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Review

Exploiting diversity to promote arbuscular mycorrhizal symbiosis and crop productivity in organic farming systems

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Abstract: Beneficial soil microbiota especially arbuscular mycorrhizal fungi (AMF) deliver essential agroecosystem services in organic farming systems, where the application externalities is often limited. Undoubtedly, organic farming provides optimal conditions for agroecological functioning due to minimal soil disturbance and limited use of agrochemicals. In this context, beneficial soil microbiota are expected to deliver optimal ecosystem services. Nevertheless, the composition, diversity and function of beneficial rhizospheric microorganisms including AMF communities vary upon agronomic practices and soil conditions. Moreover, it is well known that some modern crop cultivars are less responsive to AMF, since they are bred for high intensive agricultural systems where there is sufficient supply of nutrients especially P. Until now, the establishment and function of AMF in organic cropping systems is still poorly understood. Such information is a prerequisite for the implementation of efficient cropping systems that capitalize on biological processes, a key step towards agricultural sustainability. The overall aim of this review is to provide insights on increasing mycorrhizal symbiosis and crop productivity in organic agroecosystems through innovative, temporal and spatial manipulation of species and genetic diversity at the crop cultivar, AMF species and cover crop management levels. The bulk of this review underscores the importance of examing different levels of diversification in organic farming systems, considering functional identity (single species), composition (mixed species) and diversity (heterogeneity within species) and how such components contribute to delivery of multiple agroecosystem services.

Keywords: arbuscular mycorrhizal fungi; diversity; agroecosystem services; crop productivity; organic agriculture

1. Introduction

Agriculture today faces an exceptional challenge of producing adequate and healthy food for the burgeoning global human population, while seeking to optimize on the available natural resources. Coupled with emerging global challenges key among them, climate change, biodiversity loss and shrinking economies, the ability of contemporary agriculture to produce enough food for over nine billion people by year 2050 is unforeseen [1]. Although over the past decades, conventional agriculture is credited for improving global agricultural production [2], this, has been realized through intense economic and environmental pressure [3]. Key elements of high input agriculture include high fossil energy consumption, liberal use of agrochemicals (e.g., fertilizers and pesticides) and commercial varieties or hybrids that are by design bred to exploit such conditions. Conversely, there is growing global demand for healthier food, besides public concern about the negative ecological consequences of modern agriculture and soaring global prices of inorganic fertilizers. Therefore, to increase agricultural sustainability and conserve agroecosystems, there is growing interest in developing alternative agricultural systems that capitalize on biological processes such as organic agriculture.

Arbuscular mycorrhizal fungi (AMF) are members of a monophyletic phylum, the Glomeromycota [4] that form a mutualistic association with plant host roots. The fungal hyphae directly penetrates into the host’s cortical cells forming arbuscules where nutrition exchange takes place, with extraradical hyphae spreading from colonized roots to the surrounding soil. AMF probably form the most widespread terrestrial symbiosis with approximately 92% of plant families, which include about 80% of land plant species [5,6]. According to fossil records, AMF have been in existence for more than 400 million years morphologically unaltered [7,8], possibly qualifying as one of the most successful living fossils [9]. Often, mycorrhizal symbiosis is critical for survival, growth and development of both fungal and plant symbiont because plants depend on fungus for nutrition and protection while the fungus relies on plants for carbohydrates [10]. Moreover, AMF are crucial in ecological functioning, physiology and productivity of land plants [4]. Although AMF spores can germinate without host plants regulatory mechanisms, AMF are obligately symbiotic, and therefore, depend on photosynthates from the plant host to complete their life cycle.

2. Organic agriculture

Organic agriculture has dramatically dilated over the past two decades with 50.9 million hectares of agricultural land currently under organic management (including in-conversion areas) [11]. Presently, Australia, Argentina and the United States are among the leading countries in acreage under organic cultivation, although the largest increases of organic agricultural land are in Europe [12]. More increase is foreseen because of the tremendous rise of market opportunities and numerous government mandates and incentives [13]. This outstanding growth is principally driven by increasing domestic market, since organic foods are perceived to be healthier and financial backing for organic producers. Thus, the current organic production does not, nonetheless, meet the local and export demand requiring more rapid expansion and research.

Organic agriculture, also called ecological agriculture refers to a production system that sustains human and environmental health by capitalizing on ecological processes and biodiversity that are adapted to local agro-climatic conditions, rather than the use of external inputs (http://www.ifoam.org/en/organic-landmarks/definition-organic-agriculture, accessed on 14/03/2018).

Organic farming systems mimic natural ecosystems and rely on measures that stimulate resilience and sustainability of the agroecosystem, e.g., by enhancing crop and management diversification, incorporation of organic matter and beneficial microorganisms, to promote soil fertility, and by maximizing on nutrient cycles [14]. Crop pests and diseases are controlled through diverse rotations, while crop nutrition is maintained through the inclusion of legumes in the rotation and recycling of nutrients via crop residues and animal manures [15,16]. These tactics aim to improve sustainability of agricultural production by minimizing external inputs with adverse environmental effects while maintaining high crop yields and conserving biodiversity in agroecosystems [17,18].

Notwithstanding the tremendous rise, organic production is still limited by several agronomic and environmental factors such as varying soil fertility due to restricted application of mineral fertilizers, and lack of crop varieties adapted to organic systems. In addition, other emerging constraints to agriculture such as global climate change and resource pressure are likely to slow down the progress already made in organic farming. Therefore, novel approaches to foster local adaptation and effective exploitation of available bio-resources by organic crops are crucial. One such approach is functional agrobiodiversity recently hypothesized as potentially capable of improving crop yield and stability, produce quality, soil fertility and suppression of biotic and abiotic stresses [19].

On the other hand, conservation of sustainable soil fertility is particularly important in organic agriculture. Soil fertility and plant nutrition are enhanced through nitrogen (N) fixation by legumes and nutrient recycling of organic materials from animals and crops with limited application of external inputs [20]. The inclusion of cover crops used as green manure, living or dead mulch is important in enhancing biological processes and soil fertility, especially when farming system does not include animal husbandry [21]. Moreover, beneficial soil biota play a fundamental role in maintaining soil health and quality by regulating biogeochemical cycling of essential plant nutrients [22]. Therefore, to enhance productivity and sustainability in organic systems a more holistic approach targeting biological interactions among the main crop, cover crop and beneficial soil biota is needed.

3. Arbuscular mycorrhizal fungi and sustainable crop production

Arbuscular mycorrhizal fungi, often referred to as agroecosystem engineers, represent a key functional group of soil microbiota that are fundamental for soil fertility, crop productivity, yield quality and ecosystem resilience [23]. They form a critical symbiotic relationship with most agricultural crops improving the nutritional status of their hosts, besides protecting them against several soil-borne plant pathogens and environmental stresses. AMF enhance the uptake of phosphorus and nitrogen, and absorption of other immobile ions, such as zinc and copper by the host plant in return of about 20% of photosynthetic carbohydrates [24]. Thus this may enhance growth, production and produce quality of their hosts [25]. AMF protect their hosts against aggressive weeds [26,27], fungal, bacterial pathogens and nematodes [28], drought [29,30] heavy metals [31,32], salinity [33,34] and high temperature [35,36]. In addition, they improve soil structure and quality [37,38] mainly through the external hyphal network which creates a skeletal structure that enmeshes the soil particles [39,40], and by production of glomalin related soil protein (GRSP) which binds soil particles together [41].

4. Enhancing arbuscular mycorrhizal symbiosis in organic cropping systems

Arbuscular mycorrhizal fungi (AMF) are a crucial component of organic cropping systems, where they provide nutritional and protective benefits in exchange for photosynthetic carbohydrates. Compared to conventional systems, where nutritional requirements are compensated by external fertilizers, AMF provide essential agroecosystem services (AES) to their host in organic systems, which rely more on ecological cycles than external inputs [42]. The utilization of AMF in organic farming is promising since organic fields are often richer in indigenous AMF propagules density and diversity compared to intensively cultivated farms [43–46] probably due to lower levels of soluble P and limited use of biocides [47]. Moreover, AMF activity in organic agriculture may be enhanced through diverse crop rotations that include host cover crops and cash crops [48,49], and inoculation where native populations are insufficient or ineffective [50,51]. Besides this, we can hypothesize that innovative diversification of these elements at different levels will increase AMF functionality, promoting soil fertility, crop production and produce quality.

Unlike contemporary farming systems where soil nutrients are compensated by external mineral fertilizers, organic systems mainly rely on ecological cycles and limited organic inputs for maintenance of soil fertility and crop productivity. This requires more ingenious management of farm resources to facilitate nutrient cycling and sustainable use of the available soil nutrients. Thus, beneficial soil microorganisms and in particular AMF are fundamental in ecological functioning and crop production in organic systems. Despite theoretical recognition of AMF potential in organic agroecosytems, practical application of mycorrhizal technology is still limited. Nonetheless, we must emphasize that the future of AMF in organic agriculture seems promising since now there is a growing body of research demonstrating increased mycorrhizal activity and function in organic systems e.g., [42,45,52,53]. Furthermore, we know that organic practices are less detrimental to AMF communities [54] and also promote AMF abundance and diversity [44,55] compared to conventional systems.

To enhance mycorrhizal symbiosis in organic agriculture four critical elements ought to be considered holistically within the scope on increased functional agrobiodiversity: (1) use of mycorrhizal cover crops especially during seasonal fallow; (2) inclusion of mycorrhizal crops in the rotation; (3) management practices that favor AMF such as reduced tillage and agrochemicals; (4) inoculation with effective AMF isolates, especially when native AMF propagules are low or ineffective. Moreover, since mycorrhizal symbiosis is a complex biological association, increased diversity of these elements is imperative to augment AMF community structure, which directly affects the diversity and productivity of plants [56,57]. Increased fungal diversity in agroecosystems may enhance more ecological functions due to niche differentiation (complementarity effect) and facilitation as well as presence of a particular effective AMF species (sampling effect) [58,59].

Until now, most of AMF studies in organic systems are limited to greenhouse experiments or a handful of field experiments characterized by organic-input substitution approach that involves substitution of inorganic inputs by organic inputs. Although the potential of AMF to enhance soil fertility, crop productivity and quality in diversified organic systems is well recognized [60], relatively few studies have been dedicated to this subject. Moreover, only a few studies [61,62] have been conducted globally on functionality of mycorrhizal symbiosis at different levels (i.e., species, genetic and habitat) of agrobiodiversity in organic systems. Although such field experiments are generally considered challenging to initiate (e.g., in establishment on a non-mycorrhizal control), they can generate very useful information since seasonal variations, environmental factors and microbial interactions contribute to the experimental outcome. Thus, results from field studies may provide practical solutions to the existing knowledge on mycorrhizal technology application in organic farming. Additionally, crop diversity-related field experiments may contribute to development of germplasms that are more adapted to the local conditions, a key element in organic farming. By holistically promoting diversity at all levels, ecological processes will be more enhanced effectively increasing soil fertility and crop productivity without incurring extra environmental and economical costs [63].

4.1. Cover crops diversification

Cover crops are globally recognized as an important agronomic management practice for organic and low-input agriculture because of their contributions to soil health, reduction of nutrient leaching, weed suppression, maintaining and restoring soil biodiversity and to crop performance [64–66]. They provide a wide range of AES, including availing valuable plant nutrients, control soil erosion and nutrient leaching, interrupt pest, disease and weed cycles and maintenance of soil biodiversity [67]. Cover crops are particularly important in replacing or supplementing fertilizer N with residual N through N_2 fixation by leguminous cover crops or scavenging of residual available N by cereal cover crops or microbial decomposition of cover crop residues [68].

Cover crop management mainly depends on the intended use as green manure, living mulch or dead mulch. In countries that experience winter, cover crops are seeded in late summer or early fall and maintained in the field through winter and spring. Towards the end of spring, the cover crop biomass is either destroyed and incorporated into the soil by turning under or mowed and left on the soil surface as a dead surface mulch [21]. Turning under generally enhances microbial decomposition of the cover crop biomass compared to surface mulch, although it decreases the exposure of biomass to air and atmospheric agents. This may also negatively affect AMF symbiosis similar to tillage although this perspective has not been critically examined.

Cover crops may indirectly affect crop productivity by influencing rhizospheric soil microbiota, particularly AMF [48,69,70]. Since AMF are obligate mutualists, cover crops maintain or increase soil mycorrhizal propagules by providing them with photosynthates, especially during winter or fallow periods [64,71–74]. However, some cover crops e.g., Brassicas are nonmycorrhizal, and additionally produce mycotoxic glucosinolates upon tissue disruption negatively affecting AMF communities [75]. Until now, there are conflicting reports, either negative [76,77] or neutral [78,79], on the effects of Brassica crops (either as cover crop or main crop) on soil mycorrhizal potential and root colonization of the subsequent crop. Thus, to determine the effect of cover crops on soil mycorrhizal potential it would be necessary to have large scale field experiments incorporating contrasting host and not-host cover crops.

The intended benefits of cover crops depend on the cover crop species, composition, prevailing environmental conditions, and the management of field activities. Cover crops can be grown as monocultures or as diverse mixture of species, where the latter aims to optimize resource use efficiency and the associated AES (Figure 1). Although the use of single cover crop species is well documented [65,80,81], relatively little information is available globally on cover crop mixtures. Cover crop diversification may increase the aboveground biomass, the amount of N fixed, weed suppression, soil biodiversity and promote timely decomposition of the cover crop biomass depending on the crop needs by moderating C:N ratios [67]. Moreover, cover crops mixtures may be more tolerant to adverse environmental conditions than monocultures, thus promoting resilience especially in the present era of unpredictable weather patterns.

Cover crops benefits mainly depend on the crop species and agronomic management practices. While some cover crops, especially legumes, support a rich beneficial soil biota, others e.g., non-mycorrhizal hosts such as brassicas, contain allelochemicals that could be deleterious to beneficial soil biota, thus affecting delivery of essential ecological services to crops. Hitherto, it remains contentious whether non-host cover crops negatively affect soil mycorrhizal potential, root colonization and growth of the succeeding crops. To optimize the use of cover crops, cover crop mixtures (cocktails) are especially important (Figure 1) since they are viewed as more productive, resilient and adaptable to local conditions providing a wider range of ecological services [82,83].

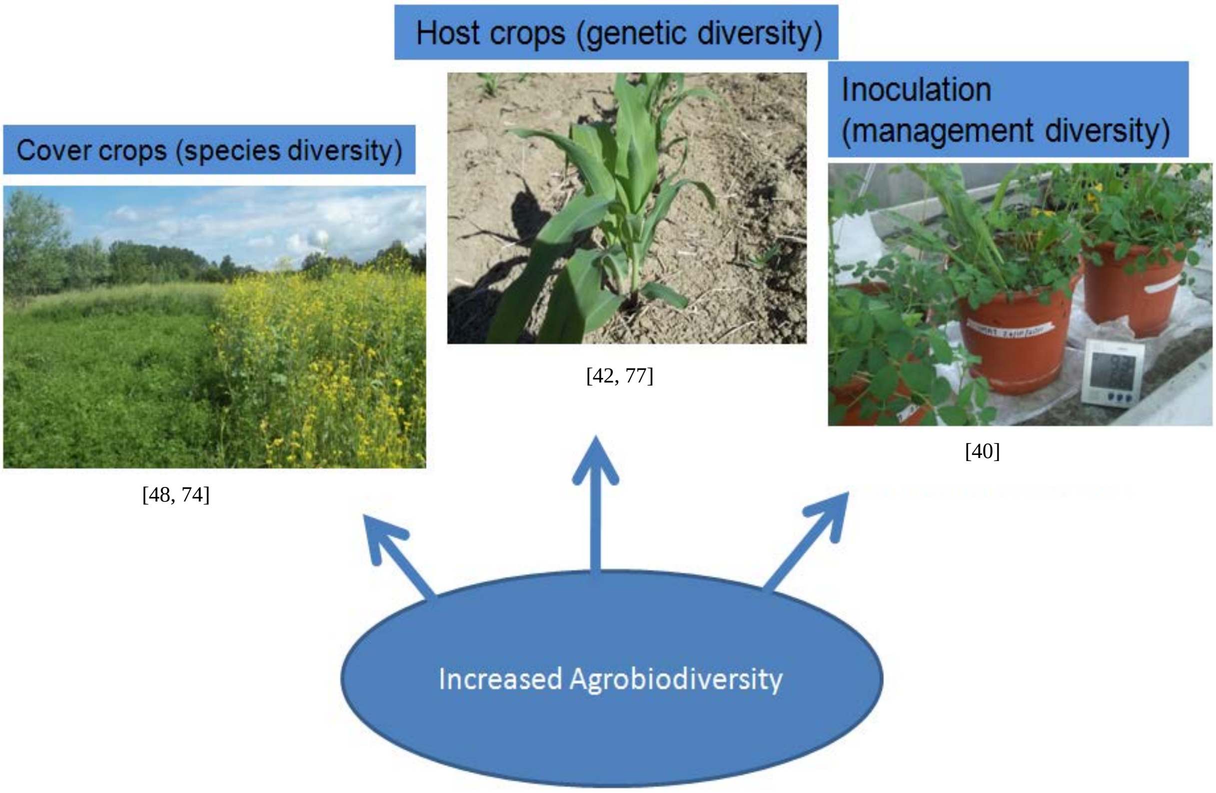

Figure 1. Key agronomic management practices that support development of functional arbuscular mycorrhizal symbiosis increasing delivery of associated agroecosystem services in organic and low input cropping systems. At each level, increased diversity of these elements, enhance mycorrhizal symbiosis which in turn increases soil biological fertility and agroecosystem resilience to climate change drivers.

4.2. Diversified crop rotations

Previous crops affect the performance of the subsequent crops through various mechanisms which include changes in water and nutrient use efficiency, pest and pathogenic microorganisms' interactions, soil quality and biodiversity. Crop rotations and sequences are aimed at obtaining stable and higher crop yields besides enhancing agroecosystem resilience. Generally, crop genotypes even within crop cultivars in a single species may have more dramatic effects on mycorrhizal symbiosis. One way of increasing

AMF propagules, diversity and functioning is through diversified crop rotations and sequences. In this case, crops that are well documented for positive plant-mycorrhizal interactions should be incorporated [22]. Some of the best bet mycorrhizal crops that augment indigenous AMF propagules include certain cultivars of cereals such as wheat (*Triticum aestivum* L.) and maize (*Zea mays* L.) [76,84]. Moreover, the previous crop mycorrhizal interaction may influence the soil mycorrhizal infection potential and root colonization of the succeeding crop as recently demonstrated using sunflower (*Helianthus annuus* L.) and mustard (*Brassica alba* Boiss) in 17 different soils [85].

On the other hand, leguminous crops have the ability to fix atmospheric nitrogen through symbiosis with rhizobia, and can also host AMF, which in return provides the plant with mineral nutrients. The presence of each microbial symbiont has been shown to affect the activity of the other and the interaction of both microbial symbionts can be detected on the host plant [24]. This interaction among the three organisms results in a mutualistic tripartite symbiosis [86]. Studies have also shown that co-inoculation of cowpea with bradyrhizobia and AMF [87,88] has synergistic effect in alleviating nutrient deficiencies through the enhancement of plant nutrients uptake [89]. Since legumes can host AMF and N fixing bacteria at the same time, the tripartite symbiosis of AMF-rhizobia-legume assumes more significance in terms of improving soil fertility and crop productivity.

Besides, agricultural weed species can either be mycorrhizal, weakly mycorrhizal or non hosts, exhibiting varied response to AMF [90]. Therefore, allowing mycorrhizal weeds to grow alongside other crops during rotations and sequences sustain AMF propagules during growth of non host crops such as Brassica or during fallow periods. This envisages an interesting perspective in organic weed management, where some weeds may form an essential component of agrobiodiversity providing alternative hosts to AMF during growth of non host crops. Moreover, weeds growing within the main crop could be beneficial where there are mycorrhizal non hosts within the rotation [91], provided they are not too competitive against the cash crop. At the time of weed termination and seedbed preparation, practices that embrace conservation tillage and reduced pesticide and fertilizer application should be prioritized since they favor plant mycorrrhizal interactions [92].

4.3. Within field crop genetic diversity

Conventional agriculture is dependent on the utilization of specific crop varieties or hybrids that are bred specifically to exploit high-input conditions. Many crop varieties (about 95%) grown in organic agriculture today were bred under high-input agriculture systems [93]. Although modern genetically uniform cultivars bred for specific characteristics are well developed to cope with certain stress, they are unlikely to cope with the greater site-to-site and seasonal fluctuations experienced in organic agriculture fields. This is overarched by the increasing challenges in agriculture, mainly as a result of climate instability, biodiversity loss and declining resources. Thus, the interaction of climate change and resource constraint dictates the need to base future agricultural production increasingly on diverse crop cultivars and ecological cycles.

Contemporary bred hybrids are usually selected for high input conditions where soil nutrients are not limiting. Consequently, modern hybrids, especially cereals [94,95], may portray reduced mycorrhizal dependency and responsiveness. Besides this, crop species and even cultivars belonging to same species may respond differently to AMF depending on the prevailing soil conditions [88,96]. By contrast, soil nutrients are often limiting in organic agriculture, necessitating optimization of ecological cycles for crop productivity. Thus, a profitable use of AMF in organic farming will require crop breeding programs that take into account existing AMF response variations within crop genotypes.

To overcome some of the challenges caused by large-scale monocultures there is growing interest to increase within field crop diversity in organic agriculture. There are two main approaches to create diversity, which include: use of varietal mixtures or Composite Cross Populations (CCPs). The two approaches differ in the way in which the cultivars are created, i.e., by crossing for CCPs, and by physical mixing seeds of different varieties for varietal mixtures [97]. CCPs are developed through evolutionary breeding by subjecting crop populations with a high level of genetic diversity to forces of natural selection for several cropping seasons [14]. Those adapted to local growing conditions are expected to contribute more seeds to the consecutive generations eventually leading to breeding of crop populations that are fully adapted to the local conditions under which they are grow. Despite the clear value of variety mixtures and CCPs [98], their adoption by organic farmers' remains limited mainly because relatively little is yet known about them in terms of adaptation, stability and productivity.

4.4. Fungal inoculants

Although AMF are ubiquitous soil microorganisms, inoculation with efficient isolates is one of the major agronomic practices that targets to improve the functionaly of indigenous AMF [99,100]. Numerous studies have reported beneficial effects of inoculation on root colonization and crop performance especially where indigenous AMF populations are infective, or low soil mycorrhizal infection potential [50,88,101,102]. However, although the introduced isolates are generally prescreened and considered more symbiotically superior to the indigenous isolates, some studies have reported minimal benefits mainly associated to less competitive AMF ecotypes compared to native species [103–105]. Besides, crop sequences or rotations that exclude AMF host crops, and extended fallow periods may hinder the establishment of introduced isolates [106].

One of the main obstacles of AMF inoculation in the field is the biotrophic nature of AMF which requires initial production of crude inoculum using different host plants. The resultant inocula is usually bulky and laborous to apply on large scale. This may steeply increase the production and application costs when large quantity of efficient and reliable AMF inoculum is needed [107,108]. Besides this, since many commercial AMF inoculants often contain a single fungal isolate mostly of Glomus genus, this may alter the community structure of the native AMF community through either positive or negative microbial interactions [109]. Moreover, competition or negative interactions with resident fungal endophytes, especially at juvenile plant stages, and environmental stress may consequently reduce the effectiveness of the introduced isolates.

An alternative strategy aimed at increasing AMF symbiosis in horticultural crops is where plantlets are pre-inoculated with AMF isolates at nursery. Here, the mycorrhizal inoculum is homogenously mixed with a sterile seeding substrate used for the pre-germination of the seedlings. Therefore, plant-AMF interaction is established at a juvenile stage and in the absence of other rhizospheric microorganisms that often compete for root space in the field [22]. At transplanting, the introduced AMF isolates have established intermittent symbiosis with the host crop and are well established to thrive in field conditions. Therefore, optimal AMF colonization at early crop stages is achieved which promotes uptake of essential plant nutrients when they are much needed. In such cases, the nursery AMF inoculants should be screened for functional diversity to incorporate AMF species that promote plant productivity, yield quality and tolerance to abiotic stresses. This approach is cheaper in cost and labor than direct field inoculation especially due mycotrophic nature of AMF, and has been proved effective for horticultural crops [110]. Moreover, since AMF colonization and responsiveness vary based on crop cultivars [95,111,112], the genotypes used in nursery should be ingeniously screened for AMF symbiosis.

In general, there is rising global trade of AMF commercial inocula and increased application of exotic AMF in both conventional and organic agriculture [100]. However, it is still unclear how the introduction of exotic AMF isolates affects the resident AMF diversity and community composition and structure. Ecologically, this may have serious consequences, due to introduction of new invasive isolates wipe out the indegenous populations altering the natural soil biodiversity [100,113,114]. Therefore, besides effectivess in promoting crop nutrition, isolates for commercial purposes should be by and large screened for other useful agroecologic effects such as their effect on soil biodiversity.

5. Conclusions

Organic agriculture is increasingly being recognized as a potential strategy to produce healthier food, conserve biodiversity and reduce off-farm inputs in agricultural landscapes [55]. Despite the remarkable rise in organic production over the last 20 years, organic farming is still faced with a number of agronomic and environmental challenges that could derail its future progress. Given the high variability in organic systems coupled with emerging global challenges like climate change, environmental pollution and biodiversity loss, novel cropping systems based on increased agrobiodiversity are imperative. These will provide better AES e.g., soil biodiversity, fertility and quality [115], weed and pest suppression [116], promoting sustainable crop production and quality [117]. Thus, agronomic practices such as diverse microbial inoculation, right choice of cover crops mixtures and incorporating highly mycorrhizal host crops in rotations and sequences (functional diversity, [19]), may have a great potential in promoting organic crop productivity via enhanced mycorrhizal symbiosis. Moreover, the development of complementary mixtures will further promote expression of both generic and specific agroecosystem functions in organic agriculture thus contributing to soil fertility, crop growth, yield and produce quality.

Conflict of interest

The author declares no conflict of interest.

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