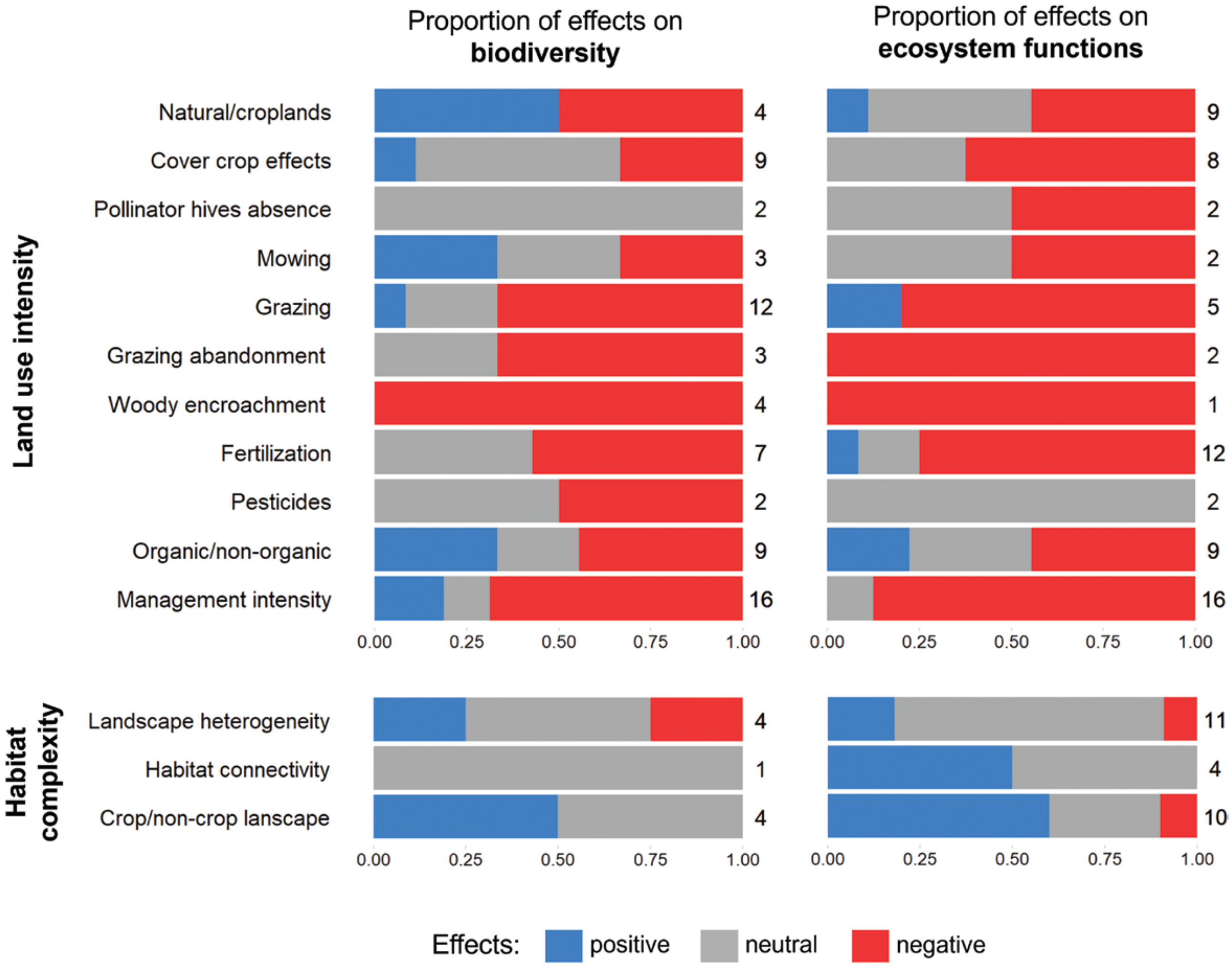

Figure 7: The proportion of positive, neutral and negative effects of the specific types of land-use intensity and habitat complexity on biodiversity (left panel) and ecosystem functions (right panel). Numbers near bars show the number of the investigated effects of each driver. For details on the investigated drivers included in each category see Supplementary Table S2.

different ecosystem functions, in many cases across our literature search the biodiversity effects on ecosystem functions depended on the studied species or on the species composition of the community. Consequently, the delivery of ecosystem services (e.g. pest control) may partly be species specific, e.g. weed control through the weed-seed predation by ground beetles in vineyards strongly depended on the species identity (Rusch *et al.* 2016).

Effects of management on multitrophic BEF

Our results provide additional evidence that land-use intensification reduces BEF, including ecosystem multifunctionality (Fernández-Guisuraga *et al.* 2022; Grass *et al.* 2020; Li *et al.* 2017; Schils *et al.* 2022). We also found that certain land-use measures are particularly negative for BEF, such as high grazing and general management intensity for biodiversity, and fertilization as well as general management intensity for ecosystem functions. We also found that BEF relationships can depend on the land-use type. For example, Meyer *et al.* (2019) found in grasslands that arthropod predation increased with grazing but decreased with mowing and fertilization intensity. Such BEF variations with land-use type may be explained by the filtering of species traits (e.g. body size, food and habitat specialization). As a result, local food-web structure and functioning reflect the selective process of community assembly from regional food webs by the local habitat conditions (Saravia *et al.* 2022). For example, agricultural land use favoured spider species with a preference for arable fields, which in turn correlated with the level of aphid predation rates (Rusch *et* *al.* 2015). Such differential responses of BEF to different management systems suggest that adverse effects of agricultural management on ecosystem services could potentially be diminished by using management practices that favour biodiversity of specific functional groups and their trophic interactions that deliver these services. There is a need of more data on the effects of land-use types and management measures on multitrophic BEF relationships. For example, we found that production forests, tree plantations and aquaculture were rarely investigated.

Knowledge gaps regarding multitrophic BEF relationships

We have identified several crucial gaps in scientific knowledge in our introductory literature review and during our systematic analyses of the literature. We already mentioned above the need for food-web level BEF studies. In addition, we found a strong geographical bias of the number of studies (generally many North American and European studies, many multifunctionality studies from China) with many areas of the world almost not represented at all (e.g. Africa, South America, Australia). With EI being relevant in all agricultural and forestry regions of the world, we call for more studies on multitrophic BEF relationships in these underrepresented countries and continents.

Remarkably, many of the studies that we analysed measured both biodiversity and ecosystem functions but made no analytical attempt to link the two variables and address how BEF relationships may be changing under certain management. Species diversity metrices were the dominant facet of biodiversity tested in the studies included in our literature search. Much less was done for functional diversity. However, functional diversity may explain a greater part of the variation in ecosystem functions and their stability than taxonomic measures (Fry *et al.* 2018) because of a greater potential for complementarity effects when considering the diversity of functional traits. In addition to functional diversity, functional composition of the community or presence of specific functional group is recognized as an important predictor of ecosystem functions, e.g. spider body size and habitat preferences determined predation rates in agricultural fields (Rusch *et al.* 2015). Therefore, how biodiversity is measured matters for the strength and direction of BEF relationships (Zirbel *et al.* 2019) and functional measurements should be considered more often.

Another limitation is that many studies focussed on aboveground diversity and functions and often neglected soil biodiversity and the related functions. However, land-use effects on biodiversity across multiple trophic levels as well as on ecosystem functions may substantially differ between aboveground and soil communities (Gossner *et al.* 2016; Pacheco *et al.* 2017). Furthermore, the responses of belowground functioning may lag behind those of aboveground functioning (Liu *et al.* 2022), and thus may be underestimated in short-term studies, where diversity effects may be masked by soil legacy effects of the former land use and plant community (Eisenhauer *et al.* 2013). We further found that very few BEF tests across the investigated literature were performed for vertebrates. However, the responses of vertebrates to land use may differ from those of invertebrates. For example, the effects of grassland management on predation rates differed between rodent and arthropod predators (Meyer *et al.* 2019).

CONCLUSIONS

We have shown in our systematic literature analysis that positive multitrophic BEF relationships are prevalent in production systems, largely across ecosystem function dimensions, trophic levels, methodologies and different ecosystem functions, however, with certain context dependencies. We also found that land management strongly affects BEF. However, large data gaps still exist (e.g. geographical bias, functional diversity and belowground *vs.* aboveground measurements). We conclude from our results that EI will need a range of measures (that are very often related to multitrophic interactions) across spatial scales to increase the multifunctionality of production landscapes. A holistic management of landscapes at the larger scale and with an ecosystem perspective will help to enhance their functioning, stability and resilience, especially under changing future conditions. It is clear that we will need an approach to agricultural production that integrates society participation (Kremen 2020; Østergård *et al.* 2009) and a more sustainable use of products, e.g. reduced waste (Bommarco *et al.* 2013). In the future, multitrophic BEF research may benefit EI by closing some of the knowledge gaps, investigating longer temporal scales, climate-change effects, larger spatial scales and possible ways for implementation. Many challenges remain for EI but depending on how valuable sustainable products and their stable supply will be in the future and how limited inputs will be

FUTURE DIRECTIONS

From our quantitative and general literature review we have derived the following ideas for future research on the multitrophic context of EI.

TRADE-OFFS AND MULTIPLE ECOSYSTEM FUNCTIONS

Our results show that management for high diversity across trophic levels increases multifunctionality despite potential trade-offs between functions. However, the management of complex ecological systems is not always straight forward. In many situations, there are antagonistic interactions (e.g. hyperparasitism or seed predation by birds) that complicate the improvement of biocontrol using trophic interactions (Khudr *et al.* 2020; Louda *et al.* 2003; Symondson *et al.* 2002); and some functions can rather be considered disservices to people (Kremen 2020). However, there are also synergies (Kleijn *et al.* 2019) that can be used to maximize desired functions and some trade-offs may decrease over time (Liu *et al.* 2022). Very often it is simply unknown how organisms interact, especially because their interaction networks are complex (Bommarco *et al.* 2013; Segre *et al.* 2020). Thus, to address or avoid these trade-offs we need more detailed knowledge of the local systems and their organisms. New solutions may also be developed that can help to avoid trade-offs in certain situations. For example, predator cues (e.g. predator scent or visual cues) may be used to deter specific plant pests (Khudr *et al.* 2017). Further trade-offs but also synergies and changes in the weighting of ecosystem functions may emerge when additional services are included in the measurements that are currently underrepresented, such as the provisioning of cultural values of permanent grasslands (Schils *et al.* 2022).

TEMPORAL DYNAMICS

We found in our systematic literature review and analysis that long-term investigations were rare and that temporal dynamics were often not addressed in multitrophic BEF studies. Annual cropping systems are inherently dynamic, but few studies have investigated how the structure of predator communities and their interactions with prey correspond with crop seasonality. Adding winter habitat, such as cover crops, contributes to seasonal habitat availability for arthropod communities, leading to functionally diverse predatory communities and their associated services (Bowers *et al.* 2020, 2021). In addition to such effects, the evolutionary adaptation to management interventions (e.g. the manipulation of trophic interactions or the increase in diversity) over time also needs to be considered to make EI stable in the long term (Gaba *et al.* 2014). Many positive BEF effects may only play out over time in production systems (Kleijn *et al.* 2019). A meta-analysis of long-term studies (but focussed on plant and soil-based measures only) indeed showed that EI measures at field scale have positive effects on yield (MacLaren *et al.* 2022). More long-term experimental studies in production systems (e.g. long-term forest diversity experiments considering multitrophic interactions such as the BEF China experiment; Bruelheide *et al.* 2011; Schuldt *et al.* 2018, 2023) are needed. Over time, EI may then not only contribute to high yield per harvest but may increase the stability and resilience of services and yield (Bommarco *et al.* 2013). This increase in stability and resilience will be especially important under changing conditions (see next section).

CLIMATE CHANGE

Our results also show that BEF relationships can change with changing environmental conditions. This is supported by the few studies specifically targeting these changes. For example, grazing can have positive effects on ecosystem services, particularly in species-rich rangelands, but these effects may become negative under a warmer climate (Maestre *et al.* 2022). In contrast, the positive effect of functional diversity on productivity (Ratcliffe *et al.* 2016) and multifunctionality (Ratcliffe *et al.* 2017) in forests have been shown to increase towards drier climates across Europe. Along these lines, studies found that greater plant species richness buffered the adverse effects of soil drought on soil multifunctionality in grasslands (Xu *et al.*

2022). One of the large benefits of diversity and an unearthed potential of EI compared with conventional intensive management may in fact be the more stable performance of high-diversity landscapes under changing climatic conditions in the future, e.g. because (plant trait) diversity has an effect on drought resistance and resilience of soil functions (Fry *et al.* 2018; Xu *et al.* 2022).

SPATIAL SCALE

Results from our analysis show that in multitrophic BEF studies measures at smaller spatial scales are investigated more frequently. However, all spatial scales, i.e. field, multiple-field and landscape level (Fig. 2; Supplementary Table S9) need to be considered (Petit *et al.* 2017). Previous studies often advocate a landscape scale for EI (Batáry *et al.* 2020; Kleijn *et al.* 2019) or even a complete redesign of the cropping system (Kremen 2020 Ratnadass and Barzman 2014). These larger spatial scales are especially important when management aims at multiple ecosystem services (Alsterberg *et al.* 2017; Isbell *et al.* 2017; Le Provost *et al.* 2023; Manning *et al.* 2018; van der Plas *et al.* 2016; Zirbel *et al.* 2019) that may be affected by trade-offs, temporal variability (Zavaleta *et al.* 2010), environmental variation (Zirbel *et al.* 2019), ecosystem boundaries (Scherer-Lorenzen *et al.* 2022) and the movement of ecosystem function providers through the landscape (Batáry *et al.* 2020; Schlägel *et al.* 2020). An increase in the area of non-crop habitat *per se* at larger spatial scales has not been shown to increase pest control (Karp *et al.* 2018) but landscape complexity may increase arthropod diversity (Marja *et al.* 2022) and especially natural enemies (Chaplin-Kramer *et al.* 2011). This increased complexity can also be an outcome of smaller field sizes, diversifying cropland with a small proportion of semi-natural habitat (Tscharntke *et al.* 2021), landscape-scale crop patchiness (Frei *et al.* 2018) and increasing crop diversity (Batáry *et al.* 2020).

IMPLEMENTATION

Surprisingly, only few multitrophic BEF studies in agroecosystems in our systematic literature review and analysis specifically measured yield as an ecosystem function or service. Since yield is one of the most important variables for farmers, this missing information may be one reason why EI and other related management types are still rarely taken up by farmers (Kleijn *et al.* 2019). Generally, previous studies have found that many recommendations for EI are not adopted by the practitioners because these recommendations do not address questions or variables that farmers or nature conservation agencies find useful (Klaus *et al.* 2020) or they consider different spatio-temporal scales (Kleijn *et al.* 2019) or underestimate the challenging logistics of certain measures (e.g. intercropping). In addition, scientists focus on functions (e.g. pollination) instead of outcomes (e.g. yield or crop quality or profits). However, a recent second-order meta-analysis by Tamburini *et al.* (2020) found that multiple ecosystem services can indeed be compatible with a high yield. Even if positive effects of biodiversity on yield are sometimes only in the range of effects of conventional management (e.g. of nitrogen fertilizer), and are substitutive, i.e. there are no additional effects at high nitrogen levels (MacLaren *et al.* 2022), we might still opt for EI in the future because of the greater sustainability and stability of this management type. To be able to do so, we will need applied long-term studies that include EI measures at large scales (i.e. ecosystem approaches) and will have to do better in translating the results into an application of specific measures (Kleijn *et al.* 2019, see Supplementary Table S9 for examples of EI measures from the literature and their effects on BEF and services).

that are needed for conventional agriculture, EI may become the first choice of agricultural production in the near future.

Supplementary Material

Supplementary material is available at *Journal of Plant Ecology* online.

Figure S1: Number of studies and their study design.
Figure S2: Number of cases in which the biodiversity of different trophic levels (a) and broad taxon categories (b) of organisms were investigated across the studies (see Supplementary Table S5).
Figure S3: Number of cases in which the ecosystem functions in the multifunctionality metrics were

measured as fluxes, soil properties and as the combinations across stocks, fluxes, rates, ratios and soil properties, and in which multifunctionality metrics included biodiversity (a).

Figure S4: Broad categories of variables that affected the biodiversity–ecosystem function (BEF) relationships across the studies; see Supplementary Table S8 for details on the variables included in the broad categories of the BEF context dependency.

Table S1: Terms used for the literature search in Web of Science.

Table S2: Information on the groupings of the drivers of biodiversity and ecosystem functions.

Table S3: Information on the categories of agroecosystem types in which the studies were carried out.

Table S4: Information on trophic groups, trophic levels and the categories of taxa for which biodiversity was investigated in the study papers.

Table S5: Information on the biodiversity measures that were investigated across the studies.

Table S6: Information on ecosystem functions (EF) that were investigated across the studies, including whether the ecosystem function was considered an ecosystem service or disservice, whether the ecosystem function was measured as rate, stock, flux, ratio, soil property or the combinations across these dimensions; and trophic group and trophic level for which the ecosystem function was measured.

Table S7: Information on whether the investigated ecosystem functions were measured above- or belowground and the details on the strata where ecosystem functions were measured.

Table S8: Information on context dependencies of BEF relationships reported across the study papers, and number of cases when each context dependency was reported.

Table S9: Examples of ecological intensification (EI) measures and their effects on biodiversity and ecosystem functions (EFs) and services (ESs).

Acknowledgements

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Conflict of interest statement. The authors declare that they have no conflict of interest.

Data Availability

Data used to support the conclusions of this study are available as Supplementary Data to this paper. The source code to produce the results is available on GitHub at https://github.com/oksanabuzh/Ecol_Intensf_Multitroph_BEF (Buzhdygan 2023).

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