Current Biology
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Review

Cascading social-ecological benefits of biodiversity for agriculture

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https://doi.org/10.1016/j.cub.2024.05.001

SUMMARY

Cultivated species diversity can provide numerous benefits to agricultural systems. Many ecological theories have been proposed to understand the relationships between plant species diversity and trophic interactions. However, extending such theories to socioeconomic systems has been rare for agriculture. Here, we establish ten hypotheses (e.g., the natural enemy hypothesis, resource concentration hypothesis, insurance hypothesis, and aggregation hypothesis) about the relationships between cultivated species diversity (i.e., crop diversification, co-cultures of crops and domestic animals, and co-cultures of crops and edible fungi) and trophic cascades of crops, invertebrate herbivores and natural enemies in cropping systems. We then explore the socioeconomic advantages (e.g., yield, economic and environmental performance) of these trophic cascades. Finally, we propose a multi-perspective framework to promote the cascading social-ecological benefits of species diversity for agricultural sustainability. Integrating the benefits of trophic cascades into agricultural socioeconomic systems requires policies and legislation that support multi-species co-culture practices and the willingness of consumers to pay for these practices through higher prices for agricultural products.

Introduction

Cropping system-based agriculture, dominated by agricultural intensification with the striking changes in land use in which complex natural ecosystems have been converted to monocultural crop production systems[1,2], has dramatically increased crop yields to support an increasing world population. However, it has also led to multiple consequences, including large increases in resource, energy, and chemical fertilizer and pesticide consumption[3,4]; decreases in biological pest control[5]; extensive damage to naturally occurring species and biodiversity loss; and increased risk to environmental health and food safety stemming from the heavy input of agrochemicals[4,6]. Intriguingly, a substantial body of evidence has demonstrated that increasing cultivated species diversity (see Supplemental methods) in crop production-based systems can alleviate these consequences and increase crop productivity and food safety[7–9].

Species diversity refers to all species of plants, animals, and microorganisms that live and interact with ecosystems, and this diversity provides multiple benefits for humans and their planet[10,11]. In crop production systems, species diversity can be achieved by adding more plant, animal, or microorganism species within and around the managed cropping systems, or by increasing the structural variations of the vegetation in the surrounding crop landscapes[12]. This increase in agrobiodiversity can promote natural pest control[13,14], reduce the use of chemical pesticides[8,15], increase crop yields[15–17], and result in greater economic benefits than monocultures[7,8]. However, the opposite results have also been reported in some cases. For example, crop diversification can decrease predatory ladybird abundance[18], increase herbivorous cabbage worm abundance[19], increase pesticide use, and decrease crop yield[20]. To elucidate broad trends and identify research gaps in different experimental results, a recent meta-analysis of 351 plant diversity experiments showed that increased plant species richness reduced herbivore abundance and damage, increased predator and parasitoid abundance, predation, and parasitism and overall enhanced plant productivity[12]. In summary, species diversity can contribute to the ecological intensification of agriculture worldwide[2,21,22] (see Supplemental methods).

To achieve the goal of cultivated species diversity increasing the well-being of crop production systems and Earth's organisms, we first review the current status of species diversity in strengthening trophic cascades and associated social-ecological benefits. Second, we explore the mechanisms linking three types of cultivated species diversity (i.e., crop diversity, co-cultures of crops and domestic animals, and co-cultures of crops and edible fungi) and trophic cascades in cropping systems. Third, we propose a 'cascade chain' linking ecological

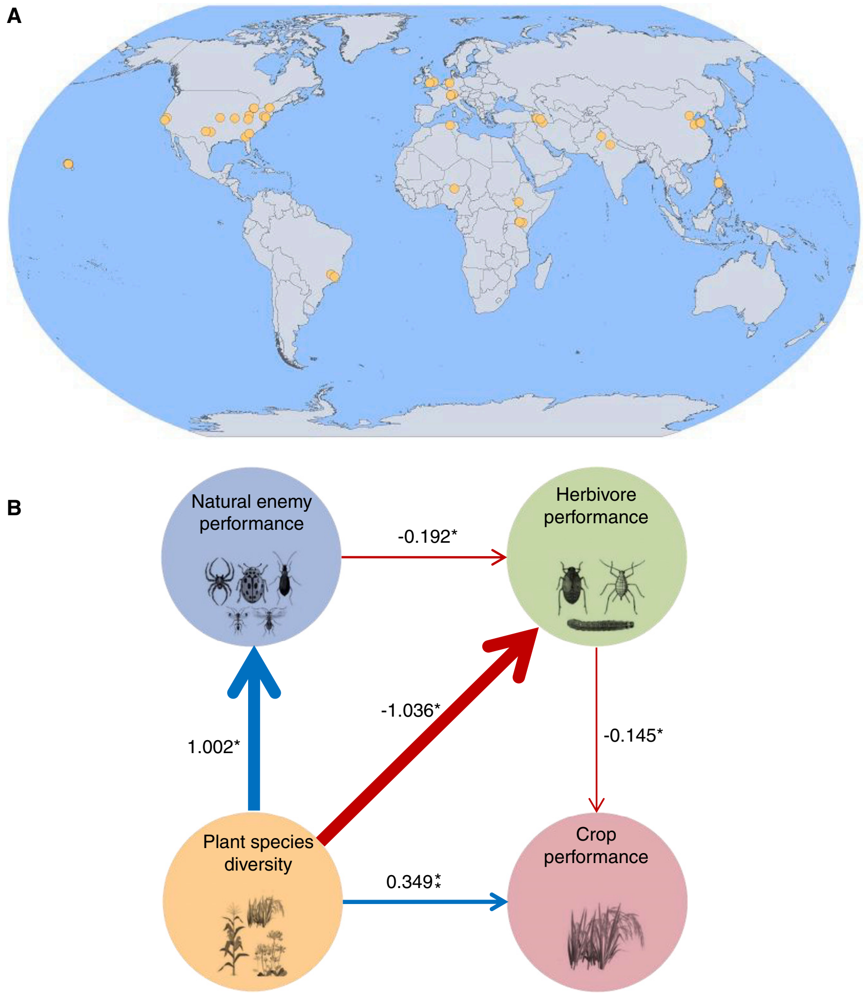

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Figure 1. Global analysis of the effects of plant species diversity on tri-trophic cascades in cropping systems.

(A) 51 global locations (from 45 articles with 215 paired observations) of plant species diversity effects on trophic cascades (world map in the World Robinson projection). (B) Piecewise structural equation model for the effects of plant species diversity on the trophic interactions of invertebrate herbivores and natural enemies and on crop performance in agroecosystems. The effects of plant species diversity were measured as the standardized mean difference between species diversity and monocrop diversity. Crop performance included the growth, reproduction and quality of crops; invertebrate herbivore performance included herbivore abundance and damage; and natural enemy performance included the abundance of predators, predation, abundance of parasitoids, parasitism, and diversity of predators and parasitoids (see Supplemental methods). * denotes significance ($P < 0.05$), and ⁑ denotes marginal significance ($0.05 < P < 0.10$). The blue and red arrows denote positive and negative relationships, respectively; the numbers next to each arrow are the estimated coefficients from piecewise structural equation models, and the line width is proportional to the magnitude of the coefficients (Tables S2 and S3). (Map © ARCGIS Software.)

processes with human well-being and, finally, integrate trophic cascade benefits into agricultural socioeconomic systems.

Species diversity strengthening trophic cascades and associated social-ecological benefits

Trophic cascades are defined as the propagation of indirect effects between non-adjacent trophic groups in a food web or food chain. A tri-trophic cascade is driven by predation (including parasitism) from the top down, with altered herbivore abundance mediating the ultimate effects on the productivity of the primary producers[22–24]. For example, in crop-farming systems, a top-down tri-trophic cascade (from predators to herbivores to plants) occurs when predators directly limit or suppress the abundance or damage of herbivores or change their behavior, phenology, or physiology[23,24]. Here, we conducted a global synthesis based on 45 primary studies in crop production systems, showing that, when 'plant species diversity' is defined as any activity that increases the richness of any species in a plant community (i.e., a binary variable assuming a value of either zero or one), the top-down tri-trophic cascade stemming from species diversity (e.g., intercrops, flower strips, and border crops) can be realized through increases in the abundance and diversity of natural enemies (i.e., predators and parasitoids), decreases in the abundance of invertebrate herbivores, and increases in crop productivity and reproductive output (Figure 1). However, this trophic cascade cannot be realized when we consider the 'number of added plant species diversity' as a continuous variable (Tables S1–S3), which indicates that the trophic cascade can be strengthened just by adding a single plant species, and that additional species may not be as important in cropping systems. Moreover, due to the paucity of long-term studies at the crop level (because of the short turnover time), it may be challenging to realize trophic cascades in cropping systems.

The effects of species diversity on trophic cascades have thus far focused only on cultivated plant species diversity[12]. However, due to a lack of sufficient information in the literature, the effects of other types of cultivated species diversity in crop production-based systems, resulting, for example, from co-cultures of crops and domestic animals or of crops and edible fungi, are unclear. In cropping systems, cultivated species diversity and the strength of trophic cascades can contribute to the development of economically and socially sustainable agriculture. This can be achieved by increasing the natural enemies of pest species, decreasing the number of invertebrate herbivores, reducing pesticide use, and increasing crop yields[8,15]. Furthermore, understanding the role of species diversity in strengthening trophic cascades and triggering potential cascade chains can help to clarify the fundamental mechanisms of how agrobiodiversity drives ecosystem function and ecological processes in general.

Linking crop diversification and trophic cascades in cropping systems

Crop diversification (e.g., intercropping, flower strips, cover crops and border crops) is the dominant type[12,25] and most popular mode[25–27] of cultivated species diversity in crop production-based systems worldwide. Several hypotheses can be used to explain the direct effects of crop diversification on invertebrate herbivores, natural enemies or crop performance and the indirect effects on herbivore–enemy and crop–herbivore interactions[28,29]. These hypotheses can be extended to understand the potential effects of crop diversification on trophic cascades (Figure 2). Here, we address the four most relevant hypotheses: the natural enemy hypothesis, the resource concentration hypothesis, the insurance hypothesis, and the push–pull hypothesis.

Natural enemy hypothesis

This is a popular hypothesis for various crop systems (e.g., food crops, cash crops, vegetables and fruits), first proposed by Root[30], which predicts that more diverse habitats provide predators and parasitoids with more resources, such as alternative prey or hosts, and suitable microclimates and habitats, increasing their abundance and diversity and leading to more efficient top-down control of herbivorous pest populations. This hypothesis is widely supported by the practices of intercropping, flower strips, cover crops and border crops in cropping systems[31,32]. A classic example is given by Letourneau[33], who studied the importance of parasitic wasps in mediating differences in pest abundance between simple and complex crop arrangements in tropical corn/bean/squash systems. She found that mixed assemblages of maize, cowpea and squash crops increased the abundance of natural enemies of herbivores and resulted in a concomitant increase in herbivore regulation[34] (Figure 2A). From an applied perspective, if crop diversification benefits natural enemies, this hypothesis works. To date, this hypothesis has been the dominant hypothesis, as there is much evidence indicating that crop diversification by intercropping[35], flower strips, border crops[8] and cover crops[21,36] can strengthen the top-down control of enemies on pests in cropping systems. This enhanced top-down control of enemies on pests will then result in a decreased top-down control of pests on crops, and ultimately, these crop diversification practices strengthen the trophic cascade.

Resource concentration hypothesis

The resource concentration hypothesis is also popular for various crops (e.g., food crops, cash crops, vegetables and fruits), and this hypothesis predicts that the density of invertebrate herbivores per plant will increase with host density and patch size because invertebrates are more likely to find and stay longer in patches where their host plants are more concentrated[30,37]. In general, this hypothesis occurs in intercropping systems and relies on larger patches[37,38]. Invertebrate herbivores that arrive in a patch of a host plant and find suitable conditions will tend to stay in that area[38]. This typically occurs in monoculture cropping systems where this accumulation of herbivores on a concentrated resource is sufficient to increase their abundance and the associated negative top-down effect on crops[38]. Conversely, in diversified cropping systems, the introduction of other plant species (e.g., non-host plants) can disturb the host recognition process in invertebrate herbivores. In particular, the presence of non-host plants can induce invertebrates to move more between plants, and repeating this behavior will lead them to abandon the main crop[35] (Figure 2B). Furthermore, in diversified cropping systems, the top-down control of herbivores by natural enemies can be more efficient in response to lower herbivore pressure, as specialist invertebrate herbivores attain a higher density per unit mass of host plant species when their food plants grow in high-density patches in monocultivated fields[30,37]; however, this process involves the direct effects of plant diversity on herbivores, as these diversification practices can provide herbivores with a more suitable habitat for oviposition and feeding (e.g., trap cropping). Consequently, crop performance can be promoted due to reduced herbivore pressure. For instance, sunflowers interplanted around peach orchards can modify the behavior of a specialist borer (e.g., *Conogethes punctiferalis*) by releasing a plant volatile (e.g., β-phellandrene) to attract adult *C. punctiferalis*[39]. Currently, sunflowers are important plants that have been tested for the control of this key pest borer in eastern China[40].

Insurance hypothesis

Compared with the use of the above two hypotheses, the insurance hypothesis is rare and occurs in larger landscapes[41–43]. This hypothesis, related to plant influence on natural enemies, proposes that species that are functionally similar for an ecosystem process at a given time may show temporal complementarity due to asynchronous responses to environmental fluctuations[41]. In this case, species diversity acts as an insurance for the functioning of the ecosystem against temporal environmental change and may enhance and buffer ecosystem processes by means of spatial exchanges between local systems in a heterogeneous landscape, even when such effects do not occur in a closed homogeneous system[41–43]. This hypothesis has evolved to understand, for instance, the effects of increased plant species diversity on the predation of natural enemies on herbivores in crops[44] (Figure 2C). In particular, increasing plant species diversity can play an important role in providing temporal and spatial insurance for natural enemies[45]. However, the insurance effects of biodiversity can also have a strong spatial component[42,43] that can extend beyond the local system. Cross-habitat spillover of natural enemies between non-crop (e.g., forest or grasslands) and crop habitats[28,46] is one example. Natural habitats with greater biodiversity and a spatiotemporal stability of resources are often a major source of natural enemy populations, in which individuals can move regularly or episodically into crop fields to exploit their resource pulses, in this case a temporary hyperabundance of prey. Therefore, non-crop habitats can provide insurance for natural pest control in crop fields[47]. Examples of this hypothesis can be found in agroforestry zones (e.g., where cauliflowers were planted adjacent to trees in which the natural enemies can provide insurance for cauliflowers on Chongming Island, China). In conclusion, this biological insurance can strengthen a trophic cascade by directly enhancing the top-down control of enemies on herbivore populations and therefore indirectly weakening the top-down effect of herbivores on crops.

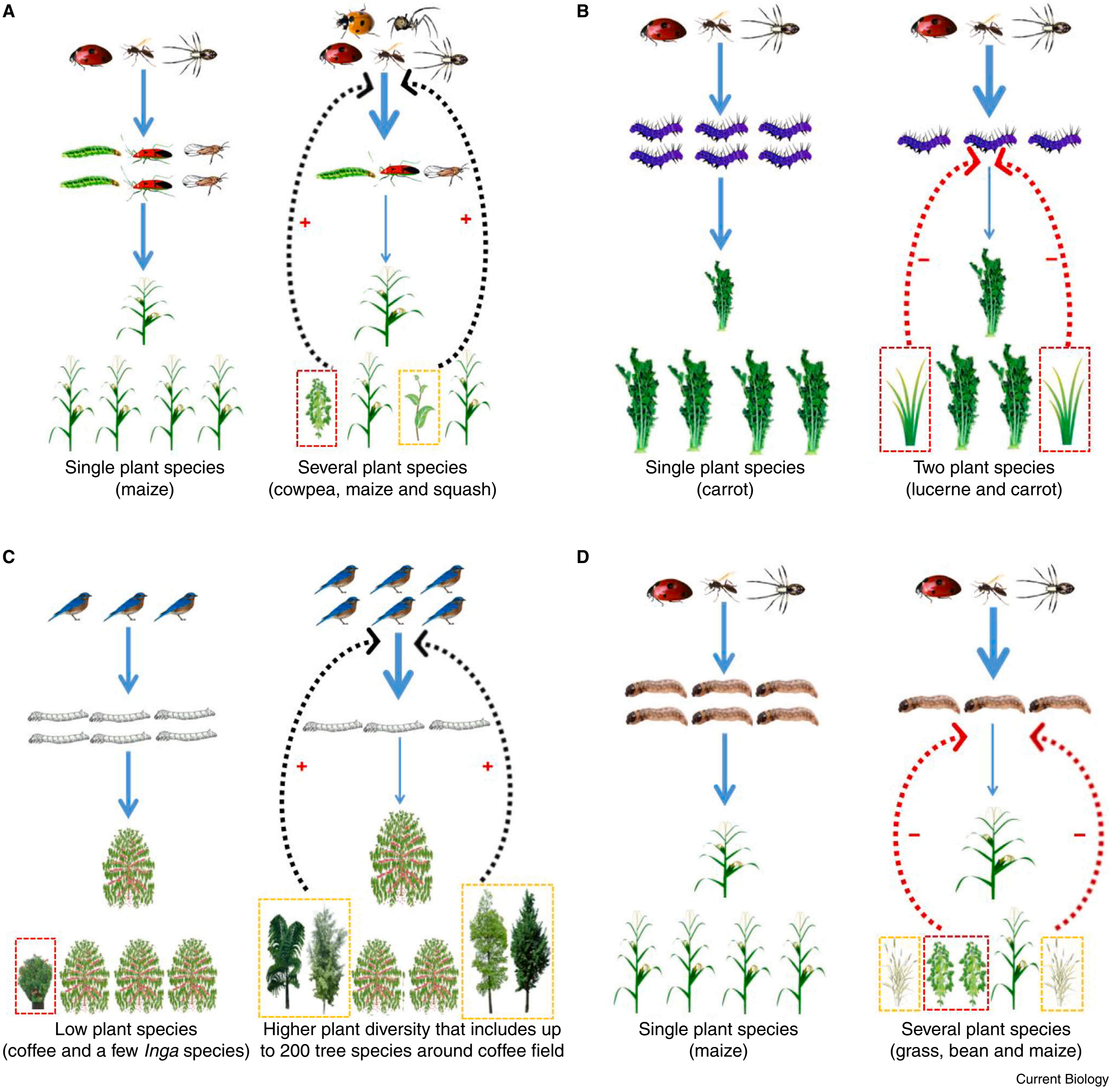

Figure 2. Hypotheses to understand the potential effects of crop diversification on trophic cascades among invertebrate herbivores, natural enemies (predators and parasitoids), and crops.
(A) Natural enemy hypothesis: the abundance and diversity of natural enemies are positively correlated with plant species diversity, resulting in a lower level of herbivores in fields with greater plant species diversity; the vegetational diversity of cowpea (red box) and squash (yellow box) increases the abundance of natural enemies of herbivores and results in a concomitant increase in herbivore regulation in maize fields[33]. (B) Resource concentration hypothesis: specialist herbivores attain a greater density per unit mass of the host plant species when their food plants grow in high-density patches in single plant species fields; a non-host plant (i.e., lucerne; red box) disrupts the sight, hearing and smell of an herbivore (carrot rust fly, *Psila rosae*) in host plants (i.e., carrots)[35]. (C) Insurance hypothesis: plant species diversity provides spatial and temporal insurance, or greater resilience and stability of ecological processes in changing environments. Tree species (yellow box) around coffee fields provide insurance for predators (i.e., birds) to feed on lepidopteran larvae in coffee trees compared with monodominant coffee fields with a few *Inga* species (red box). In this case, environmental changes (i.e., a sudden increase in the number of lepidopteran larvae in coffee) and predation on these larvae are significantly greater in diverse fields than in monospecific fields[44]. (D) Push–pull hypothesis: a combination of behavior-modifying stimuli (two plant species) is used to manipulate the distribution and abundance of herbivores within and around primary crop fields (e.g., one added plant species is used to pull herbivores, and the other is used to show the opposite function); a bean (*Phaseolus vulgaris*; red box) pushes and an attractant grass (*Pennisetum purpureum*; yellow box) pulls the stemborers in maize fields[57]. The black and red dotted arrows denote the positive (+) and negative (–) effects, respectively, of crop diversification on the trophic groups. The widths of the blue solid arrows indicate the hypothesized relative strength values (higher plant species diversity vs. lower plant species diversity) of the interactions among the trophic levels of invertebrate herbivores, natural enemies, and crops. (Insect, plant and bird images © 16pic.com.)

Push–pull hypothesis

The push–pull hypothesis requires specialized conditions because it requires resources ('push') and attraction ('pull') and occurs in the crop diversification of intercropping, flower strips and border crops in agricultural systems. A distance that is too great or too low apart from the push and/or pull will not support this hypothesis, as this distance affects the behavioral selection of target invertebrate herbivores and their natural enemies. For example, the effective distance of edible sunflowers, a trap plant used to attract the borers (e.g., *C. punctiferalis*), is 20–30 meters in fruit orchards[39,40].

The hypothesis predicts that invertebrate herbivores are repelled or deterred away from the resource (push) by using stimuli that repel the invertebrates or mask the host, or they are attracted (pull) to other areas by using stimuli that attract arthropods (including attracting herbivores out of primary crops and attracting natural enemies from non-crop plants or habitats to primary crops) (Figure 2D)[48]. The use of a push–pull strategy to protect crops has generally included intercropping with repulsive non-crop plants (or with flowering non-crop plants that attract natural enemies of pests) combined with attractive trap crops[49,50], and the use of semio-chemical repellents combined with attractive pheromone traps[48,51]. In plant-based strategies, the function of push components can be achieved through the use of stimuli that negatively influence the location and acceptance of the host. This process acts by regulating the sensory organs of herbivores through visual or chemical signals[48]. Some examples are manipulation of host color, shape or size to inhibit host orientation and acceptance behaviors of pests[52,53] or the use of non-host volatiles that mask host odors or evoke non-host avoidance and repellent behaviors[54]. In pull strategies, attractive stimuli are used to divert pests from the protected resource to a trap crop[48]. In this case, visual stimulants[55] or host volatiles[48,56] can be used to attract pests to trap crops. However, the combined application of push and pull strategies is likely essential for promoting more effective biological control[57] and has been shown to be the key technology for developing organic tea in tropical zones (e.g., Baishang County, Hainan Province, China). Push–pull directly involves attractive or repelling effects of plant diversity on herbivores, and this weakens herbivore top-down effects on primary crops. Moreover, push–pull involves the attraction of natural enemies from non-crop plants or habitats to primary crops, which strengthens enemy top-down effects on herbivores. In summary, the synergistic effects of push–pull strategies (i.e., repulsive non-crop plants combined with trap plants) can strengthen enemy top-down effects on herbivores and weaken herbivore top-down effects on plants, triggering a trophic cascade of primary crops, herbivores, and their natural enemies. Compared with the above three hypotheses, this hypothesis might work best because push–pull can achieve the triple win of directly controlling pests, directly increasing natural enemies, and indirectly enhancing the insecticidal effect of natural enemies on pests. Due to its multiple advantages, the Ministry of Agriculture and Rural Affairs of China[58] advocated this push–pull strategy, supported by the fact that China has been extending the combined application of vetiver grass (*V. zizanioides*) as a trap plant to attract rice stem borers; flowering plants (e.g., sesame, soybean, cosmos, sulfur chrysanthemum and alfalfa) as trap plants to attract natural enemies from non-crop plants or habitats to rice fields; and the application of a plant (*Ruta graveolens*) as a repellent plant to repel rice pest invertebrates in paddy fields.

Linking co-cultures of crops and domestic animals and trophic cascades in crop-production-based systems

Co-cultures of crops and domestic animals have been developed in southeast Asia for >2,000 years (e.g., crop–aquatic animal co-culture[59,60]) and have been an emerging industry in Europe (e.g., crop–livestock co-culture[61]). Importantly, the integration of crops and domestic animals (e.g., poultry and livestock) has become a useful tool for economic development in Africa[62]. Due to multiple advantages, such as maintaining soil fertility and reducing pest pressure[63,64], southeast Asia has been gradually extending this practice (e.g., China had an area of 2.86×10^6 hm^2 under rice–aquatic animal co-culture in 2022). Rice–fish co-cultures in particular have become typical in global agriculture, as this practice was recognized as one of FAO's Globally Important Agricultural Heritage Systems[9,65]. From a trophic perspective, these new integrated systems can affect different trophic groups and their interactions[60,66,67], potentially triggering trophic cascades. However, there are no popular hypotheses to explain the effects of co-cultures of crops and domestic animals on the interactions among crops, invertebrate herbivores and their enemies. Here, we propose several candidate hypotheses to explain the potential effects of co-culturing crops and domestic animals on trophic cascades (Figure 3): the predation hypothesis, the aggregation hypothesis, the environmental regulation hypothesis, and the crop resistance hypothesis.

Predation hypothesis

The predation hypothesis is based on the behavior of domestic animals in co-culture systems, which predicts that domestic animals (e.g., aquatic animals and livestock) can directly prey on invertebrate herbivores in crops (Figure 3A). To date, this hypothesis has been tested mainly in co-cultures of aquatic animals with particular crops (i.e., rice and vegetables), such as co-cultures of rice with fish[9,59], wild rice with turtles[67], rice with frogs[68], cress with loach[69], cucumber with tilapia[70] and cauliflower with fish[64,71]. Likewise, it has been tested in co-cultures of livestock with rice or orchards, such as co-cultures of rice with ducks[66], tea orchards with chickens[72], olive orchards with goats[73], and pear orchards with sheep[74]. These co-culture systems can trigger a trophic cascade through two different pathways. On the one hand, decreased invertebrate herbivore abundance due to predation by domestic animals could improve the strength of top-down control due to an increased ratio of natural enemies to herbivores[60,63] and simultaneously weaken the top-down effect of herbivores on crops due to a reduced density of herbivores per crop plant[59,60,63]. Compared with the following three hypotheses, this hypothesis might work best for pest control because the predation by domestic animals can result in greater suppression (e.g., fish decreased herbivore insect abundance by 24.1%[63]).

Aggregation hypothesis

This hypothesis, proposed by Wan *et al.*, is still poorly studied and was first tested in rice–fish (*Carassius auratus*) co-culture systems[60] with spatial geostatistics. It suggests that fish can

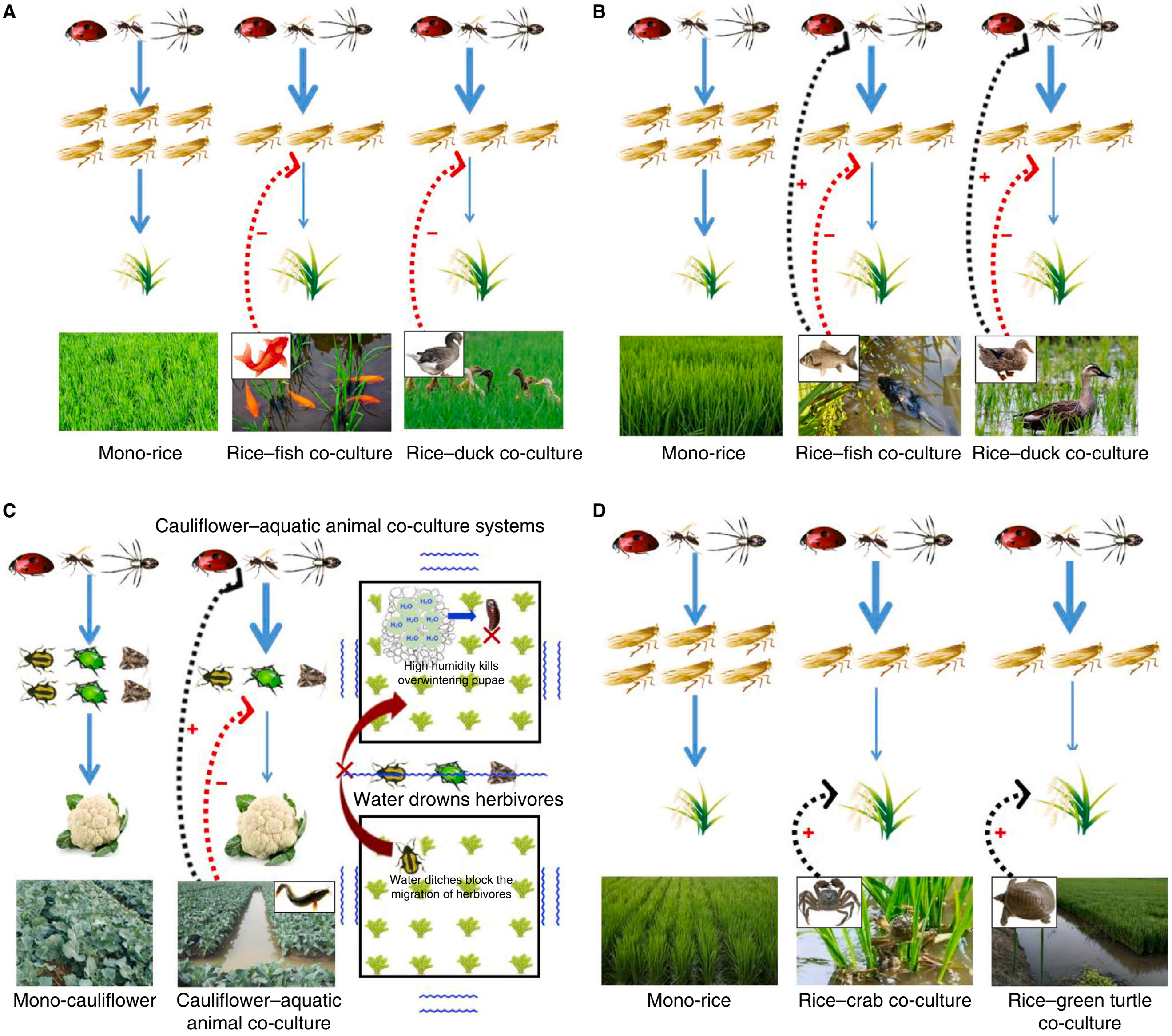

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Figure 3. Hypotheses to understand the potential effects of co-cultures of crops and domestic animals on trophic cascades among invertebrate herbivores, natural enemies (predators and parasitoids), and crops.

(A) Predation hypothesis: domestic animals (e.g., aquatic animals and livestock) can directly prey on invertebrate herbivores on crops; rice herbivores are preyed upon by fish in rice–fish co-culture systems[59] or preyed upon by ducks in rice–duck co-culture systems[66]. (B) Aggregation hypothesis: domestic animals can strengthen the tri-trophic cascade by increasing the spatial aggregation of predators and herbivores; in rice–fish co-culture plots, fish (i.e., fish are predators of rice planthoppers and their predatory spiders) increase the aggregation of herbivores (i.e., rice planthoppers) and predatory spiders in response to fish predation threat[12]. (C) Environmental regulation *hypothesis*: a suitable environment can inhibit invertebrate herbivores and benefit their predators[64,71]. (D) Crop resistance hypothesis: introducing domestic animals into monocrop systems or microclimates can increase crop resistance against invertebrate herbivores. The black and red dotted arrows, respectively, denote the positive (+) and negative (−) effects of co-cultures of crops and domestic animals on the trophic groups. The width of the blue solid arrows indicates the hypothesized relative strengths (co-culture systems vs. monocrop systems) of the interactions between invertebrate herbivores and natural enemies and between plants and invertebrate herbivores. (Insect, plant and bird images © 16pic.com.)

strengthen the tri-trophic cascade by increasing the spatial aggregation of predators and herbivores (e.g., aggregations of predatory spiders can improve their foraging efficiency, and aggregations of rice insect pests can reduce predation risk by spiders), causing increased top-down control of predators on herbivores, decreased herbivore abundance and increased crop productivity (Figure 3B). Although this hypothesis has been tested only in rice–fish co-culture systems, it can also be extended to other types of co-culture systems of aquatic crops (e.g., lotus roots and water bamboo) and aquatic animals (e.g., fish and crab) but not to co-cultures of terrestrial crops (e.g., brassicaceous vegetables) and aquatic animals, as aquatic animals fail to move freely among different terrestrial crop habitats. Imaginably, when ducks (i.e., ducks are the predators of rice planthoppers and their predatory spiders) are ushered into rice fields, aggregations of herbivores (i.e., rice planthoppers) and predatory spiders might arise in response to duck predation threat, as it has been shown that predator presence increases the aggregation level of prey[75]. Spiders are also predators of rice planthoppers; thus, increased aggregation of predatory spiders due to the presence of ducks can further strengthen planthopper aggregation in rice fields. In conclusion, this biological aggregation can directly enhance the top-down control of herbivores by predators and ultimately weaken the top-down effect of herbivores on crops via a trophic cascade.

Environmental regulation hypothesis

It is inevitable that local environmental conditions change when aquatic animals or livestock are ushered into cropping systems; thus, the environmental regulation hypothesis is widespread and applies to both terrestrial and aquatic crops. This hypothesis can be applied to understand the effects of local environmental factors on trophic cascades and implies that a suitable environment can promote biological pest control in co-culture systems (Figure 3C). On the one hand (here, we take crop–aquatic animal or rice–livestock co-cultures as examples), the local environment increases predator performance because higher water levels and adjacent ditches can improve the habitat for predatory spiders, as evidenced by increasing movement, predation and mating probability[76], or because water-rich habitats increase the abundance of alternative prey (e.g., non-pest chironomids in rice fields) of predatory spiders in co-culture systems[77]. On the other hand, higher water levels (e.g., in rice–fish co-culture systems) decreased the feeding areas of herbivores (e.g., rice planthoppers feeding at the base of rice plants) and thus decreased herbivore abundance and damage to crops[59]. In addition, in vegetable–aquatic animal co-culture systems, water ditches serve as a natural barrier that prevents some lepidopteran and coleopteran herbivores from migrating among vegetable plots (e.g., some herbivores drown in the water)[64]. Finally, compared with monocropping systems, higher soil moisture in co-culture systems of crops and domestic animals (e.g., aquatic animals and livestock) can suppress the occurrence of invertebrate herbivores in crops, as high humidity negatively affects the growth, survival, habitation and overwintering of invertebrate herbivores (e.g., lepidopteran noctuid pests of crops) (Figure 3C)[78,79]. In summary, environmental factors such as microclimates (e.g., humidity, light intensity and temperature) and habitat heterogeneity (e.g., higher water levels and added water ditches) can directly or indirectly enhance the top-down control of predators on herbivores, decrease the top-down control of herbivores on crops, and ultimately strengthen a trophic cascade. As local environmental regulation is a relatively lengthy process, the effects of such environmental regulation on crops, herbivores, their natural enemies and their interactions may be subtle.

Crop resistance hypothesis

The values of biochemical indicators related to crop resistance might change when aquatic animals or livestock are used in cropping systems[63,69]. Thus, the crop resistance hypothesis is widespread and applies to both terrestrial and aquatic crops. This hypothesis is applied to understand the effects of crop physiological conditions on the trophic cascade, indicating that introducing domestic animals into monocropping systems or local microclimates can increase crop resistance against invertebrate herbivores (crops' ability to defend against herbivores and reduce damage[80]) (Figure 3D). On the one hand, the activities of aquatic animals (e.g., fish, crayfish, frogs and crabs) and livestock (e.g., ducks, chickens and geese) affect soil conditions through their feeding, burrowing, digging and grazing activities. The change in soil physical and chemical properties due to the activities of these domestic animals increases the tendency of soil nutrients to come into contact and be efficiently absorbed by crop roots[81]. This process might increase crop resistance against herbivores by simultaneously activating phytohormonal pathways, such as jasmonic acid-dependent signaling pathways[82] and salicylic acid-dependent defenses[83]. One possible case is that loaches introduced into floating-bed cress might increase cress resistance against insect herbivores by changing the N:P ratio[69]. On the other hand, local microclimates (e.g., water levels) affect crop resistance. For instance, higher water levels are associated with higher levels of total phenolics, individual and total flavonoids, and greater antioxidant capacity, and all these substances are important for increasing vegetable resistance to insect herbivores[84]. In other words, this hypothesis concludes that increased crop resistance strengthens the bottom-up effect of crops on herbivores, generates improved enemy top-down control of herbivores due to an increased ratio of natural enemies to herbivores, and ultimately strengthens the trophic cascade.

Linking co-cultures of crops and edible fungi and trophic cascades in crop-production-based systems

The co-culturing of crops and edible fungi has become a promising emerging technology to ensure food safety and increase farm income in some regions, such as in China[85], Goa[62] and Egypt[86], and has been practiced in some regions of the United States since the 1990s[87]. In Goa, farmers voluntarily used the integration of edible fungi (e.g., mushroom) production in grain and orchard systems to boost incomes[62]. This mode, such as intercropping of maize and mushrooms, grapes and Polyporaceae fungi, rice and *Auricularia* fungi, and mulberry and Morchellaceae fungi, has become a leading industry in the development of the rural economy in China. In practice, edible fungi (e.g., mushrooms, truffles, boletus, and matsutake) can be interplanted with crops (vegetable, rice, maize, orchard fruits, etc.)[85,88]. However, there is no proposed hypothesis to explain the effects of co-cultures of crops and edible fungi on the interactions among crops, invertebrate herbivores and their enemies. Here, we summarize two potential hypotheses for understanding the effects of co-culturing crops and edible fungi on trophic cascades (Figure 4): the natural enemy hypothesis and the crop resistance hypothesis.

Natural enemy hypothesis

Here, we refer to this hypothesis as crop diversification (see the above analysis), which is prevalent in crop–edible fungus symbiotic systems. When edible fungi are introduced into cropping systems (e.g., food crops, cash crops, vegetables and fruits), the invertebrate herbivores living on the edible fungi can provide alternative prey for predators in these systems. For instance, the mushroom gall midges (*Mgcophila* spp.) that damage macrofungi (*Auricularia polytricha*) but not rice provide additional food resources to natural enemies in rice fields; thus, macrofungi contribute to the abundance and diversity of predators, leading

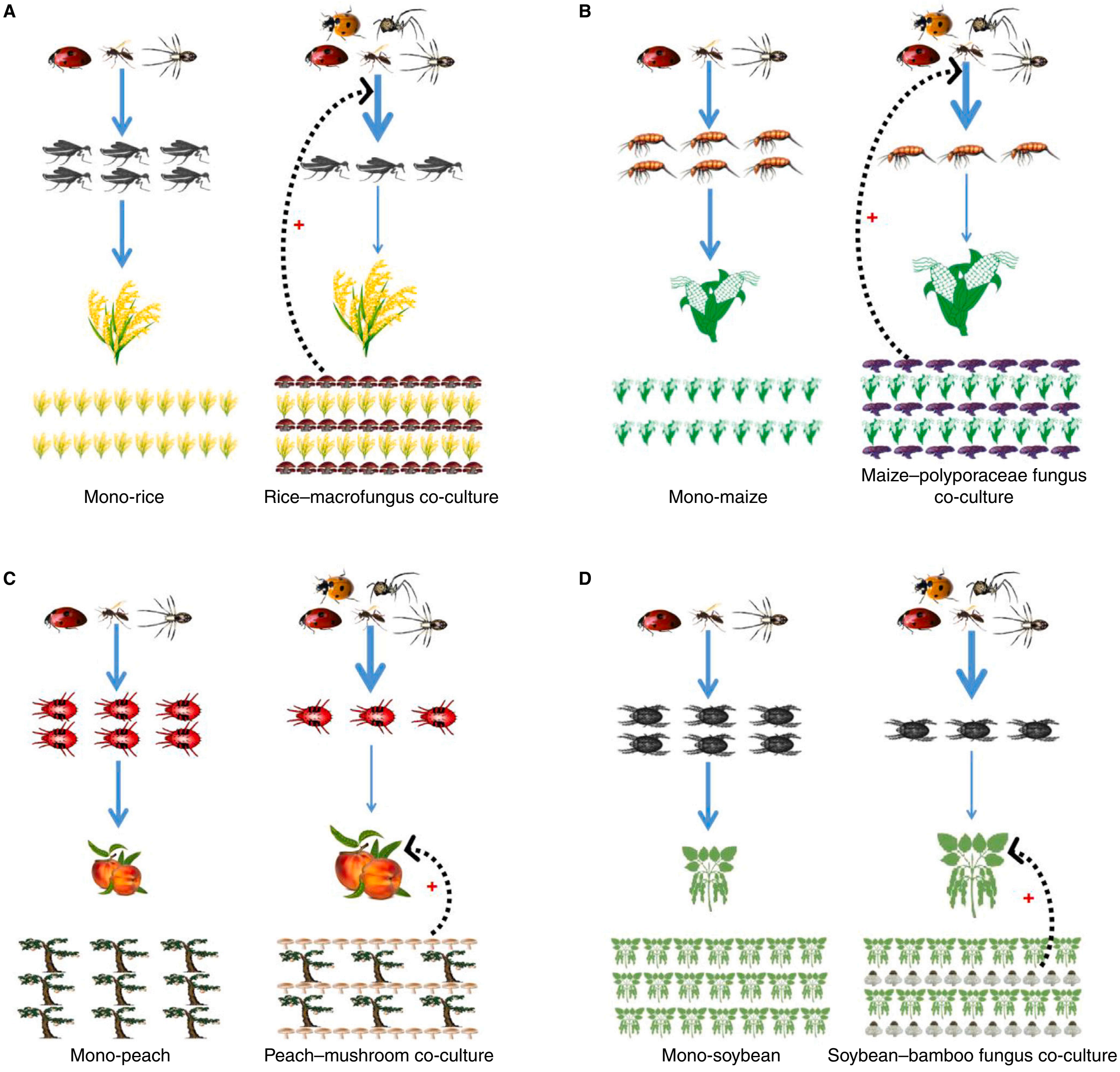

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Figure 4. Hypotheses to understand the potential effects of co-cultures of crops and edible fungi on trophic cascades among invertebrate herbivores, natural enemies (predators and parasitoids), and crops.

(A,B) Natural enemy hypothesis: co-cultures of crops and edible fungi increased the abundance and diversity of natural enemies in target crop systems, resulting in a lower level of invertebrate herbivores in these co-culture fields; in (A), herbivory gall midges in an edible macrofungus (*Auriculariapol ytricha*) provide food resources for natural enemies in rice, and this edible macrofungus provides a refuge for natural enemies in rice[89]; and in (B), herbivory mites in an edible polyporaceae fungus (*Ganoderma lucidum*) provide food resources for natural enemies in maize, and this edible fungus provides a refuge for natural enemies in maize[91]. (C,D) Crop resistance hypothesis: introducing edible fungi into monocrop systems or micro-climates can increase crop resistance against invertebrate herbivores. As shown in (C), the cultivated materials and residues of a mushroom (*Lentinus edodes*) after *L. edodes* were harvested can improve soil fertility by improving soil structure and increasing soil decay and ultimately benefitting peach trees by improving resistance to herbivores[92]. As shown in (D), soybeans absorb CO_2 released through the respiration of a bamboo fungus (*Dictyophora indusiata*), and this process benefits soybeans by enhancing soybean resistance against invertebrate herbivores[90]. The black dotted arrows denote the positive (+) effects of co-cultures of crops and edible fungi on the trophic groups. The widths of the blue solid arrows indicate the hypothesized relative strengths (co-culture systems vs. monocrop systems) of the interactions between invertebrate herbivores and natural enemies and between plants and invertebrate herbivores. (Insect, plant and bird images © 16pic.com.)

to more efficient top-down control of herbivorous pest populations in rice fields[89]. Furthermore, edible fungi can serve as a supplementary refuge for natural enemies[90] and to some extent provide additional natural enemies to consume herbivores in crops (e.g., rice)[89] (Figure 4A). A similar increase in the top-down control effect of the enemy on invertebrate herbivores was observed in maize interplanted with a Polyporaceae fungus (*Ganoderma lucidum*) (Figure 4B)[91].

Crop resistance hypothesis

Here, we reviewed the hypothesis that is similar to the above hypothesis regarding co-cultures of crops and domestic animals. The crop resistance hypothesis applies to food crops, cash crops, vegetables and fruits[90–94]. Edible fungi can provide supplementary nutrients to crops and ultimately strengthen the bottom-up effect of crops on invertebrate herbivores. For example, mushroom residues increase peach growth via the improvement of soil fertility[92] (Figure 4C). Edible fungi can also provide additional CO_2 through the respiration process[93], and this CO_2 can be absorbed by crops through photosynthesis[90]. Both of these two-sided supplementary resources from edible fungi can increase the level of chemical resistance (e.g., phenolics) of crops to defend against herbivores[94], thus strengthening the bottom-up effect of crops on herbivores (Figure 4D). All these mechanisms can directly or indirectly trigger a trophic cascade in cropping systems.

A ‘cascade chain’ linking ecological processes with human well-being

We reviewed all the literature available and found that crop diversification strengthens trophic cascades (Figure 1) through potential mechanisms (e.g., the natural enemy hypothesis, the resource concentration hypothesis and the insurance hypothesis) in cropping systems. However, due to a lack of global experiments or sufficient data, whether co-cultures of crops and domestic animals or co-cultures of crops and edible fungi also strengthen such trophic cascades is still unknown. Trophic cascades occur from the indirectly positive effects of natural enemies on crops and can be strengthened through intercropping, flower strips, cover crops and border crops[12]. Enhancing the top-down control of invertebrate herbivores by natural enemies can, in turn, increase crop yield, reduce dependence on insecticide use, and ultimately increase economic profits[95]. Therefore, there is a potential ‘cascade chain’ that links ecological processes to human well-being (Figure 5A). Here, we present two practical interventions that could support this ‘cascade chain’ in crop production-based systems.

A cascade chain from cultivated plant species diversity

Recent studies have revealed many potential benefits of increasing plant diversity (e.g., intercropping, flower strips, cover crops and border crops) in cropping systems, including pest suppression, crop yield, and yield stability (see Isbell *et al.* for a review[96]). For example, Gurr *et al.* reported that the growth of nectar-producing plants around rice fields reduced the populations of two key pests, reduced insecticide application by 70%, increased grain yield by 5% and provided an economic advantage of 7.5%[7]. In addition, they found that predators and parasitoids of the main rice pests, together with detritivores, were more abundant in the presence of nectar-producing plants. Similarly, Wan *et al.* found that crop diversification gave rise to a cascade chain, as the presence of border crops increased invertebrate predator abundance, decreased pest abundance and dependence on insecticides, and increased rice yield and economic profits in paddy systems[8] (Figure 5B). In general, there is growing evidence that increasing plant diversity around or within crops can increase the natural enemies of crop pests[97], improve pest control[14,98], decrease insecticide use[76,99], and promote crop yield[76] and economic profits[100]. These findings suggest a possible trigger for the cascade chain due to cultivated plant species diversity (Figure 5A,B)[8].

A cascade chain from co-culture of crops and aquatic animals

Increasing cultivated species diversity through co-culture of crops and aquatic animals can be another tool to benefit modern agriculture[63,101]. Previous studies have shown that co-culture of rice and aquatic animals, such as fish[63,65,102], shrimp[103], and ducks[104], has the potential to increase rice yields while reducing insect pests and thus reducing the use of insecticides[63]. Similarly, co-culture of vegetables and aquatic animals (i.e., fish)[70,71] has the same ecological functions in suppressing herbivores and decreasing the use of pesticides[64] (Figure 5C). In this case, we also expect a possible cascade chain triggered by the integration of animals into crop-based systems.

Integration of trophic cascade benefits into agricultural socioeconomic systems

A cascade chain linking ecological processes with socioeconomic factors in agriculture can be triggered by diversification practices that enhance key elements of biodiversity. However, this cascade chain cannot occur under all conditions, given that cultivated species interactions are sensitive to different environmental conditions and that some farming techniques are not compatible with nature-based solutions. Therefore, we should first integrate socioeconomics and ecology with a thoroughly new perspective and then adopt compatible cultivation strategies, as well as specific policies, to achieve direct benefits that arise from cultivated species diversity and indirect benefits that arise specifically from trophic cascades (Figure 6).

A new perspective integrating socioeconomics and ecology

When we recognize the cascade chain, we should integrate socioeconomics and ecology[105] and consider a certain agroecosystem as a complex system integrated with social, economic and natural subsystems[106,107]. When weighing the advantage of cultivated species diversity over monocrop systems, we should not only pay attention to the biological performance values of trophic groups (e.g., increased crop yield, natural enemy diversity, decreased invertebrate abundance and damage) but also weight nonbiological significance (e.g., environmental protection, biodiversity loss risk and social welfare). When assessing these integrative effects of cultivated species diversity on socioeconomic and ecological factors, we can adopt several quantitative methods (e.g., random utility models and contingent valuation methods)[105].

Cultivation strategies

The promotion of cultivation strategies based on rational selection of co-existing species (i.e., multispecies co-culture) can support mutual benefits among different species. This action is likely to be beneficial for intercropping because certain crop

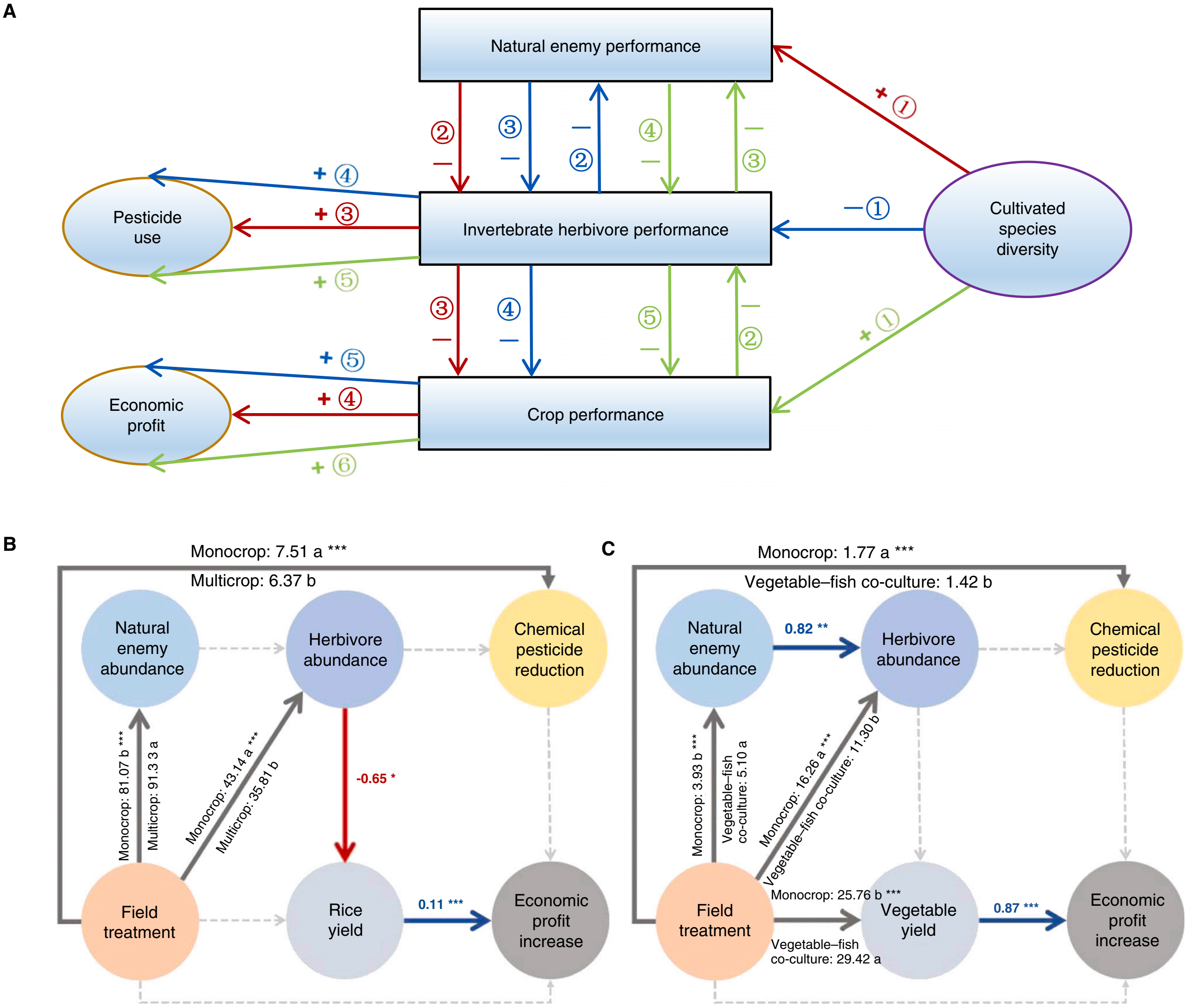

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Figure 5. A conceptual flowchart and an example analysis of the 'cascade chain' linking ecological processes with human well-being.
(A) A conceptual flowchart of the cascade chain linking ecological processes with human well-being through direct and indirect top-down tri-trophic cascades. (B) Effect of crop diversification on the cascade chain among invertebrate herbivores, natural enemies, rice, reduction of pesticide use and economic increases in microcosm experiments (i.e., multi-crop systems vs. mono-rice systems)[8]. (C) Effect of species diversity on the cascade chain among invertebrate herbivores, natural enemies, vegetables, reduction of pesticide use and increased economic profit in microcosm experiments (i.e., vegetable–fish co-culture systems vs. mono-vegetable systems)[63]. In (A), + denotes positive relationships, and – denotes negative relationships; the red arrows indicate the cascade chain via a direct top-down tri-trophic cascade, while the blue and green arrows indicate two separate cascade chains via two indirect top-down tri-trophic cascades; and the numbers in the circles denote each step of the cascade chain. In (B,C), SEMs fitted with scale-standardized coefficients were adopted. Solid lines indicate that the driver influences the likelihood of the model through a χ^2 likelihood ratio test, dashed paths indicate no detectable influence of the driver ($P > 0.05$), standardized coefficients are presented for each path, and letters a and b denote groupings through post hoc tests. * $P < 0.05$, ** $P < 0.01$, and *** $P < 0.001$.

species cannot be grown together due to interspecific competition for nutrients and other resources. In addition, cultivation strategies should cover other factors (e.g., maximum economic profit and effective pest control). Thus, the correct selection of co-existing species — such as wheat–maize–cotton intercropping[108], leguminous cover crops in maize fields[109], wildflower strips around cereal fields[110], rice–fish co-culture[59], and maize–mushroom intercropping[85] — is crucial because not all species (or their combination) introduced into a monoculture system have a real benefit on ecological processes (e.g., natural pest control) and socioeconomic factors (e.g., crop yield or insecticide use)[7,8]. It is also possible that these new species can do a disservice by, for example, increasing the abundance of invertebrate herbivores, with associated negative consequences on crops[19,20]. Therefore, the development of a cascade chain strictly depends on the rational selection of co-existing species that directly or indirectly promote the top-down control of invertebrate herbivores. These new diversification practices should be based on the following principles. First, the herbivore resistance of co-existing main crops should be increased by

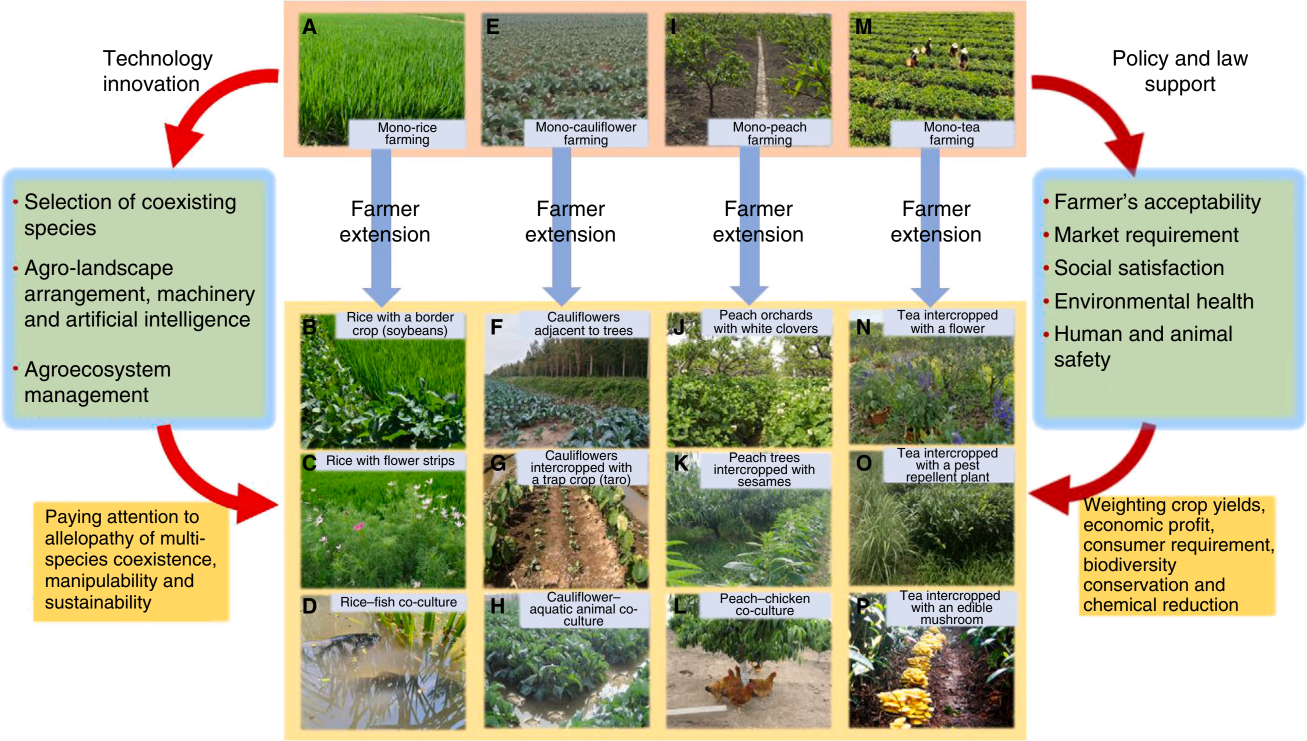

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Figure 6. Design for the application of cascade chain theory to the development of economically and socially sustainable crop production.
(A) Mono-rice farming. (B) Rice with a border crop (soybeans) in which predators (e.g., spiders and ladybirds) can spill over from soybeans to rice fields. (C) Rice with flower strips in which predators (e.g., spiders and ladybirds) can spill over from flowers to rice fields. (D) Rice–fish co-culture in which fish prey on rice pests (e.g., planthoppers). (E) Mono-cauliflower farming. (F) Cauliflower adjacent to trees in which the natural enemies can provide protection for cauliflower. (G) Cauliflower intercropped with a trap crop (taro) in which the taro plants attract tobacco cutworm from the cauliflower plants. (H) Cauliflower–aquatic animal co-culture in which ditches served as a natural barrier that prevented lepidopteran herbivores from migrating between the plots. (I) Mono-peach farming. (J) Peach orchards with white clover plants that provide food and refuge for predators. (K) Peach trees intercropped with sesame plants in which the sesame plants provide food resources for predators and parasitic wasps. (L) Peach–chicken co-culture systems in which the chickens prey on orchard herbivores. (M) Mono-tea farming. (N) The tea is intercropped with a flower (*Salvia japonica*), which provides food resources for predators and parasitic wasps. (O) Tea intercropped with a pest repellent plant (*Nardus lemongrass*) to repel the pest geometrid in teas. (P) Tea intercropped with an edible fungus (*Pleurotus citrinopileatus*), in which *P. citrinopileatus* increases tea plant resistance to insect herbivores in teas.

improving plant resistance characteristics. Second, they should promote natural enemies by providing alternative resources or refuge sites. Third, they should suppress invertebrate herbivores by regulating herbivore behaviors via organism-released volatiles (i.e., keeping herbivores away from target plants through push–pull strategies). For instance, China has been extending the cultivation of trap plants (i.e., *Chrysopogon zizanioides*) in rice fields nationwide, as *C. zizanioides* is a dead-end trap plant that can effectively attract adult female stem borers to oviposit, but stem borer larvae are unable to complete their life cycle on this plant[111]. Moreover, such plant diversity with trap plants decreases rice insect pests and associated pesticide use and increases rice yield and economic profits due to the indirect weakening of the herbivore top-down effects on rice. In addition to diversification strategies, other important operational practices need to be considered, such as compatible mechanization. For example, field trenching and water management differed between rice–fish co-culture systems and mono-rice systems because rice and fish have different growth and survival conditions in co-culture systems (Figure 6D). The development of an integrated operational program considering both mechanization and practical cultivation techniques is certainly needed. In monoculture systems (Figure 6A,E,I,M), operational practices are simplified compared with those in multispecies co-existence systems (Figure 6B,D,F–H,J–L,N–P), where more aspects must be considered simultaneously.

Progressive policies and laws

Governments should also enact specific policies and laws that help implement multispecies co-culture practices in agriculture, such as was done for organic farming, for which different policies have been promoted worldwide to implement this practice. Examples of such policies in the United States include the adoption of crop species diversification (e.g., intercropping, cover crops, or flower strips) to conserve beneficial arthropods[112], control pests[113] and improve crop productivity and quality[114]. Likewise, similar policies have also been implemented in the European Union that, to have access to greening payments, oblige medium (10 to 30 ha) to large (>30 ha) farms to grow at least two or three crops, respectively[115,116]. Some studies have shown the potential of crop diversification to suppress insect pests by natural enemies, alleviate pesticide pollution[117] and increase crop yield[118]. In China, a similar policy (Action Plan for Zero Growth in Pesticide Use by 2020) was launched to promote crop diversification in different regions[119]. Another example is “The

14th Five-Year Plan for the National Green Development of Agriculture'' in China, which states that farmers should further apply environmentally friendly and higher-profit technologies (e.g., crop–aquatic animal co-cultures) nationwide to reduce pesticide use, increase crop yields and improve economic profits[58].

Financial support

Financial benefits may also be generated by more holistically considering the non-target environmental long-term damage caused by agrochemicals if public financial compensation or incentives are advocated. A successful case is the European Union's Common Agricultural Policy (CAP) measures[120]. For example, Payments for Ecosystem Services (PES) have been proposed to maintain and adopt plant diversification in the European Union[120], China[121], Brazil[122], Ecuador[123], as well as parts of western and central Africa[124]. The application of PES measures specifically for agricultural biodiversity (Payments for Agrobiodiversity Conservation Services) is another example[125,126]. Incentives are also very important for farmers to implement these practices. To motivate farmers to improve food production and reduce environmental pollution, Zhejiang Province in China has applied agricultural diversification practices to the main cropping systems (i.e., rice, tea, wheat, and rapeseed) by providing specific subsidies for the implementation of these practices[127]. Consequently, the use of agrochemicals has decreased seven years ahead of China's goal to achieve zero growth in chemical fertilizer and pesticide application[127]. In particular, incentives related to short-term economic benefits might result in a higher adoption rate than those aimed solely at providing an ecological service to motivate farmers to adopt crop diversification[128]. Thus, farmers may be prone to adopt species diversity practices, as economic benefits can be obtained through a decrease in both herbivory damage and pesticide input and an increase in yields. However, these economic benefits do not fully offset the increased labor costs of these practices. New subsidies for covering (total or in part) these extra costs might be proposed to motivate farmers to implement these practices. In turn, farmers might be inclined to adopt co-culture practices by the imposition of a pesticide tax[129], fertilizer tax[130], or carbon tax[131] or by the implementation of an administrative penalty on the overuse of agrochemicals.

Societal acceptance

The cascading social-ecological benefits of biodiversity for agriculture (e.g., quality and healthy food due to decreased pesticide use) should also be recognized by society (i.e., farmers and city dwellers). First, farmers should be willing to adopt biodiversity-based practices. Second, consumers should be willing to pay for these practices through higher prices for agricultural products, as most of the cascading social-ecological benefits of biodiversity will accrue to consumers who will be able to enjoy the healthy food provided by farmers. Furthermore, with increasing awareness of sustainability issues[132,133], societal acceptance of these additional costs will be accelerated[134]. Currently, stakeholders can play a critical role in disseminating the cascading social-ecological benefits of biodiversity from farm to fork to improve societal acceptance.

Conclusions

Here, we reviewed three ways of increasing cultivated species diversity — crop diversification, co-cultures of crops and domestic animals and co-cultures of crops and edible fungi — which were chosen based on their popularization and contribution to global crop production. Co-culturing of crops and domestic animals and co-culturing of crops and edible fungi are not well practiced globally, but these two practices play key roles in food safety for increasing populations and local economies in developing countries. Even in developed Europe, the 'AGFORWARD' project was developed to adopt co-cultures of crops and domestic animals (i.e., integrating crops and grazing livestock)[135].

We reviewed how enhancing species diversity in cropping systems can trigger trophic cascades that lead to the top-down control of invertebrate herbivores by natural enemies, resulting in positive, indirect effects on crops (Figure 1 and Tables S2 and S3). These advantages can spread to cover socio-economic benefits (i.e., yield, economic and environmental performance)[95]. However, there are also situations in which enhancing species diversity can fail to yield these benefits or even have a negative effect[18–20]. In this context, further studies are needed to explore the mutual benefit mechanism among multi-species co-existence systems and how to avoid the negative effects of species diversity on social-ecological benefits. In cropping systems, cultivated species diversity can also decrease the abundance of other pests (e.g., crop pathogens) through a potential 'dilution effect' by which crop diversity dilutes pathogen concentration and prevents pathogen spread[136]. Decreased crop pathogen abundance triggered by crop diversity results in a decrease in pesticide use and economic input and thus gives rise to an increase in crop productivity and economic profit. Thus, we believe that such a linking chain can also be extended to the effects of crop diversity on crop–pathogen interactions.

Here, we focused on the top-down and bottom-up effects of cultivated species diversity to understand the links between them. Such a chain can also be obtained by non-trophic effects (e.g., soil mutualists and pollinators). For example, crop diversity promotes crop productivity and economic profit through direct effects from soil arbuscular mycorrhizal fungi (AMF), as AMF mediate positive plant diversity–productivity relationships[137,138], or from the pollination services of honey bees[139,140].

Here, we summarized ten hypotheses and propose a cascade chain linking ecological processes with human well-being. However, such a chain cannot be realized, which can be explained by the 'more individuals hypothesis', in which the increased herbivore abundance and herbivory are due to greater availability of more nutritionally balanced or less temporally variable food resources[141], or can be evidenced by decreased crop productivity as trait-dependent complementarity becomes more negative at higher plant species richness[142].

The large-scale application of these co-culture systems may be limited by several factors: phenological mismatches between co-cultured crops that can affect mechanical harvest efficiency[143]; differences in cultivation requirements between co-cultured species (e.g., crops and aquatic animals) that can limit agricultural practices; increased operational costs in co-cultured crops compared with monoculture[71]; and benefits of diversification practices that are often not immediate, so farmers might lose interest. Thus, there is an urgent need to develop diversified planting technology, and smart agricultural machinery that is compatible with mechanization.

Although farmland is the main source for human food production, we should consider not only the economic interests of farmers but also the negative effects of agrochemical pollution. Therefore, stakeholders at all levels should strengthen cooperation in publicizing, disseminating, and implementing policies that promote the benefits of co-existing species diversity to harness biodiversity to provide healthier food and environments for humans. In this regard, it would be important to focus not only on the direct benefits that arise from species diversity, but also on the indirect effects that arise from trophic cascades. Here, we propose a cascade chain theory that links cascading social-ecological benefits of biodiversity for agriculture, and such a theory could also be applied in other fields, such as forestry and grassland management and wildlife protection.

SUPPLEMENTAL INFORMATION

Supplemental information containing one figure, five tables, and methods can be found with this article online at https://doi.org/10.1016/j.cub.2024.05.001.

ACKNOWLEDGEMENTS

We thank Professor Teja Tscharntke for providing useful suggestions and Dr. Fengfei Xin for designing the map. N.-F.W. was supported by the Shanghai Agriculture Applied Technology Development Program, China (Grant No. 2023-02-08-00-12-F04586), the Natural Science Foundation of Shanghai (22ZR1417200), Fundamental Research Funds for the Central Universities (JKY01231718), the Shanghai Science and Technology Innovation Action Plan from the Shanghai Municipal Science and Technology Commission of China (22015821000) and the National Ten Thousand Plan-Young Top Talents of China. M.D. was supported by the SusCrop-ERA-NET FACCEJPI - 2022 Joint Call on Agrobiodiversity project IMPRESS ('Improving Agrobiodiversity for Resilient Pest Control Services Across Landscapes') with national funding from the MASAF.

AUTHOR CONTRIBUTIONS

N.-F.W. developed the initial idea of the conceptual framework, which was elaborated upon and finalized by all the authors. N.-F.W. drafted the article. N.-F.W., M.D. and Y.-Q.W. collected and analyzed the data. N.-F.W., M.D., Y.-Q.W. and M.L. wrote the manuscript. All authors prepared and edited the final drafts.

DECLARATION OF INTERESTS

The authors declare no competing interests.

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