



Combining *Milpa* and Push-Pull Technology for sustainable food production in smallholder agriculture. A review

Felipe Librán-Embíd¹ · Adewole Olagoke¹ · Emily A. Martín¹

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Abstract

Achieving food security remains a pressing challenge for small-scale farmers, especially in sub-Saharan Africa and Latin America. Ongoing climate change, invasive noxious weeds, and crop pests further exacerbate the situation. Optimizing traditional cropping systems for sustainable yields and climate-resilient production is imperative in order to address this challenge. The pre-Columbian *milpa* system of intercropping maize with companion crops such as beans (*Phaseolus vulgaris*) and squash (*Cucurbita* spp.) is one effective system that has been shown to produce outstanding yields per unit area compared to monoculture systems. The Push-Pull Technology developed in East Africa, based on the use of repellent and trap companion plants intercropped with maize (and to a lesser extent sorghum), is seen to be similarly effective in minimizing the impact of major pests on yields, including striga weed (*Striga* spp.), maize stemborers, and the fall armyworm (*Spodoptera frugiperda*). Although both systems have the potential to compensate for each other's limitations, there has been no cross-system learning between the Mesoamerican *milpa* and the East African Push-Pull Technology. Here, we review both systems and present the advantages likely to be obtained by combining these technologies in small-scale farming. The proposed *milpa push-pull* system could adapt to different gradients of altitude, rainfall, and soil nutrient levels, in addition to controlling pests, and therefore has the potential to become a fundamental cropping technique in Latin America and sub-Saharan Africa.

Keywords *Desmodium* · *Brachiaria* · Napier grass · Fall armyworm · Striga weed · Stimulo-deterrent · Diversionary strategy · Stemborer · Maize · Squash · Beans

1 Introduction: Maize, Mesoamerican *Milpa*, and the Push-Pull Technology

Food insecurity remains a pressing issue for many small-scale farmers, especially in sub-Saharan Africa and Latin America (Silvestri et al. 2015; Espinosa-Cristia et al. 2019). Varying rainfall patterns under climate change, in addition to threats such as invasive noxious weeds and crop pests, further deepen the problem (Khan et al. 2014; Gazal et al. 2018). Therefore, optimizing agricultural techniques for the production of staple foods, such as maize (*Zea mays* ssp. *mays*), becomes imperative.

Maize origins trace back nearly 9000 years to the Mesoamerican region when it was domesticated from its wild relative teosinte by early settlers (Matsuoka et al. 2002). It became the staple food source for many indigenous American societies (Staller 2021) and a crucial component of the diets of subsistence farmers across the Americas and Africa (Shiferaw et al. 2011). In fact, maize accounts for more than 20% of the calorie intake in Eastern Africa, Central America, and Mexico (Shiferaw et al. 2011). At the same time, these regions are also likely to suffer disproportionately from the impacts of climate change on agricultural production through increases in droughts and the pressure of native or invasive pests (McGuigan et al. 2002; Mainka and Howard 2010). The mean global maize losses due to pests and pathogens stand at 22.5% but increase to 30.1% in sub-Saharan Africa (Savary et al. 2019). The predicted range expansion, severity, and emergence of pests and pathogens with ongoing climate change further threaten long-term food security (Bebber 2015; Ristaino et al. 2021).

✉ Felipe Librán-Embíd
feliem3@gmail.com;
Felipe.Libran-Embíd@allzool.bio.uni-giessen.de

¹ Institute of Animal Ecology and Systematics, Justus Liebig University of Gießen, Heinrich-Buff-Ring 26, 35392 Gießen, Germany

Agricultural intensification and land-use change have increased the pressure that pests and pathogens exert on crops, especially in non-origin areas, where natural enemies are usually absent (Bianchi et al. 2006; Chaplin-Kramer et al. 2011). For example, the invasion of the fall armyworm (*Spodoptera frugiperda*, FAW) in Africa in 2016 was dramatic as this pest attacks common cereal crops, including maize and sorghum (Davis et al. 2018; Baudron et al. 2019); whereas in the Americas, the species is a generalist pest of almost all main staple crops (Montezano et al. 2018). Climate change and FAW have been the main threats to food security in sub-Saharan Africa in recent years (Gebreziher 2020; Matova et al. 2020; Timilsena et al. 2022).

Several strategies have been developed across the tropics to deal with the susceptibility of maize to soil fertility, climatic stressors, and pest pressures (Altieri and Nicholls 2003; De Groot et al. 2010). One such strategy involves enriching the system with edible and/or beneficial companion plants. The traditional *milpa* system in Mesoamerica, based on intercropping maize with beans and squash, and the Push-Pull Technology (PPT) developed in Eastern Africa in 1997, are key among available technologies based on companion cropping strategies. Both technologies have shown great promise, most conspicuously through strong increases in yield, but also through a range of other benefits (Khan et al. 2014; Lopez-Ridaura et al. 2021). While the *milpa* system is founded on diversified food crop production, the push-pull system makes use of attractive and repellent properties of companion plants to reduce the pressure of pests on the crop. However, to date, *milpa* use has remained mostly limited to smallholder indigenous farmers in Mexico and Central America (Molina-Anzures et al. 2016), although there are reports of cereal-legume (Layek et al. 2018; Maitra et al. 2020) and cereal-legume-pumpkin (Baudron et al. 2019) combinations from other parts of the world, including Asia and Africa.

Widespread adoption of the PPT, on the other hand, has been limited by several factors including access to seeds of companion plants, lack of flexibility for crop rotation/diversification, and the amount of labor required at the initial stages (Fischler 2010). While very efficient in controlling pest and weed infestations, one main constraint of PPT lies in the fact that the recommended companion plants are not utilized as food, making the system produce only maize and fodder from plots that would otherwise be intercropped with other food plants such as common beans in addition to maize. Meanwhile, the *milpa* system is not designed to withstand high levels of insect pests and/or striga weed infestation. Surprisingly, to date, there has been little or no cross-system learning between the Mesoamerican *milpa* and the East African PPT, despite the fact that both systems have the potential to compensate for each other's limitations.

Here, we review the available literature on the characteristics of *milpa* and the PPT. We followed a qualitative review methodology that was not designed to be exhaustive, but rather to represent a consistent sample of the literature. Articles that described both systems, as well as those with evidence to support the potential benefits of combining *milpa* and PPT, were reviewed and synthesized. Based on the above, we present the advantages likely to be obtained by combining these technologies in small-scale farming in Latin America and sub-Saharan Africa.

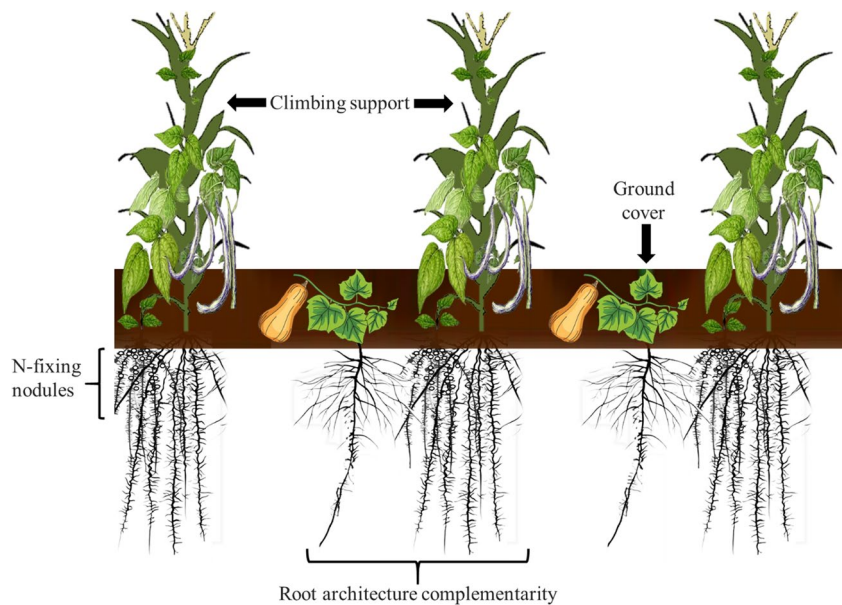
2 *Milpa* in Mesoamerica: a highly successful traditional mixed-cropping system

The pre-Columbian civilizations in Mesoamerica did not grow maize in extensive monocultures but rather used complex multi-cropping systems (Zizumbo-Villarreal and Colunga-GarcíaMarín 2010). By 4400 BP, they developed a planting technique known as *milpa* or “three sisters” (Zizumbo-Villarreal and Colunga-GarcíaMarín 2010). The term *milpa* may be broadly used to refer to any kind of maize-producing system (Lopez-Ridaura et al. 2021), but its more strict and original meaning involves intercropping maize with beans (*Phaseolus vulgaris/Phaseolus lunatus*) and squash (*Cucurbita* spp.) (Parsons et al. 2009; Zizumbo-Villarreal and Colunga-GarcíaMarín 2010) (Fig. 1). The basis of the *milpa* system lies in the fact that the bean plant climbs the maize, increasing its access to light, and at the same time fixates nitrogen in the ground, which is then available for the other plants of the system (Zhang et al. 2014). The squash, with its broad leaves, shades the soil, protecting it against erosion, retaining soil moisture, and preventing competitive weeds from entering the system (Lopez-Ridaura et al. 2021).

Maize, beans, and squash were domesticated contemporaneously in Mesoamerica and experienced natural and artificial selection leading to a high level of ecological adaptation to each other (Zizumbo-Villarreal and Colunga-GarcíaMarín 2010). The *milpa* adapts to diverse soil and climatic conditions and suffers from fewer pests and diseases than monocrop maize, also proving particularly efficient in terms of nutritional output (Van Rheenen et al. 1981; Morales and Perfecto 2000; Lopez-Ridaura et al. 2021). Indeed, the component plants in a typical *milpa* system differ in their root crown architecture and vertical root distribution, leading to a high degree of complementarity and efficiency in terms of nutrient uptake, particularly nitrogen, and phosphorus (Zhang et al. 2014).

Smallholders in Latin America mostly use traditional agricultural systems based on polycultures such as *milpa* (Aldama et al. 2015; Suárez et al. 2022). Smallholder farming (farms with < 5 ha in production) in Latin America

Fig. 1 Maize (*Zea mays* ssp. *mays*), beans (*Phaseolus vulgaris*), and squash (*Cucurbita* spp.) in the most traditional setting of the *milpa* system. The principles of *milpa* are depicted, showing beans' N-fixing nodules and root architecture complementarity (optimization of nutrient uptake), climbing support for beans (optimizing light interception and photosynthesis), and ground cover by the leaves of *Cucurbita* spp. (moisture retention and soil erosion prevention). Root architecture modified from Postma and Lynch (2012).



represents circa 60% of the share of farms in the region, but only extends over less than 2% of the agricultural area (Lowder et al. 2021). However, the contribution of smallholder agriculture to the general food supply in the region reaches on average 7% of the food calories produced, indicating that smallholders have greater productivity per hectare than larger farms (Samberg et al. 2016). When “family farming” is considered (farms held by a family unit and not a commercial company), this type of farming’s contribution to the regional food supply is considerably larger (Schneider 2014; Lowder et al. 2021). The widespread use of *milpa* by smallholder and family farmers, especially in low-input cropping systems, is notably based on a 30% over-yield advantage over the average yield of the respective monocultures (Altieri et al. 2012; Zhang et al. 2014). Compared to monocultures, *milpa* allows small-scale farmers to produce more food on the same land, while maintaining the yield of the main crop, maize (Altieri et al. 2012; Ebel et al. 2017; Lopez-Ridaura et al. 2021).

In Latin America, several native and exotic arthropods are considered pests of economic importance, in particular the lepidopterans *Spodoptera* spp., *Helicoverpa* spp., *Agrotis ipsilon*, and *Diatraea saccharalis* (Blanco et al. 2016; Varón de Agudelo et al. 2022). *Spodoptera frugiperda* (FAW) is commonly referred to as the most important maize pest in Latin America (Blanco et al. 2016; Hruska 2019). However, these pests are only problematic in large-scale maize farming (conventional and transgenic maize) and are not even mentioned among the most common herbivorous arthropods by traditional smallholder farmers (Morales and Perfecto 2000). In fact, no herbivorous arthropod is classified as a “pest” (i.e., surpassing economic threshold damage) by small-scale *milpa* farmers (Morales and Perfecto 2000).

Due to the increasing resistance of FAW to many insecticidal proteins of *Bacillus thuringiensis* (Bt), multiple insecticide applications, even in transgenic maize, are required to control FAW in large-scale maize farming (Blanco et al. 2016). Blanco et al. (2016) cite potential losses of 100% in conventional large-scale maize plantations as a consequence of FAW attacks if left unattended. Regarding weed control, herbicides, such as glyphosate, are usually used in large-scale maize farming and particularly in association with herbicide-tolerant biotech (Round-UP Ready technology) maize (Gianessi 2013; ISAAA 2018). In contrast, manual interventions are usually sufficient for smallholders to control noxious weeds (Parsons et al. 2009), as many naturally occurring weeds in *milpa* are used for food, medicinal or other purposes, and companion crops (e.g., beans and squash) already control the spread of most noxious weeds (Caamal-Maldonado et al. 2001; Lima et al. 2010; Le Garff 2017). Although no parasitic specialist cereal weeds, such as those from the genus *Striga*, are known to occur in Latin America *Striga* spp. did invade the USA and Australia (Mohamed et al. 2006).

3 The African cereal-based Push-Pull Technology

Maize arrived in Africa during the seventeenth century and spread rapidly throughout the continent, substituting traditional native cereals such as sorghum (*Sorghum bicolor*), pearl millet (*Pennisetum glaucum*) and finger millet (*Eleusine coracana*) as the preferred crop in many parts of the continent (Cherniwchan and Moreno-Cruz 2019). As in Mesoamerica, maize is the main source of

calories within cereals in sub-Saharan Africa and is fundamental for the food security of smallholders (Shiferaw et al. 2011). In sub-Saharan Africa, smallholders represent circa 90% of the share of farms and occupy approximately 55% of the agricultural land, producing 50% of the calories in the region (Samberg et al. 2016; Lowder et al. 2021). Additionally, medium-sized farms (5–15 ha) account for another 26% of production (Samberg et al. 2016).

In Africa, maize production is severely limited by lepidopteran pests, such as stemborers *Busseola fusca*, *Chilo partellus*, the fall armyworm (*Spodoptera frugiperda*, FAW), and by the obligate root parasite *Striga* weed (i.e., *S. hermonthica* and *S. asiatica*, Midega et al. 2018). Stem-borers alone can cause up to 40% yield losses and striga weed can lead to a 100% yield loss if unattended (Khan and Pickett 2008). In the late 1990s, a stimulo-deterrent system for sustainable maize production was developed by the International Centre of Insect Physiology and Ecology (icipe) in Kenya, originally to control stemborers and striga weed without using pesticides or herbicides (Khan et al. 2000; Khan and Pickett 2008). The so-called Push-Pull Technology integrates into the maize field a set of repellent companion and “dead-end” trap plants (Khan et al. 2001, 2003) (Fig. 2). The PPT has proven to be highly efficient in increasing yields in an environmentally friendly manner not only by controlling pests but also because of its

benefits in terms of soil moisture retention and soil fertility improvement. Average yield increases of 50% and 20% were attained in areas with and without striga weed, respectively (Khan and Pickett 2008).

The PPT is based on intercropping maize with *Desmodium* spp., a plant genus native to the Americas. *Desmodium* spp. have pest repellent properties and also the capacity to control *Striga* spp. by provoking abortive germination of its seeds (Khan et al. 2003). At the same time, the properties of *Desmodium* spp., as a legume, enhance soil fertility by fixing nitrogen in the soil, and its extensive cover between the rows of maize helps retain soil moisture in otherwise dry conditions. Additionally, a dead-end trap plant (i.e., a plant attractive to female moths but in which larvae cannot develop), such as Napier grass (*Pennisetum purpureum*) or *Brachiaria* spp., is used around the plot edges to act as a “pull” for the pests (Khan et al. 2014; Cheruiyot et al. 2021a). Both companion plants also represent valuable sources of fodder for dairy animals. Different versions of PPT have been developed, including highly successful first-, second-, and third-generation “climate-smart” variants (Cheruiyot et al. 2021a). Besides controlling both stem-borers and striga weed, PPT has proven effective against the recent invasion of polyphagous FAW from America (Midega et al. 2018).

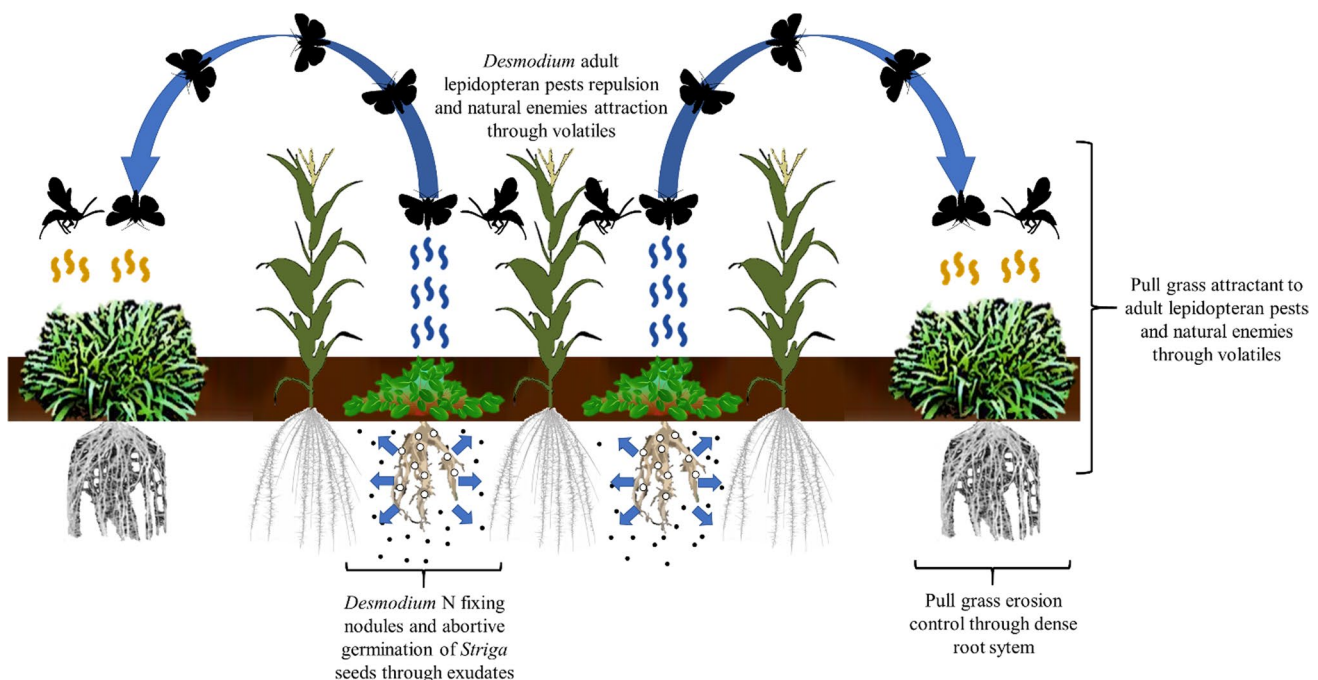


Fig. 2 Push-pull mechanism showing the repellent effects of *Desmodium* spp. on maize stemborers and the attractant properties of trap plants such as *Brachiaria* spp. and Napier grass *Pennisetum purpureum*. The attraction of natural enemies by companion plants is also shown, as well as the capacity of *Desmodium* spp. to fix nitrogen

and stimulate abortive germination of *Striga* weeds through root exudates. Maize roots modified from Postma and Lynch (2012), *Desmodium* roots modified from Hooper et al. (2015), and *Brachiaria* roots modified from Galdos et al. (2020).

There is currently an open debate on the exact mechanisms by which the PPT controls FAW. On the one hand, Sobhy et al. (2022) found that all companion plants tested (*D. uncinatum*, *D. intortum*, and *Brachiaria brizantha* cv Mulato II) constitutively emit volatile compounds that repel adult FAW moths and attract parasitoids. On the other hand, Erdei et al. (2022) propose that the fundamental mechanism is based on the preference of first instar FAW larvae on *D. intortum* over maize as the host plant although the plant does not allow FAW development (i.e., causes 100% larval mortality). Instead of repelling adult FAW moths, these authors report evidence of *D. intortum* acting as a pull plant for neonate-dispersing FAW larvae in search of a new host (Erdei et al. 2022). Although there is general agreement on the efficiency of PPT to control FAW, the elucidation of specific mechanisms is of major importance in order to develop natural pest control strategies in other crops and regions of the world. Decoding the reasons behind these seemingly contradictory findings will bring to light a deeper mechanistic understanding of PPT.

4 *Milpa* push-pull as a versatile solution to key agronomic limitations

We propose that a combination of traditional indigenous *milpa* with recent advances in PPT would represent a highly effective synergy for the biological control of maize pests and weeds, high yields, and diversified production. Both systems can be easily combined and adapted to region-specific farming conditions, with large potential benefits in terms of reduction of agrochemical inputs, crop yields, revenue, protection of biodiversity and cultural traditions. A *milpa* push-pull combination has the potential to robustly mitigate weeds and pests while also providing smallholder farmers with optimal food production and a diverse nutritionally-balanced harvest. Here, we describe how the *milpa* principles can be combined with the PPT to attain their mutual benefits. Furthermore, we critically assess the characteristics of the plants involved in the *milpa* and push-pull systems and discuss the possibility of using alternative plants in certain scenarios.

4.1 Parallels of the two systems: intercropping of cereals and legumes

In sub-Saharan Africa and Latin America, maize and leguminous plants, including beans (*Phaseolus vulgaris*), soybean (*Glycine max*), cowpea (*Vigna unguiculata*), pigeon pea (*Cajanus cajan*), bambara nut (*Vigna subterranea*), green gram (*Vigna radiata*) and groundnut (*Arachis hypogaea*) are commonly planted together for their ecological complementarity and associated

overyielding (Mucheru-Muna et al. 2010; Muoni et al. 2019). This overyielding is partly explained by the capacity of legumes to fix nitrogen in the soil, which is then available to other plants, such as maize. Additionally, cereal-legume associations tend to have fewer pests and pathogens than their respective monocultures (Van Rheenen et al. 1981; Fininsa 2003), including reduced severity of FAW attack (Hailu et al. 2018; Udayakumar et al. 2021). These properties explain why cereal-legume associations, particularly climbing beans and maize/sorghum, are so popular among smallholder farmers in Africa and Latin America and constitute the backbone of smallholder production.

4.2 Lessons from Mesoamerican *milpa* for African push-pull systems: diversification of food production, nutritional balance and the fight against FAW

Arguably, the strongest virtue of *milpa* systems is the high diversification of food production, the derived nutritional balance, and the “insurance” against total production failure. In other words, *milpa* systems maximize the volume and diversity of food elements, leading to a high nutritional balance in terms of macro- and micronutrients (Lopez-Ridaura et al. 2021). The accumulation of long-term knowledge on the most suitable plant combinations can be extremely valuable to enrich and accelerate the more recent efforts at food plant diversification currently underway in Africa (Chidawanyika et al. 2023).

One such example is the incorporation of *Cucurbita* spp. to cereal-legume smallholder production in Africa. The role of *Cucurbita* spp. within *milpa* systems partially overlaps that of *Desmodium* spp. within PPT, as both are responsible for soil moisture retention, reduction of soil erosion, and prevention of noxious weeds entering the system. But while *Desmodium* spp. are only used as fodder, *Cucurbita* spp. are a source of micronutrients, especially vitamin A, which are fundamental for an appropriate nutritional balance (Ndoro et al. 2007; Lopez-Ridaura et al. 2021). *Cucurbita* spp. are not unfamiliar to African smallholder farmers; maize-pumpkin intercropping is very common in southern Africa where farmers use all parts of the plant for food, including leaves, flowers, and seeds (Silwana and Lucas 2002; Maereka et al. 2009). However, its combination with cereal-legume intercropping is rare (Baudron et al. 2019), especially in other African regions.

Non-surprisingly, most knowledge on agroecological strategies against FAW comes from Latin American smallholders (Harrison et al. 2019). *Cucurbita* spp., for example, have been found to reduce FAW attack when intercropped with maize in Latin America (García González et al. 2010, 2013). On the contrary, the only study that

analyzed the effect of maize-pumpkin intercropping on FAW in Africa found increased FAW damage in maize-pumpkin treatment and no effect in the pumpkin-pulse-maize treatment compared to monocrop (Baudron et al. 2019). There is currently no clear explanation for this contradiction, which signals that complex interaction mechanisms are at play in these systems that are not yet understood and require additional research. Notably, this may signal context-dependent effects and non-trivial relationships among natural enemies in each local food web underpinning pest control services (Chen et al. 2017).

Among small-scale farmers in Latin America FAW does not usually reach economic thresholds (Wyckhuys and O'Neil 2006) and is commonly considered a herbivore of lesser importance that requires no particular management, especially in the highlands (Morales and Perfecto 2000; Wyckhuys and O'Neil 2007). The situation is different in large-scale maize monocultures in Latin America where FAW is usually a serious problem (Blanco et al. 2014). Smallholders in Latin America benefit from pest control services provided by a diverse array of predators and parasitoids that have coevolved with FAW (Molina-Ochoa et al. 2004; Rios-Velasco et al. 2011). These include wasps, flies, carabids, ants, spiders, and bats that are associated with native vegetation in the surroundings of plantations from which they can spillover to maize crops (Wyckhuys and O'Neil 2010; Maine and Boyles 2015; Cinel and Taylor 2019). This network of specialist and generalist natural enemies also profits from the multicropping systems used by small-scale farmers in Latin America due to the presence of alternative food resources and nesting sites (Nicholls and Altieri 2004; Altieri et al. 2012). Although specialist natural enemies of FAW, such as Hymenoptera (e.g., *Eiphosoma laphygmae*, Allen et al. 2021) and Diptera parasitoids are not expected to occur in Africa and Asia, where it has recently spread (Roy et al. 2011), a number of generalist natural enemies have been identified so far in its new range, including several parasitoids and ants (Abang et al. 2021; Mohamed et al. 2021; Kenis et al. 2022). Considering that other *Spodoptera* spp. are native to Africa such as *Spodoptera exempta* and *Spodoptera littoralis* host switching by indigenous parasitoids of *Spodoptera* spp. or other noctuids, could open an opportunity for biological pest control of FAW (Roy et al. 2011; Mohamed et al. 2021), as has already occurred with *Telenomus remus* in Asia (Kenis et al. 2019; Liao et al. 2019; Colmenarez et al. 2022) and with *Cotesia sesamiae* and *Cotesia icipe* in Africa (Fia-boe et al. 2017; Agbodzavu et al. 2018; Sisay et al. 2018; Abang et al. 2021; Mohamed et al. 2021). Additionally, the dependency of these natural enemies on proximal natural vegetation has recently been proven in Africa (Clarkson et al. 2022; Jordon et al. 2022). Hruska (2019) and Harrison et al. (2019) have extensively described a number of

strategies that smallholders in Africa and Asia could use, inspired by the American experience, that can contribute to palliate FAW damage, such as which, when and how to intercrop plant species and several cultural and landscape management recommendations and also have pointed to the most important knowledge gaps and research priorities.

4.3 Widening perspectives: centers of origin and traditional agroecological knowledge as foundations for sustainable intensification

To understand how agroecological systems work, it is essential to study them at their centers of origin (Chen et al. 2017). A good example of this comes from the election of *Desmodium* species in the African push-pull systems. Originally, the species *D. uncinatum* was used as a repellent plant (Cook et al. 2007), but as this species could not resist long periods of drought, it has been substituted with *D. intortum*, *D. incanum*, and other drought-resistant species during the last decade (Midega et al. 2018; Cheruiyot et al. 2021a). In fact, *D. uncinatum* is a forest species in its native range in South America, which may explain why it is not as tolerant to drought as other species in the genus (Vanni 2001). The drought-tolerant *D. incanum* (Midega et al. 2017) is a grassland-adapted species from the south of South America, which may explain its higher tolerance to drought and frost (Crosa et al. 1999). *D. incanum* is currently the recommended push plant of the so-called third-generation PPT (Cheruiyot et al. 2021a).

Local traditional knowledge is also key, particularly in millenary cultivation systems such as the *milpa*, because much can be learnt from the empirical experiences of farmers (Morales and Perfecto 2000; Lopez-Ridaura et al. 2021). Knowledge from centers of origin is also fundamental in terms of pest management (Altieri 1980) and will be especially important in Africa and Asia to learn how to better deal with the noxious FAW invasion from the American experience (Hruska 2019). This is particularly relevant considering that exotic FAW is displacing native stemborers such as *Busseola fusca* and *Sesamia calamistis* in some parts of Africa (Sokame et al. 2020, 2021). For example, it has been demonstrated in American systems attacked by FAW that beans should be planted considerably earlier than maize to achieve better protection against FAW (Altieri 1980). The same recommendation has been made regarding trap plants for FAW in African systems (Cheruiyot et al. 2021b).

Unfortunately, knowledge is often lost because a great deal of information is only available in local languages. In *milpa* systems, for example, knowledge is usually only available in Mayan languages and, if at all, translated and published in Spanish (Morales and Perfecto 2000; Ebel et al. 2017). This may also be the case for some native plants in

Africa that could potentially be used for *milpa push-pull* systems but whose usage is stored in local languages (Muoni et al. 2019), such as *Cleome* (= *Gynandropsis gynandra*) as a repellent plant for spider mites (Nyalala and Grout 2007). The protection of local indigenous languages and populations is likely to mean the protection of invaluable agricultural knowledge at the foundation of global food security.

4.4 Lessons from African PPT for Mesoamerican *milpa* systems: fight against *Striga* spp., control of lepidopteran pests and fodder production

Although currently absent in Latin America, striga weed has been found to have a high invasive potential in Latin America, and an invasion of the region in the near future cannot be excluded (Mohamed et al. 2006). In fact, striga weed was introduced and spread through the states of Florida, North and South Carolina (USA), and was eventually eradicated after several decades of interventions and significant expenditures from the local governmental agencies (Mohamed et al. 2006). To avoid major yield losses, as happened with the vertiginous FAW spread in Africa, Asia, and Oceania, Latin American farmers should be aware of the African experience with this parasitic weed. Many small-scale farmers in Africa rotate maize with beans (or other legumes) to fight striga weed, given that legumes stimulate striga weed germination, which later dies in the absence of a cereal host (Oswald and Ransom 2001). Among legumes, the use of *Desmodium* spp. in push-pull systems as an intercrop is particularly effective when striga weed is a problem and when maize is to be planted continuously throughout the seasons, without crop rotation (Khan et al. 2007). This is because *Desmodium* spp., unlike most other legumes, not only induces striga weed seeds to abortive germination but also prevents *Striga* from attaching to maize roots via allelopathic effects of their root exudates (Khan et al. 2007, 2014). A further advantage of *Desmodium* spp. is that they are perennial legumes and can fix more nitrogen in the soil than annual legumes provided that they can establish mutualistic interactions with specific rhizobia (Khan and Pickett 2008; Granada et al. 2014). Also *Desmodium* spp. intercropping has been found to induce increased plant defense through plant-soil feedback (Mutyambai et al. 2019; Erdei et al. 2022). The edible *Crotalaria brevidens* and *Crotalaria ochroleuca* have also been found to induce suicidal germination and prevent *Striga hermonthica* radicle development (Mwakha et al. 2020). In addition, *D. intortum* and *C. ochroleuca* were found to be the only two intercrop legumes, among several tested, to significantly reduce the emergence of *S. hermonthica* and increase maize height (Khan et al. 2007). Given the well-studied allelopathic effects of *C. juncea* (Skinner et al. 2012; Bundit et al. 2021) and the demonstrated allelopathy of root extracts in several other *Crotalaria* spp. (Rugare et al. 2021), it is possible that

C. ochroleuca and *C. brevidens* also rely on the same mechanism to control *S. hermonthica*.

Despite being native to the Americas, *Desmodium* spp. are largely ignored in their potential to control FAW and other pests on that continent, and to our knowledge, are not used as a repellent intercrop in any traditional Latin American cultivation system so far. Considering the increasing pressure of FAW attack on maize and the weakening of natural enemies' networks resulting from pesticide overuse in large-scale farms, deforestation, and climate change, *Desmodium* spp. may also be a candidate intercrop for smallholders to consider in Latin America. In fact, the inclusion of *Desmodium* spp. or other push plants may also allow for the sustainable intensification of maize crops and contribute to the control of other lepidopteran pests such as *Helicoverpa* spp. and *Agrotis ipsilon*. Moreover, it could be an option to produce more fodder without losing pest control properties or even be an alternative to Bt maize (Midega et al. 2006). The grasses used as trap plants in Africa (i.e., *P. purpureum*, *Brachiaria* cv Mulato II and *Brachiaria* cv Xaraes) have proven effective over the years for controlling African stemborers (Khan et al. 2003; Midega et al. 2015). However, they are found to perform poorly as pull trap plants for the American FAW, in particular the most commonly used trap plant, *Brachiaria brizantha* cv Mulato II (Guera et al. 2020; Scheidegger et al. 2021; Cheruiyot et al. 2021b). Guera et al. (2020) found that only *Panicum maximum* cv. Mombasa was significantly preferred by adult FAW moths for oviposition over maize, while also having a low survival rate of the larvae (15%). Cheruiyot et al. 2021b reported that FAW laid more eggs on *B. brizantha* cv. Xaraes and *P. purpureum* cv. South Africa than on maize in two-choice tests, but only when these grasses were double the size of maize. Overall, FAW larvae do not prefer any of the tested pull grasses over maize in two-choice tests (Guera et al. 2020) and all of them attracted significantly less larvae than maize after 48 h (Cheruiyot et al. 2021b). This means that, until better alternative trap plants for FAW are found, a trap plant may not be convenient in the Americas, as it may not compensate the opportunity costs of the land used for it in the absence of fodder requirements for dairy animals. Similarly, considering that FAW is displacing native stemborers such as *Busseola fusca* and *Sesamia calamistis* in some parts of Africa (Sokame et al. 2020, 2021), the importance of trap plants in African push-pull systems, especially in regions affected mainly by FAW should be revisited. Recently, Sobhy et al. (2022) found that none of the climate-smart PPT companion plants act as a pull trap plant for adult FAW moths, but rather all of them (including the border grass *Brachiaria brizantha* cv Mulato II) act as push plants for the pest and attractants to two of its natural enemies in Africa. Erdei et al. (2022) studied FAW

larval behavior towards *D. intortum* and found that this perennial legume functions as a dead-end trap plant for FAW larvae. Taken together, these studies show that PPT control of FAW does not occur by the same mechanisms as African stemborers, thus opening a range of possibilities to further maximize the efficacy of the system to control FAW through variations in the choice of companion plants, plant densities and spatial arrangement of PPT components.

4.5 The *milpa* push-pull system

Considering the above and the fact that beans intercropping has been shown to be compatible with PPT (Khan et al. 2009), we propose that already a basic form of a combined *milpa* push-pull system, i.e., a multi-crop association including maize planted in alternating rows with *Desmodium* spp. and *Cucurbita* spp. and enriched within the same row with climbing beans (Fig. 3), would be a useful framework to consider for further intensification of smallholder maize production. Furthermore, such a system could use a trap plant such as *P. maximum* cv. Mombasa or *B. brizantha* cv. Xaraes, where fodder production is desired and/or FAW pressure is high.

Other legume-enriched push-pull systems that diversify food production, increase nitrogen fixation, and enhance pest control might also be envisioned. We propose that a flexible *milpa* push-pull can be developed that builds on the benefits of species combinations classically found both in *milpa* and in PPT. Such a system should allow flexibility according to the

most appropriate combination of push-and-pull plants given variables such as rainfall pattern, *Striga* pressure, FAW and stemborer pressure, nutritional needs, and cultural and food preferences of the farmers. Both the *milpa* and PPT show a high capacity to be adapted to cope with different challenges including varying climatic regimes (Murage et al. 2015; Midega et al. 2015, 2018). The same properties of flexibility and adaptability are likely to be transferred to their combination.

A basic *milpa* push-pull system could use all plant combinations traditionally practiced in *milpa* systems, including the addition of potato, faba bean, amaranth, peas, tomato, pepper, and other green vegetables (Lopez-Ridaura et al. 2021). Such a system would largely benefit from the knowledge generated recently on push-pull intensification with vegetables, including cabbages, kales, cowpeas, African nightshade, tomatoes, and onions (Chidawanyika et al. 2023).

Drought-resistant intercrop species such as *Desmodium incanum* may be selected preferentially in areas with long droughts (Midega et al. 2017). In areas with low or no incidence of striga weeds and low to moderate FAW occurrence, or where farmers practice crop rotation between legumes and cereals, *Desmodium* spp. may be optionally substituted with other repellent intercrops, particularly species of high value as food (Table 1). In the presence of annual legumes (e.g., beans) in the system, non-legume-repellent intercrops could also be considered as candidates without compromising nitrogen fixation and associated high soil fertility (Guera et al. 2020, 2021).

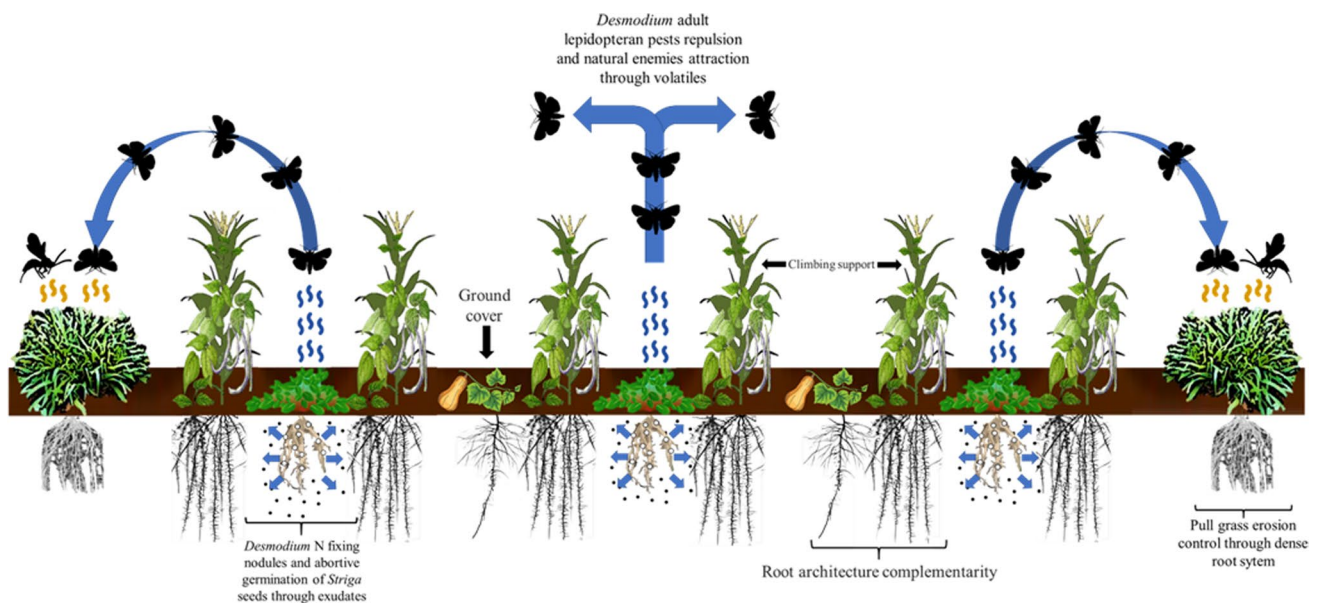


Fig. 3 *Milpa* push-pull showing a possible arrangement of the merged system, especially for regions affected by striga, including intercropped maize, beans climbing the maize stalks, squash, *Desmodium*, and a trap plant surrounding the plot. In this system, the combination of maize, *Desmodium*, and the trap plant originates from the

push-pull cropping system (Fig. 2), whereas the maize, beans, and squash mixture is the basic foundation of the Latin American *milpa* (Fig. 1). Maize, beans and squash roots modified from Postma and Lynch (2012), *Desmodium* roots modified from Hooper et al. (2015) and *Brachiaria* roots modified from Galdos et al. (2020).

Table 1 General properties of candidate plant species for *milpa push-pull*. Identified or potential “push” and “pull” properties refer to plants’ action on lepidopteran pests, with “push” indicating a repellent and “pull” an attractive effect on pests, respectively. These traits are described in more detail in Table 2. Some plants found to have both “push” and “pull” activity are listed in both categories. Question marks indicate knowledge gaps

Plant	Common name	Family	Origin	Food	Fodder	Lifespan	Drought resistant	Comments	References
Plants with identified or potential “push” properties for lepidopteran pests									
<i>Dysphania ambrosioides</i>	Mexican-tea, paico, epazote	Amaranthaceae	Latin America	Yes	No	Annual or short-lived perennial	Yes	-	(Guera et al. 2020, 2021)
<i>Tagetes erecta</i>	Marigold	Asteraceae	Mexico	Yes	Yes	Annual	No	-	(Njunie et al. 2022)
<i>Clitoria ternatea</i>	Butterfly pea, blue pea	Fabaceae	Asia	No	Yes	Perennial	Yes	-	(Polhill 1968; Uiso and Johns 1996)
<i>Crotalaria brevidens</i>	Mitoo, Marejea, Alaju	Fabaceae	Africa	Yes	Yes	Annual or short-lived perennial	No	More drought tolerant than <i>C. ochroleuca</i>	(Tripathi et al. 2013; Guera et al. 2020, 2021)
<i>Crotalaria juncea</i>	Sunn hemp	Fabaceae	India	No	Yes	Annual	Yes	-	(Morton 1994)
<i>Crotalaria longirostrata</i>	Chipilín	Fabaceae	Mesoamerica	Yes	Yes	Annual or short-lived perennial	?	-	(Polhill 1968; Sikuku et al. 2013)
<i>Crotalaria ochroleuca</i>	Mitoo, Marejea, Alaju	Fabaceae	Africa	Yes	Yes	Annual or short-lived perennial	No	-	(Manzanero-Medina et al. 2020)
<i>Crotalaria pumila</i>	Low Rattlebox	Fabaceae	Mexico and southern USA	Yes	?	Annual or short-lived perennial	Yes	-	(Crosa et al. 1999; Vanni 2001; Ma et al. 2011; Midega et al. 2017)
<i>Desmodium incanum</i>	Greenleaf Desmodium	Fabaceae	Latin America	No	Yes	Perennial	Yes	More drought resistant than <i>D. intortum</i> .	
<i>Desmodium intortum</i>	Greenleaf Desmodium	Fabaceae	Latin America	No	Yes	Perennial	Yes	-	
<i>Desmodium uncinatum</i>	Silverleaf Desmodium	Fabaceae	Latin America	No	Yes	Perennial	No	-	
<i>Brachiaria brizantha</i> cv. ‘Mulato II’	Brachiaria	Poaceae	Africa	No	Yes	Perennial	Yes	Repellent of FAW adults	(Sobhy et al. 2022)
<i>Melinis minutiflora</i>	Molasses grass	Poaceae	Africa	No	Yes	Perennial	Yes	-	(Cheruyot et al. 2021b, a; Erdei et al. 2022)
Plants with identified or potential “pull” properties for lepidopteran pests									
<i>Desmodium intortum</i>	Greenleaf Desmodium	Fabaceae	Latin America	No	Yes	Perennial	Yes	-	(Erdei et al. 2022)
<i>Desmodium uncinatum</i>	Silverleaf Desmodium	Fabaceae	Latin America	No	Yes	Perennial	No	-	

Table 1 (continued)

Plant	Common name	Family	Origin	Food	Fodder	Lifespan	Drought resistant	Comments	References
<i>Brachiaria brizantha</i> cv. 'Mulato II'	Brachiaria	Poaceae	Africa	No	Yes	Perennial	Yes	-	(van den Berg 2006b; Truong et al. 2008; Guera et al. 2020, 2021; Shamim et al. 2021; Cheruiyot et al. 2021a, b)
<i>Brachiaria brizantha</i> cv. 'Xaraes'	Brachiaria	Poaceae	Africa	No	Yes	Perennial	Yes	-	
<i>Melinis minutiflora</i>	Molasses grass	Poaceae	Africa	No	Yes	Perennial	Yes	-	
<i>Panicum maximum</i> cv. Mombasa	Guinea grass	Poaceae	Africa	No	Yes	Perennial	Yes	-	
<i>Paspalum notatum</i>	Bahia grass	Poaceae	Latin America	No	Yes	Perennial	Yes	-	
<i>Pennisetum purpureum</i> cv. Ouma II	Napier grass, Elephant grass	Poaceae	Africa	No	Yes	Perennial	No	-	
<i>Pennisetum purpureum</i> cv. South Africa	Napier grass, Elephant grass	Poaceae	Africa	No	Yes	Perennial	No	-	
<i>Vetiveria zizanioides</i>	Vetiver	Poaceae	India	No	Yes	Perennial	Yes	-	
High food value plants commonly intercropped with cereals									
<i>Amaranthus</i> spp.	Amaranth	Amaranthaceae	Worldwide	Yes	Yes	Annual	Yes	Seeds and leaves are edible	(Fomsgaard et al. 2011; Alemayehu et al. 2015)
<i>Cleome gynandra</i>	Spider plant	Cleomaceae	Africa	Yes	Yes	Annual	Yes	Contains high levels of proteins	(Nyalala and Grout 2007)
<i>Cucurbita</i> spp.	Squash/Pumpkin	Cucurbitaceae	Mesoamerica	Yes	No	Annual	No	Source of vitamin A. Flowers and fruits are edible	(Novotny et al. 2021; Lopez-Ridaura et al. 2021)
<i>Arachis hypogaea</i>	Groundnut	Fabaceae	South America	Yes	Yes	Annual	Yes	-	(Mucheru-Muna et al. 2010; Villordo-Pineda et al. 2015; Iqbal et al. 2018; Muoni et al. 2019; Manzanero-Medina et al. 2020; Drinkwater et al. 2021)
<i>Cajanus cajan</i>	Pigeon pea	Fabaceae	India	Yes	Yes	Short-lived perennial	Yes	Very drought resistant	
<i>Crotalaria longirostrata</i>	Chipilín	Fabaceae	Mesoamerica	Yes	Yes	Annual or short-lived perennial	?	-	
<i>Crotalaria pumila</i>	Low Rattlebox	Fabaceae	Mexico and southern USA	Yes	?	Annual or short-lived perennial	Yes	-	
<i>Glycine max</i>	Soybean	Fabaceae	East Asia	Yes	Yes	Annual	No	-	
<i>Phaseolus</i> spp.	Bean	Fabaceae	Mesoamerica	Yes	Yes	Annual	No	-	
<i>Vicia faba</i>	Broad bean, faba bean	Fabaceae	West Asia	Yes	Yes	Annual	No	-	
<i>Vigna radiata</i>	Green gram	Fabaceae	India	Yes	Yes	Annual	Yes	-	
<i>Vigna subterranea</i>	Bambara nut	Fabaceae	West Africa	Yes	Yes	Annual	Yes	-	
<i>Vigna unguiculata</i>	Cowpea	Fabaceae	West Africa	Yes	Yes	Annual	Yes	Very drought resistant	

4.6 Other potential plant candidates and combinations for effective *milpa push-pull*

Many *Desmodium* spp. are edible and used for human consumption, among various uses, in some parts of the world (Ma et al. 2011), but this is neither common in America nor Africa. In Latin America, since striga weed is not yet present (Mohamed et al. 2006), other edible legumes with pest-repellent properties may represent better options as “push” components in an adapted *milpa push-pull*. For instance, recently, a maize push-pull system, inspired by the African experience, has been adapted in Mexico (Guera et al. 2021). Instead of *Desmodium* spp., these researchers used two native plants (*Tagetes erecta* and *Dysphania ambrosioides*) and the introduced legume (*Crotalaria juncea*) as repellent intercrops. They found that the system successfully reduced the incidence and severity of FAW up to 70% and 60% compared to a monocrop, respectively. Additionally, the system retained soil moisture and more than doubled maize yields (Guera et al. 2021). Interestingly, all repellent plants used in Guera et al. (2021) are edible (mostly used as condiments) and have multiple other purposes. *Tagetes erecta* for example, is cultivated to be used as feed, food pigment, ornament (including the famous Mexican Day of the Dead), and a medicinal plant (Hadden et al. 1999; Shetty et al. 2015). Furthermore, its roots produce secretions that have insecticidal and nematocidal effects that were found to suppress nematode pests when intercropped with cowpea (Olabiyi and Oyedunmade 2007). *Dysphania ambrosioides* is also frequent in the Mexican markets for its popularity as a condiment in a wide variety of regional foods although it is also consumed raw (Manzanero-Medina et al. 2020). *Crotalaria*, notably, is a drought-resistant genus of leguminous plants with hundreds of species, most of them native to East Africa, India, and America (le Roux et al. 2013). In addition to fixing nitrogen and repelling FAW, *C. juncea* attracts beneficial insects like parasitoids and pollinators, retains soil moisture, and prevents the development of noxious weeds (Guera et al. 2021; Bundit et al. 2021).

Specifically, *Crotalaria juncea* has been shown to attract predatory wasps (Vespidae) from the genera *Polistes*, *Brachygastra*, and *Protonectarina*, increasing the predation rates of the coffee-leaf-miner (*Leucoptera coffeella*), an important lepidopteran pest in coffee (Rosado et al. 2021). Given that the genera *Polistes* and *Polybia* have been found to attack both FAW and coffee leaf miner (Carvalho et al. 2005; Pereira et al. 2007; Held et al. 2008; Saraiva et al. 2017; Southon et al. 2019; Rosado et al. 2021), *Crotalaria juncea* may thus also increase predation rates of FAW in maize in addition to its pest repellent effects. Similar synergistic effects between coffee and maize regarding biological pest control could be mediated by the presence of Chrysopidae, such as *Chrysoperla externa*, the larvae of which are known

to prey on both *L. coffeella* and FAW (Tavares et al. 2012; Silva et al. 2022). Coffee volatiles can also attract predatory wasps and other FAW predators, producing synergistic effects between coffee and maize intercropped with *C. juncea* in terms of predator presence and predation rates, as these are commonly planted in close vicinity in many tropical regions (Fernandes et al. 2010). Other potential *milpa push-pull* intercrops may also have attractive effects on natural enemies, notably squash (García González et al. 2013), but they remain largely to be investigated (Table 2). Additionally, *milpa push-pull* and versions thereof are likely to also be a valuable resource for pollinators and for biodiversity in general given the variety of flowers, pollen, and other resources it can shelter (Nicholls and Altieri 2013), as known in similar mixed cropping systems. However, the value of these multicropping cereal-based systems for wild and managed bees has only recently started to be studied (Hüber et al. 2022; Kirsch et al. 2023). Some *Crotalaria* species (e.g., *C. ochroleuca*, *C. arenaria*, *C. juncea*) also provide nematocidal effects against certain pathogenic nematodes (Kushida et al. 2003; Germani and Plenchette 2005; Wang et al. 2002), including the root-knot nematodes (Do Nascimento et al. 2020). However, *Crotalaria juncea*, is also reported to be a host to *Microtechnites bractatus* (Hemiptera: Miridae) (Ribeiro et al. 2020) and *Dalbulus maidis* (Hemiptera: Cicadellidae) (Tavares et al. 2011; de Lange et al. 2014) that are also known maize pests. Nonetheless, intercropping *C. juncea* at adequate planting timings and densities does not affect maize yields and is superior to other legume cover crops in terms of biomass productivity (Dzvene et al. 2022). Hence, it is essential to be selective and ensure proper planting and management routines that avoid unintended negative effects when choosing *Crotalaria* species. *Crotalaria* spp., such as *C. longirostrata* (locally known as “chipilin”) and *C. pumila*, are already a frequent part of *milpa* systems in America, where they are planted mainly for human consumption (Morton 1994; Le Garff 2017; Manzanero-Medina et al. 2020). Furthermore, the leaves of *C. brevidens* and *C. ochroleuca* (commonly known as “Marejea” or “Mitoo” in Tanzania and Kenya and “Alaju” in Uganda) are also consumed as leafy vegetables and condiments in some African countries (Maundu et al. 1999; Oluoch et al. 2009; Mwakha et al. 2020; Muli et al. 2020). In fact, the market value of indigenous African leafy vegetables (including *C. brevidens* and *C. ochroleuca*) is calculated to be worth billions of US dollars (Weinberger and Pichop 2009) and is especially important in East Africa (Imathiu 2021). It should be tested whether the repellent effects of *C. juncea* against FAW (Guera et al. 2021) are exhibited by other *Crotalaria* spp., as has been found for some *Desmodium* spp. (Cheruiyot et al. 2021a), and particularly edible *Crotalaria* species. If edible *Crotalaria* species

Table 2 Pest control related properties of candidate plant species for *milpa push-pull*. Identified or potential “push” and “pull” properties refer to plants’ action on lepidopteran pests, with “push” indicating a repellent and “pull” an attractive effect on pests, respectively. Some plants found to have both “push” and “pull” activity are listed in both categories. Question marks indicate knowledge gaps

Plant	Repels FAW adults	Repels stemborer adults	Dead-end trap for FAW larvae	Dead-end trap for stemborer larvae	Attractive to parasitic wasps	Attractive to other natural enemies	Nematicidal effect	Comments	References
Plants with identified or potential “push” properties for lepidopteran pests									
<i>Dysphania ambrosioides</i>	Yes	?	No	?	?	Yes	No	-	(Olabiya and Oyedunmade 2007; Guera et al. 2020, 2021)
<i>Tagetes erecta</i>	Yes	?	No	?	Yes	Yes	Yes	-	(Njunie et al. 2022)
<i>Clitoria ternatea</i>	Yes	Yes	?	?	?	?	No	-	(Wang et al. 2002; Kushida et al. 2003; Germani and Plenchette 2005; Do Nascimento et al. 2020; Guera et al. 2020, 2021)
<i>Crotalaria brevidens</i>	?	?	?	?	?	?	?	-	(Midega et al. 2017; Cheruiyot et al. 2021a; Sobhy et al. 2022; Erdei et al. 2022)
<i>Crotalaria juncea</i>	Yes	?	?	?	Yes	Yes	Yes	-	(Sobhy et al. 2022; Erdei et al. 2022)
<i>Crotalaria longirostrata</i>	?	?	?	?	?	?	?	-	(Sobhy et al. 2022)
<i>Crotalaria ochroleuca</i>	?	?	?	?	?	?	Yes	-	(Sobhy et al. 2022)
<i>Crotalaria pumila</i>	?	?	?	?	?	?	?	-	(Sobhy et al. 2022)
<i>Desmodium incanum</i>	Yes [§]	Yes [§]	?	?	?	?	No	§ See recent debate related to control mechanisms (Sobhy et al. 2022; Erdei et al. 2022)	(Midega et al. 2017; Cheruiyot et al. 2021a; Sobhy et al. 2022; Erdei et al. 2022)
<i>Desmodium intortum</i>	Yes [§]	Yes [§]	Yes	?	Yes	Yes	No	-	(Sobhy et al. 2022)
<i>Desmodium uncinatum</i>	Yes [§]	Yes [§]	Yes	?	Yes	Yes	No	-	(Sobhy et al. 2022)
<i>Bracharia brizantha</i> cv. ‘Mulato II’	Yes	No	Yes	Yes	Yes	Yes	No	Susceptible to spider mites (<i>Tetranychus</i> spp.)	(Scheidtger et al. 2021; Sobhy et al. 2022)
<i>Melinis minutiflora</i>	Yes	Yes	?	?	Yes	?	No	-	(Tolosa et al. 2019; Cheruiyot et al. 2021b, a; Erdei et al. 2022)
Plants with identified or potential “pull” properties for lepidopteran pests									
<i>Desmodium intortum</i>	Yes [§]	Yes [§]	Yes	?	Yes	Yes	No	§ See recent debate related to control mechanisms (Sobhy et al. 2022; Erdei et al. 2022)	(Erdei et al. 2022)
<i>Desmodium uncinatum</i>	Yes [§]	Yes [§]	Yes	?	Yes	Yes	No	-	(Sobhy et al. 2022; Erdei et al. 2022)

Table 2 (continued)

Plant	Repels FAW adults	Repels stemborer adults	Dead-end trap for FAW larvae	Dead-end trap for stemborer larvae	Attractive to parasitic wasps	Attractive to other natural enemies	Nematicidal effect	Comments	References
<i>Brachiaria brizantha</i> cv. 'Mulato II'	Yes	No	Yes*	Yes	Yes	Yes	No	Susceptible to spider mites (<i>Tetranychus</i> spp.). *Does not retain FAW larvae.	(Ofomata et al. 2000; Khan et al. 2006, 2007; Van den Berg 2006a; Van den Berg 2006b; Van den Berg et al. 2006; van den Berg 2006b; Koji et al. 2007; Hassanali et al. 2008; Bruce et al. 2010; Brauman et al. 2014; Midega et al. 2015; Cheruiyot et al. 2018, 2021b, a; LU et al. 2019; Guera et al. 2020, 2021; Scheidegger et al. 2021; Flausino et al. 2022; Sobhy et al. 2022; Erdei et al. 2022)
<i>Brachiaria brizantha</i> cv. 'Xaraes'	?	No	Yes*	Yes	Yes	Yes	No	Resistant to spider mites (<i>Tetranychus</i> spp.). *Does not retain FAW larvae.	
<i>Melinis minutiflora</i>	Yes	Yes	?	?	Yes	?	No	Low food assimilation by FAW larvae. Survival not tested	
<i>Panicum maximum</i> cv. Mombasa	No	No	No	Yes	?	Yes	No	15% survival rate of FAW	
<i>Paspalum notatum</i>	No	?	No	?	?	?	No	10-15% survival rate of FAW	
<i>Pennisetum purpureum</i> cv. Ouma II	No	No	Yes*	No ⁺	No	Yes	No	*Does not retain FAW larvae. ⁺ Very low survival rate of stemborers	
<i>Pennisetum purpureum</i> cv. South Africa	No	No	Yes*	No ⁺	No	Yes	No	*Does not retain FAW larvae. ⁺ Very low survival rate of stemborers	
<i>Yvetiveria zizanioides</i>	No	No	?	Yes*	Yes	?	No	*Dead-end for <i>Chilo partellus</i> and <i>C. suppressalis</i> but not <i>Busseola fusca</i>	
High food value plants commonly intercropped with cereals									
<i>Amaranthus</i> spp.	No	No	No	No	?	Yes	No	-	(Reddy 2017)
<i>Cleome gynandra</i>	No	No	No	No	?	?	No	Repellent to spider mites (<i>Tetranychus</i> spp.)	

Table 2 (continued)

Plant	Repels FAW adults	Repels stemborer adults	Dead-end trap for FAW larvae	Dead-end trap for stemborer larvae	Attractive to parasitic wasps	Attractive to other natural enemies	Nematicidal effect	Comments	References
<i>Cucurbita</i> spp.	No	No	No	No	Yes	Yes	No	-	(García González et al. 2010, 2013, 2022; Baudron et al. 2019)
<i>Arachis hypogaea</i>	No	No	No	No	Yes	Yes	No	-	(Reddy 2017; Mon-tezano et al. 2018; Hailu et al. 2018; Scheidegger et al. 2021; Udayakumar et al. 2021)
<i>Cajanus cajan</i>	No	No	No	No	?	?	No	-	
<i>Crotalaria longirostrata</i>	?	?	?	?	?	?	?	-	
<i>Crotalaria pumila</i>	?	?	?	?	?	?	?	-	
<i>Glycine max</i>	No	No	No	No	?	Yes	No	Inferior to other studied legumes in controlling stemborers and FAW	
<i>Phaseolus</i> spp.	No	No	Yes	No	Yes	Yes	No	-	
<i>Vicia faba</i>	No	No	No	No	?	Yes	No	-	
<i>Vigna radiata</i>	No	No	No	No	?	?	No	-	
<i>Vigna subterranea</i>	No	No	No	No	?	?	No	-	
<i>Vigna unguiculata</i>	No	No	No	No	?	?	No	-	

show repellency against FAW, they could be considered candidates in addition to *Desmodium* spp. in *milpa push-pull* systems in Africa and America. Other *Crotalaria* spp. such as *C. grahamiana* have already been studied because of their potential usefulness e.g., in reducing Striga weed (Gacheru and Rao 2005). But to our knowledge, no study other than Guera et al. (2021) has focused on *Crotalaria* spp. repellency as intercrops toward lepidopteran pests of cereals so far. Similarly to *Desmodium* spp. in America, the potential of *Crotalaria* spp. as lepidopteran repellents in push-pull systems has to date been largely ignored in Africa, even though its potential to control striga weed has been previously studied (Khan et al. 2007).

Another prime candidate companion crop for the *milpa push-pull* system is pigeon pea (*Cajanus cajan*, Fabaceae). It is an important tropical grain legume traditionally cultivated in many parts of Africa, Asia, and the Americas (Saxena 2008). Pigeon pea is known for multiple benefits, and its compatibility with cereal crops in intercropping, perennial and rotational cropping, or improved fallow practices are also well documented (Abunyewa and Karbo 2005; Mwila et al. 2021). Intercropping maize with pigeon pea increases crop productivity (Myaka et al. 2006; Ngwira et al. 2012; Mwila et al. 2021), resulting in a land equivalent ratio of up to 1.77 (Asiwe and Madimabe 2020). It is a highly edible crop to humans and livestock, rich in protein and other essential nutrients, which can provide nutritional and economic benefits to farmers (Odeny 2007). Moreover, many cultivars of pigeon pea have drought-resistant and nitrogen-fixing qualities (Njira et al. 2017). As a hardy plant, some cultivars possess traits to thrive in drought and low fertility conditions, making the crop an ideal “climate-proof” crop for farmers in drought-prone regions (Valenzuela and Smith 2002; Renwick et al. 2020). Pigeon pea has proven to be a reliable source of grain yield, even during prolonged dry spells when other field legumes may have withered (Odeny 2007). With nitrogen fixation by pigeon pea intercrop, farmers can improve soil fertility and reduce the need for synthetic fertilizers, which can be expensive and also harmful to the environment.

Studies have tested the potential of pigeon pea as a trap companion crop for reducing crop damage by polyphagous lepidopterans such as *Helicoverpa (Heliothis)* spp. (Tann 2011; Ratnadass et al. 2014), which are serious pests of many field crops including pulses, vegetables (e.g., tomato and okra), cotton, some cereals, and oilseeds (Ali et al. 2006; Bentivenha et al. 2016). A push-pull strategy was reported for controlling *Heliocoverpa (Heliothis)* pests in cotton fields, which involved the use of a repellent (neem extract) to “push” the moths away from the cotton plants and “pull” them towards the trap crop (pigeon pea) (Pyke et al. 1987). Moreover, cereal-pigeon pea intercropping has potential to reduce Striga weed infestations (Oswald and Ransom

2001; Odeny 2007), although it is inferior to *Desmodium distortum*, *Sesbania sesban*, *S. cinerascens*, *Crotalaria grahamiana*, and *Tephrosia vogelii* to reduce Striga attack and increase maize yields (Gacheru and Rao 2005).

While the aforementioned points provide support for integration of pigeon pea into *milpa push-pull* systems, it is important to note that selecting the appropriate pigeon pea varieties is crucial, as certain short-duration varieties may be susceptible to insect pest attack (Jones et al. 2002; Kaoneka et al. 2016). Shading and light competition effects of some perennial cultivars on other crops may also raise concerns, but implementing timely ratooning could make an effective management strategy (Rusinamhodzi et al. 2017). Nonetheless, realizing the full benefits of pigeon pea in *milpa push-pull* systems calls for further research and development.

Four other plants have high potential for *milpa push-pull*, namely molasses grass (*Melinis minutiflora*), Vetiver grass (*Vetiveria zizanioides*), Amaranth (*Amaranthus* spp.), spider plant (*Cleome gynandra* Synonym: *Gynandropsis gynandra*). In the absence of striga weed, molasses grass has been recommended as an alternative repellent (i.e., push) plant in Africa to fight stemborers (Storkey et al. 2019) and FAW (Cheruiyot et al. 2021b), despite its lack of the nitrogen-fixing benefits of legumes. The potential of *M. minutiflora* intercrop as a “push” plant in PPT has been previously investigated (Khan et al. 1997). *M. minutiflora* integration as a one-to-one intercrop without changing the row spacing of maize crop reduced stemborer damage from 39.2 to 4.6% (Khan et al. 1997). *M. minutiflora* intercrop:crop ratio can even be reduced to a ratio of 1:10 and still produce significant stemborer reduction (Khan et al. 2000). As Tolosa et al. (2019) noted, intact *M. minutiflora* neighbouring maize field releases volatile organic compounds (VOCs) that repel stemborers from maize and enhance parasitism by *Cotesia sesamiae* (Cameron). Erdei et al. 2022 also reported that *M. minutiflora* constitutively releases a variety of terpenes with the ability to deter common maize pests, and this further reinforces its potential as a viable alternative to *Desmodium* intercrop where Striga weed is less prevalent. *M. minutiflora* has also been successfully used as “push” intercrop to the sugarcane stemborer (*Eldana saccharina*) and attractant of one of its parasitoid natural enemies (*Xanthopimpla stemmator* Thunberg (Hymenoptera: Ichneumonidae) (Cockburn et al. 2014). Outside of its native range, the use of *M. minutiflora* should be discouraged due to its high invasive potential (Hoffmann et al. 2004; Hoffmann and Haridasan 2008).

Vetiver grass has been found to be a good trap plant for *Chilo partellus* in Africa (van den Berg 2006b), it is also important in preventing soil erosion and has value as animal feed (Truong et al. 2008). Additionally, Vetiver grass attracts several parasitic wasps such as *Telenomus* spp. and *Trichogramma* spp. (Lu et al. 2019). In terms of food diversity, Amaranth (*Amaranthus* spp.) adapts well to multicropping

systems such as the *milpa* and is highly appreciated and used in Africa and America for its nutritional value (Fomsgaard et al. 2011; Alemayehu et al. 2015). Nonetheless, caution should be given to the fact that *Amaranthus* spp. are a host of African *Spodoptera* spp. such as *S. littoralis* and *S. exigua* (Fiaboe et al. 2017). *Cleome gynandra* is another nutritious and popular plant that could be incorporated into *milpa push-pull* systems in Africa, especially as a source of protein and vitamin A in regions where cucurbits are not preferred (Mishra et al. 2011). *Cleome gynandra* is a fast-growing leafy vegetable that is widespread in West and Eastern Africa and is increasingly valued as a commercial crop (Achigan-Dako et al. 2021). *Cleome gynandra* is also effective as a repellent plant for spider mites (*Tetranychus* spp.), which represents a serious problem for the trap plant *Bra-chiaria brizantha* cv Mulato II (Nyalala and Grout 2007). However, *C. gynandra* has also been found to be an alternate host of *Eurystylus oldi* (Hemiptera, Miridae), a pest of sorghum (Ratnadass et al. 2012).

5 Remaining questions

There are several knowledge gaps that require further research in order to fully leverage the potential and adaptability of mixed push-pull and *milpa* systems for sustainably intensified smallholder cereal farming. In Tables 1, 2, and 3, we review and summarize the diversity of plants with a documented potential to play effective roles in intensified mixed cereal systems according to socio-cultural needs and local environmental pressures and conditions. As outlined above, some of these species have been tested for effectiveness under selected conditions, while others remain to be investigated. However, only a fraction of potentially promising interacting species is currently used in the context of traditional *milpa* and push-pull systems.

Through a qualitative literature review, we identified 30 plants that are either already classically employed in smallholder cereal mixed cropping systems in America and Africa, or have been referenced and/or tested for their potential to play an active role in these systems (Table 1). Among these, species combinations with high potential effectiveness for various agroecologies remain to be trialed (Tables 2 and 3). For example, possible repellent effects of *Crotalaria* spp. apart from *C. juncea* on FAW are not yet known, especially *C. longirostrata* and *C. pumila* in Latin America and *C. brevidens* and *C. ochroleuca* in Africa. With ongoing climate change, FAW invasion may reach other regions of the world such as Europe and Canada that were previously too cold for its survival. Striga is also forecast to attack the south of Europe (Mohamed et al. 2006). Therefore, research on European maize and other

cereal production, such as wheat (Vasey et al. 2005), could focus on agricultural strategies to prevent the likelihood of crop damage due to these threats in the near future. *Spodoptera* spp., *Helicoverpa* spp., and *Agrotis ipsilon* are cereal crop pests in both America and Africa which opens opportunities for further cooperation and research on best practices for biological pest control enhancement (Tay et al. 2013; Jones et al. 2019; Hruska 2019; Rodingpuia and Lalthanzara 2021).

Molasses grass is known to repel adult stemborer and FAW moths, limiting oviposition in their main host maize (Storkey et al. 2019; Cheruiyot et al. 2021b). Moreover, similarly to what Erdei et al. (2022) observed with *Desmodium* spp., Cheruiyot et al. (2021b) have recently demonstrated that *M. minutiflora* is the only plant preferred by FAW larvae over maize among the six potential pull grasses tested, although it is not suitable for larval development. Considering that after hatching FAW larvae can move to alternative hosts (Rojas et al. 2018), Cheruiyot et al. 2021b propose a novel intercropping design based on FAW larval behavior and preferences that remains to be tested.

The poor performance of the trap plants tested so far for FAW, which fail to preferentially attract adult FAW moths over maize and/or to retain and kill FAW larvae (Guera et al. 2020; Cheruiyot et al. 2021b), highlights the necessity to test other species for this purpose. This could be an opportunity to experiment with plants that, beyond the function of trap plants for FAW, may also have value as a food source. In particular, millets from the genera *Panicum*, *Pennisetum*, and *Paspalum* may be explored, as species within these groups are recognized for their nutritional value and broadly planted in various regions of the world (e.g., Proso millet *Panicum miliaceum*, little millet *Panicum sumatrense*, Sonoran panicgrass *Panicum sonorum*, pearl millet *Pennisetum glaucum* and Kodo millet *Paspalum scrobiculatum*). Some species in these genera are known to control FAW to some degree, including *Panicum maximum*, *Pennisetum purpureum*, *Paspalum ionanthum*, and *Paspalum notatum* (Tables 1, 2, and 3) (Braman et al. 2014; Guera et al. 2020; Cheruiyot et al. 2021b).

An important open question also remains about the effects of different densities of push plants on maize pest infestation, particularly *Desmodium* spp. and the FAW attack but also *Crotalaria* spp. (Dzvene et al. 2022). If a lower density of *Desmodium* is sufficient to repel FAW, higher flexibility may be offered for the integration of other food plants with the *Desmodium* intercrop. However, no studies are currently available testing the impact of varying *Desmodium* planting ratios on pest repellence. Although the optimum plant densities for maize-beans, maize-squash, and maize-beans-squash are well understood (Altieri 1999; Silwana and Lucas 2002), further research is needed in order

Table 3 Weed control and soil properties of candidate plant species for *milpa push-pull*. Identified or potential “push” and “pull” properties refer to plants’ action on lepidopteran pests, with “push” indicating a repellent and “pull” an attractive effect on pests, respectively.

These traits are described in more detail in Table 2. Some plants found to have both “push” and “pull” activity are listed in both categories. Question marks indicate knowledge gaps

Plant	Provokes Striga germination	Prevents Striga radicle development	Other weed prevention	N-fixation	Erosion control	Comments	References
Plants with identified or potential “push” properties for lepidopteran pests							
<i>Dysphania ambrosioides</i>	No	No	No	No	No	-	(Guera et al. 2020, 2021)
<i>Tagetes erecta</i>	No	No	No	No	No	-	
<i>Clitoria ternatea</i>	Yes	?	?	Yes	No	-	(Njunie et al. 2022)
<i>Crotalaria brevidens</i>	Yes	Yes	Yes	Yes	Yes	-	(Mwaka et al. 2020)
<i>Crotalaria juncea</i>	Yes	Yes	Yes	Yes	Yes	Very effective at competitively displacing weeds	(Fischer et al. 2020; Guera et al. 2020, 2021; Bundit et al. 2021)
<i>Crotalaria longirostrata</i>	Yes	?	?	Yes	?	-	(Morton 1994)
<i>Crotalaria ochroleuca</i>	Yes	Yes	Yes	Yes	Yes	-	(Mwaka et al. 2020)
<i>Crotalaria pumila</i>	Yes	?	?	Yes	?	-	(Manzanero-Medina et al. 2020)
<i>Desmodium incanum</i>	Yes	Yes	Yes	Yes	Yes	-	(Khan et al. 2014; Midega et al. 2017; Cheruiyot et al. 2021a)
<i>Desmodium intortum</i>	Yes	Yes	Yes	Yes	Yes	-	
<i>Desmodium uncinatum</i>	Yes	Yes	Yes	Yes	Yes	-	
<i>Brachiaria brizantha</i> cv. ‘Mulato II’	No	No	No	No	Yes	-	(Cheruiyot et al. 2021b)
<i>Melinis minutiflora</i>	No	No	No	No	Yes	-	(Cheruiyot et al. 2021b, a; Erdei et al. 2022)
Plants with identified or potential “pull” properties for lepidopteran pests							
<i>Desmodium intortum</i>	Yes	Yes	Yes	Yes	Yes	-	(Khan et al. 2014; Midega et al. 2017)
<i>Desmodium uncinatum</i>	Yes	Yes	Yes	Yes	Yes	-	
<i>Brachiaria brizantha</i> cv. ‘Mulato II’	No	No	No	No	Yes	-	(Truong et al. 2008; Tolosa et al. 2019; Guera et al. 2020; Cheruiyot et al. 2021b, a)
<i>Brachiaria brizantha</i> cv. ‘Xaraes’	No	No	No	No	Yes	-	
<i>Melinis minutiflora</i>	No	No	No	No	Yes	-	
<i>Panicum maximum</i> cv. Mombasa	No	No	No	No	Yes	-	
<i>Paspalum notatum</i>	No	No	No	No	Yes	-	
<i>Pennisetum purpureum</i> cv. Ouma II	No	No	No	No	Yes	-	
<i>Pennisetum purpureum</i> cv. South Africa	No	No	No	No	Yes	-	
<i>Vetiveria zizanioides</i>	No	No	No	No	Yes	-	
High food value plants commonly intercropped with cereals							
<i>Amaranthus</i> spp.	No	No	No	No	No	-	(Alemayehu et al. 2015; Reddy 2017)
<i>Cleome gynandra</i>	No	No	?	No	No	-	(Reddy 2017)
<i>Cucurbita</i> spp.	No	No	Yes	No	Yes	-	(Novotny et al. 2021; Lopez-Ridaura et al. 2021)

Table 3 (continued)

Plant	Provokes Striga germination	Prevents Striga radicle development	Other weed prevention	N-fixation	Erosion control	Comments	References
<i>Arachis hypogaea</i>	Yes	No	No	Yes	No	-	(Khan et al. 2007; Ndayisaba et al. 2020)
<i>Cajanus cajan</i>	Yes	No	No	Yes	No	-	
<i>Crotalaria longirostrata</i>	Yes	No	No	Yes	?	-	
<i>Crotalaria pumila</i>	Yes	No	No	Yes	?	-	
<i>Glycine max</i>	Yes	No	No	Yes	No	-	
<i>Phaseolus</i> spp.	Yes	No	No	Yes	No	-	
<i>Vicia faba</i>	Yes	No	No	Yes	No	-	
<i>Vigna radiata</i>	Yes	No	No	Yes	No	-	
<i>Vigna subterranea</i>	Yes	No	No	Yes	No	-	
<i>Vigna unguiculata</i>	Yes	No	No	Yes	No	-	

to integrate other plant combinations with optimal densities and configurations. Also, further research on adequate planting timings in intercrops is needed because this can have major impacts on yield and pest damage (Altieri 1980).

Finally, studies that exploit the apparent incongruence between larval and adult FAW host selection are needed to maximize the efficiency of integrated pest management strategies (Rojas et al. 2018; Sotelo-Cardona et al. 2021). Furthermore, context-dependent effects and non-trivial relationships among natural enemies must be further explored when selecting appropriate species for intercropping.

6 Conclusion

The Mesoamerican *milpa* and East African PPT systems have the potential to complement each other and promote sustainable food production, but there has been little to no cross-system learning to date. We reviewed extant literature on both systems and present the likely advantages of combining them in small-scale farming in the Americas and sub-Saharan Africa. Designing effective combinations of *milpa* with PPT has the potential to reduce poverty, address food security challenges and provide farmers with increased flexibility to adapt and rotate crops. This can be achieved by merging the respective benefits of different companion plants for crop protection against pests, increased food production, and diversified nutrition, along with improved soil moisture, fertility, and other benefits such as fodder production. The larger range of possibilities provided by the *milpa push-pull* system to adapt the composition and configuration of its components is likely to increase the resilience of smallholders to socio-environmental challenges. Based on existing knowledge of both cropping systems, we show that there is a

large potential for such configurations to be highly adaptive according to the key pressures influencing production in different regions. Through the selection of plant species and cultivars with specific traits, integrated *milpa push-pull* systems could be adapted to different gradients of altitude, rainfall, and soil nutrient levels. *Milpa push-pull* is likely to combine the benefits of the *milpa* and push-pull systems to robustly increase yields, yield stability, and soil fertility in the long term, even under predicted scenarios of climate change and increasing pest pressure. Co-development and testing of the *milpa push-pull* concept by farmers and scientists will bring further insight into its effectiveness and optimal design. We conclude that a fruitful exchange of knowledge on sustainable and traditional cropping systems practiced by smallholders in different parts of the world is an essential approach for key insights and inspiration toward further development of biodiversity-friendly farming practices with a high capacity for resilience and social-ecological adaptation.

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Data availability Data sharing is not applicable to this article as no datasets were generated or analyzed during the current study.

Code availability Not applicable.

Declarations

Conflict of interest The authors declare no competing interests.

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Consent for publication Not applicable.

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