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Review

Endophytes as Permanent or Temporal Inhabitants of Different Ecological Niches in Sustainable Agriculture

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Abstract: Local adaptation of plants to environmental conditions is gaining attention, particularly in the context of climatic change and the microbiota that are associated with it. It should be noted that endophytes play a large role in shaping plants. These are microorganisms that reside within plant tissues without causing any apparent harm to their host. It should also be highlighted that endophytes play an essential role in ecosystems by contributing to plant health through multiple mechanisms. We suggest that endophytes affect some animals, as they are used in the ecological niche in which animals thrive. Thus, we analyzed this aspect of endophytes as persistent but impermanent inhabitants of various ecological niches. Therefore, the aim of the current review is to present the knowledge (from the last 10 years) on plant endophytes, their applicability in agriculture and endophytes affecting animals. We focused on bioproducts and biofertilizers containing endophytes, which are indirectly connected with agrobiotechnology, and the legal conditions associated with the marketing of these products, which also impact some animals, as they are used in the ecological niche in which animals thrive.

Keywords: endophytes; persistence; plant; animal; microbiota

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1. Introduction

Endophytes are microorganisms that reside within plant tissues without causing any apparent harm to their host [1]. They form symbiotic relationships with plants, inhabiting spaces such as roots, stems, leaves, flowers, fruits and seeds [2–4]. Endophytes can contribute to overall soil health by promoting beneficial soil microbiota and improving soil structure [5]. Healthier soils support better crop growth and yield.

It should be emphasized that microorganisms can be strictly bound to plants and complete a major part or even their entire life cycle inside plants. Hardoim et al. [6] indicated that microorganisms requiring plant tissues to complete their life cycle are classified as "obligate". Part of these belong to the so-called 'core microbiome' and are vertically transmitted from one generation to the next through seeds [7–9]. The second group of endophytes are rhizosphere-competent colonizers. Between these two is an intermediate group, which comprises the vast majority of endophytic microorganisms, the so-called "facultative" endophytes [6].

The study of endophytes has gained significant attention in recent years due to their potential applications in sustainable agriculture, such as reducing the reliance on synthetic fertilizers and pesticides while improving crop yields [10]. Their role in enhancing plant health indirectly benefits animals that consume these plants by providing more nutritious and resilient forage [5]. Consequently, it should be emphasized that endophytic effects do not just end with plants but also apply to animals and humans. Christian et al. [11] argue that community ecology demonstrates complex species interactions across space and time. These authors suggested that the animal-bacterial and plant-fungal microbiomes should be compared and contrasted using six core theories in community ecology: succession, community assembly, metacommunities, multi-trophic interactions, disturbance, and restoration. (i.e., succession, community assembly, metacommunities, multi-trophic interactions, disturbance, restoration) [11].

Therefore, we propose that the aim of the current review is to present the knowledge (from the last 10 years) on plant endophytes, their applicability in agriculture and the effects of endophytes on animals. Importantly, the relationship between plant endophytes and animal microbiomes has been described relatively little and most of the published papers concern plants, so this review attempts to present the current state of knowledge also in terms of animal endophytes. According to the One Heath theory, all these aspects overlap and exhibit common interactions.

2. Endophytes–Current State of the Art

2.1. The Basic Characteristic of Endophytes

Liu et al. [12] mentioned that endophytic organisms have been found in virtually every plant. In this context, plants are hosts of various endophytes and form a range of relationships with them including symbiotic, mutualistic, commensalistic and trophobiotic [13]. Plant–endophyte interactions are thought to date back over 400 million years, and they have proven to be so successful that plants still interact with and even require endophytes to live in demanding environmental conditions [3]. It is worth remembering that plants have the potential to "select" endophytes of microorganisms from their above-ground or below-ground plant-associated microbial communities that provide them with some benefit [3]. Plant endophytes are usually represented by various microbial taxa, including both bacteria and fungi, and also archaea, algae and viruses [3,14]. Their main sources are microorganisms associated with the rhizosphere, phyllosphere and seeds [2].

Bacteria from the plant root zone (rhizosphere) enter the root interior through lateral root formation sites, damaged tissues and micropores. They then migrate inside the plant through the apoplast and conductive tissues [15]. In this way, they can colonize the intercellular spaces, the xylem, and the cell interior of organs such as roots, stems, leaves, flowers, fruits and seeds [16]. Some studies demonstrated that many endophytic bacteria can infiltrate roots and give rise to new endophyte populations in other plant organs [17,18].

As far as endophytic fungi are concerned, in many plants they are the most diverse and commonly occurring microorganisms. Fungal endophytes are found in the roots and above-ground parts of plants, with considerable diversity [19]. As in the case of bacteria, fungi can colonize plants systemically up until the flowering organs [19]. In addition, endophytes can be transmitted by seeds [19]. Many fungal endophytes, such as Epichloae, are seed-transmitted because they are completely reliant on the host's reproductive strength for their survival and dissemination [19]. It is worth mentioning that studies have shown that endophytic fungi never colonize very early embryos and that infection by endophytes mainly takes place at a later stage, during seed formation [19]. It is also important to note that the first stages of growth are generally critical for the overall microbiota, and plants should utilize the microbes present in seeds to ensure proper ecological functions in later developmental stages [20]. Kuźniar et al. [20] evidenced greater biodiversity of seed-borne endophytes in the seed endosperms than in the embryos and concluded that the seed-born microbiome is not statistically significantly dependent on the wheat cultivars; however, it cannot be claimed that every wheat seed is the same [20].

It should be pointed out that the endophytic microbiome of a plant is a function of factors such as plant species, growth stage, plant tissue, soil physicochemical factors (especially pH and moisture), physiological and nutritional status of the plant, the growing season and environmental factors [6]. The root tissues were found to contain the largest numbers of endophytic microorganisms, meanwhile the aerial parts of the plant are characterized by lower abundances of endophytes [12], whereas the generative organs of plants are the least rich in endophytic microorganisms [21].

Through the use of next-generation sequencing (NGS) techniques, it has been established that the endophytic structure of most plants is dominated by six phyla of bacteria (Figure 1): Proteobacteria, Actinobacteria, Firmicutes, Bacteroidetes, Acidobacteria and Deinococcus-Thermus [22,23]. The most common phylum of bacteria isolated from plants is Proteobacteria. Actinobacteria, Bacteroidetes and Firmicutes also belong to phyla frequently encountered as endophytes [24,25]. Opposingly, Acidobacteria, Planctomycetes and Verrucomicrobia occur at a somewhat lower frequency, most often as associated microbiota [24,26].

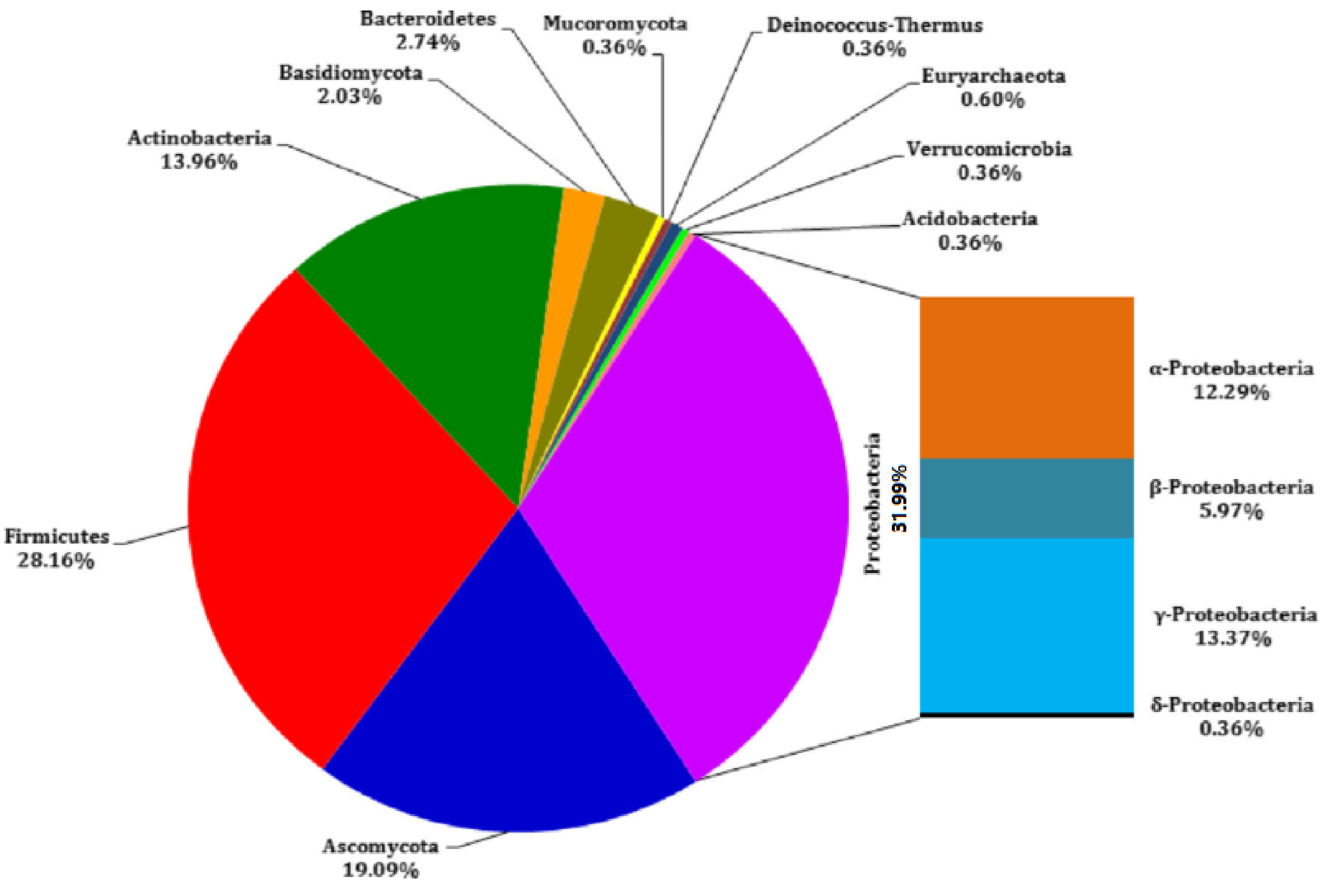

Figure 1. The abundance of endophytic microorganisms belonging to different phyla, according to Rana et al. [27].

Within Proteobacteria, α-, β-, γ- and δ- classes can be distinguished, with the γ-Proteobacteria being the most diverse and containing the highest number of bacterial endophytes [28]. Most endophytic γ-Proteobacteria belong to the following genera: *Acinetobacter*, *Enterobacter*, *Pantoea* and *Pseudomonas* [6]. α-Proteobacteria is also characterized by high abundances of the genera *Rhizobium*, *Methylobacterium*, *Sphingomonas* and *Bradyrhizobium* [29]. Numerous studies have shown that the most commonly known endophytic genera of bacteria include *Bacillus*, *Burkholderia*, *Microbacterium*, *Micrococcus*, *Pantoea*, *Pseudomonas* and *Stenotrophomonas* [28], *Achromobacter*, *Azoarcus*, *Collimonas*, *Curtobacterium*, *Enterobacter*, *Flavobacterium*, Gluconoacetobacter, *Herbaspirillum*, *Klebsiella*, *Microbiospora*, *Micromomospora*, *Nocardioides*, *Planomonospora*, *Serratia*, *Streptomyces* and *Thermomonospora* [6,29].

Endophytic fungi are classified into three main ecological groups: mycorrhizal, balansicaeous or pasture fungal endophytes and non-pasture fungal endophytes [30]. Endophytic fungi can also be divided into the two groups: non-*clavicipitaceous* endophytes (NC-endophytes) and *clavicipitaceous* endophytes (C-endophytes) [31]. C-endophytes are grouped into Class 1 and are commonly found in plant shoots, where they cause systemic intracellular infections [32]. There are three categories of C-endophytes: symptomatic and pathogenic species (Type I), mixed-interaction and asymptomatic endophytes, and asymptomatic endophytes (Types II and III, respectively). NC-endophytes are divided into the three subclasses: 2, 3 and 4 [32]. Class 2 fungi, also known as Ascomycetes, are a significant group of fungi that often serve as endophytes in various plants. Class 3 is exceptionally diverse, with its members belonging to the Basidiomycota and the fungal group Dikaryomycota [32]. Class 4 are facultative biotrophic fungi that penetrate plant roots and are distinguished by melanized dark septate hyphae [32]. The endophytic fungi of Class 4 are classified mainly in the phylum Zygomycetes [3,32]. The largest group in Class 4 are the Dark Septate Endophytes (DSE). They can be found in probably all land plants worldwide [33]. For an endophytic fungus to be classified as a DSE, it should create the specialized structures in the roots of the host and occur in plant roots as asexual, both melanised and septate hyphae [32]. Genera belonging to Class 4 but not to the DSE are, for example, *Ilyonectria*, *Fusarium*, Cylindrocarpon, *Gibberella*, Neonectria and the Sebacinales [32]. The diversity of endophytic microorganisms described for many plant species are summarized in Table 1.

Table 1. Examples of identified endophytic microorganisms from different plants.

Phylum/Class/Species	Host	References
BACTERIA α-Proteobacteria		
Rhizobium wenxiniae sp.	maize	[34]
Rhizobium sp. MP1	chickpea	[35]
Acetobacter diazotrophicus *Azospirillum* sp.	maize, wheat, rice	[36]
β-Proteobacteria		
Burkholderia sp. GE 17-7	ginseng	[37]
Achromobacter insolitus	wheat	[38]
Herbaspirillum seropedicae	rice	[39]
γ-Proteobacteria		
Acinetobacter xylosoxidans	pink cataranth	[40]
Citrobacter sp. RPT	fern	[41]
Enterobacter ludwigii	tomato	[42]
Actinobacteria		
Corynebacterium sp.	maize	[43]
Microbacterium sp. LKL04	rod millet	[44]
Micrococcus sp.	tomato	[45]
Firmicutes		

Table 1. *Cont.*

Phylum/Class/Species	Host	References
Bacillus sp. *Staphylococcus* sp.	wheat tomato	[46] [42]
FUNGI		
Class 1		
Epichloë sp. *Pestalotiopsis* sp. 9143	tall fescue cypress plants	[47] [48]
Class 2		
Phoma sp. *Fusarium* spp. *Aspergillus* spp. *Neothypodium* spp.	tropical plants grasses, legumes maize, rice grasses, Poaceae	[49] [50] [51] [52]
Class 3		
Ganoderma spp. *Tricholoma* spp.	tree species trees and shrubs	[53] [54]
Class 4		
Mortierella spp. *Rhizopus* spp.	maize wheat, potato	[55] [55]

2.2. Endophytes as Inhabitants of Agricultural Plants

Among endophytic bacteria, the so-called plant growth-promoting endophytes (PGPE) are of particular interest. These microorganisms, through a number of different mechanisms, can directly or indirectly influence the growth of their host [24,56]. They facilitate the extraction of N, P and Fe from the environment and are responsible for the production of phytohormones (auxins, gibberellins, cytokinins, abscisic acid and jasmonic acid) and the synthesis of 1-aminocyclopropane-1-carboxylic acid deaminase (ACC) [57]. They also produce compounds that inhibit pathogen growth, produce antibiotics and biosurfactants, induce systemic immunity, and provide plants with essential vitamins [58]. Endophytic microorganisms also support plant growth as a result of mitigating many types of abiotic stresses such as drought, excessive salinity, too low or high temperature, or the presence of heavy metals in the soil [59]. All the above endophyte features improve the yield and condition of crops.

2.2.1. Biotic and Abiotic Stresses Related to Crop Productivity

The major constraints to crop productivity, food quality and global food security are biotic and abiotic stresses [6]. Stress affects several physiological, biochemical and molecular parameters of plants resulting in loss of microbial diversity and soil fertility and competition for nutrient resources [10]. As endophytes have the ability to improve their host's tolerance to stress factors, researchers highlighted their potential use to alleviate plant stress in a rapidly changing climate where plants will be exposed to frequent flooding, water and nutrient deficiencies, low or high temperatures, excessive salinity or the presence of heavy metals in the soil [60].

Drought is a major environmental stress that has caught the attention of ecologists and agricultural scientists. Excessively high temperatures reduce germination rates, growth and plant productivity. In contrast, water deficiency reduces cell size and cell membrane integrity, impairs photosynthetic activity and enzyme function, and causes changes in plant hormone concentrations [10]. Drought stress-tolerant microorganisms have the ability to improve plant growth and development under water-deficit conditions. These microorganisms can form a thick cell wall, enter a dormant state, accumulate osmolytes, produce exopolysaccharides (EPS) and provide access to nutrients [10]. Naveed et al. [61] observed positive effects of endophytic bacteria on metabolic balance and a reduction in negative effects of drought stress in wheat grown under unfavorable irrigation conditions. In contrast, Gonzalez-Teuber et al. [62] investigated how root colonization by endophytic fungi affects *Chenopodium quinoa* and its ability to cope with extended periods of drought. The endophytic fungus *Penicillium minioluteum* was used for this purpose. It was shown that under drought conditions, *Penicillium minioluteum* had a positive effect on quinoa root growth and improved root formation [62]. On the other hand, low temperatures are also associated with many threats to plants. Acclimatization to low temperatures aims to minimize cell damage and increase photosynthetic activity and the accumulation of metabolites, such as phenolic compounds, proline and starch, associated with cold stress tolerance [63]. Numerous endophytes have been shown to increase plant tolerance to low temperatures. For example, the endophytic *Burkholderia phytofirmans* strain PsJN modified photosynthetic activity and carbohydrate metabolism involved in cold stress tolerance in grapevine plants [58], and improved growth and strengthened cell walls of *Arabidopsis* sp. [63].

Another growing problem faced by the agricultural sector is salinity. It lowers microbial activity due to ion toxicity and osmotic stress, leading to reduced plant growth and development [64]. Despite this, endophytes have been successfully used to protect various plants under salt-stress conditions. Plants under salinity stress tend to produce higher levels of ethylene, which can be prevented by the action of the enzyme ACC deaminase, produced by many plant-associated bacteria. It was shown that two bacterial endophytes, *Pseudomonas fluorescens* YsS6 and *Pseudomonas migulae* 8R6, isolated from tomatoes, can provide protection and growth stimulation to plants at very high (185 mM) salt stress. These endophytic bacteria produce ACC deaminase, IAA and siderophores. Under salinity stress, plants inoculated with these endophytes showed significantly higher chlorophyll content, yield and lower sodium (Na) content compared to plants inoculated with endophytic strains not synthesizing ACC deaminase [65]. Meanwhile, among fungi, endophytic *Epichloe* sp. play an important role in improving salt tolerance of wild barley (*Hordeum brevissubulatum*) by modifying polyamine metabolism [66].

Environmental stress also includes trace element pollution (metals and metalloids) of soils, the presence of which results in disruption of numerous biochemical and physiological processes, including photosynthesis, cellular respiration, N metabolism and nutrient uptake [67]. Nevertheless, endophytic bacteria can mitigate the effects of toxic concentrations of trace elements. As most of the techniques used for soil remediation are very costly and detrimental to soil structure, methods using plants and associated microorganisms to lower levels of trace elements are being used [68,69]. Armendariz et al. [70] reported that two bacterial strains *Bradyrhizobium japonicum* E109 and *Azospirillum brasilense* Az39 effectively colonized As-polluted soil and accumulated it in cellular biomass, stimulating plant growth [70].

2.2.2. An Essential Nutrient Associated with Endophytes in Plants

Plants require a continuous supply of macro- and micronutrients, most importantly N, P, K and Fe, in order to grow properly [28]. Of all the essential plant nutrients, N is the most important growth-limiting factor, and its deficiency is a major cause of low agricultural productivity worldwide [71]. Endophytes are essential for plant N feeding. They improve the ability of plants to acquire N from both organic and inorganic sources [72]. Other macronutrients also largely affect plant growth and yield [4].

P plays a role in metabolic processes, signal transduction, macromolecular biosynthesis, photosynthesis and cellular respiration [73]. Unfortunately, most of the available P quickly form complexes with other elements in the soil making it unavailable to plants [74]. Some endophytic microorganisms have been shown to possess the ability to convert insoluble forms of P into a usable form [4,74]. Among the bacteria capable of phosphate solubilization, the genera *Rhizobium*, *Agrobacterium*, *Pseudomonas*, *Burkholderia*, *Erwinia*, *Paenibacillus*, *Bacillus*, *Enterobacter*, *Klebsiella*, *Kluyvera*, *Streptomyces*, *Pantoea*, and *Lysinibacillus* can be distinguished [74].

On the other hand, Muthuraja and Muthukumar [75] obtained three species of *Aspergillus* sp. fungi capable of solubilizing K. In addition, the researchers showed that inoculation of maize seedlings with K-solubilizing fungi (KSF) significantly improved plant growth and K uptake in maize and increased the population of KSF in the soil [75].

2.2.3. Plant Phytohormones Connected with Plant Growth and Yielding

Phytohormones are signaling molecules that coordinate cell activity and control plant growth and developmental processes [4]. The major plant hormones include auxins, ethylene, gibberellins, cytokinins and abscisic acid [76]. Auxins are particularly important. They play a significant role in almost every stage of the plant's growth and life. They regulate many important physiological processes such as seed germination, cell division and elongation, and root development. They are also involved in organogenesis and gene regulation [4]. The most common naturally occurring auxin is indolyl-3-acetic acid (IAA), which can be produced by plants, bacteria and fungi in tryptophan-dependent and tryptophan-independent pathways [77]. Areas of IAA action mainly include cell signaling, cell division, elongation and differentiation, initiation of root, leaf and flower systems, and fruit development and aging [78]. IAA also induces plant defense systems, mediates responses to stimuli, affects photosynthesis and biosynthesis of metabolites, and may even control the synthesis of other plant hormones, e.g., ethylene [28,77]. It is a fact that IAA is commonly secreted by endophytic microorganisms. The most active strains of IAA-producing endophytic bacteria include the following genera: *Pseudomonas*, *Rhizobium*, *Azospirillum*, *Enterobacter*, *Azotobacter*, *Klebsiella*, *Alcaligenes*, *Pantoea*, *Acetobacter*, *Herbaspirillum*, *Burkholderia*, *Bacillus*, *Rhodococcus* and *Streptomyces* [4,77]. Endophytic fungi are also capable of synthesizing auxins, including IAA. For example, the endophytic fungus *Aspergillus awamori* Wl1 isolated from *Withenia somnifera* leaves was capable of producing important secondary metabolites including IAA, phenols and sugars. Furthermore, this strain effectively colonized maize roots and improved the growth of the host plant and finally maize yields [79,80].

Other plant hormones are also commonly synthesized by endophytic microorganisms [80]. Bean et al. (2022) showed that endophytic *Trichoderma* strains produce cytokinins that stimulate plant growth, influence colonization strategies by symbiotic fungi and increase plant resistance to pathogens [81]. As endophytic microorganisms can synthesize cytokinins, they can also influence the increase in cytokinin levels in both the soil and the plants growing on it [81]. Etminani and Harighi [82] isolated more than 60 endophytic bacteria belonging to the genera *Pseudomonas*, *Stenotrophomonas*, *Bacillus*, *Pantoea* and *Serratia*, capable of producing gibberellins and auxins. The strains tested evidenced inhibitory effects on bacterial phytopathogens, significantly increased root length and promoted plant growth [83].

2.2.4. Endophytes as Plant Defense Against Pathogens

Endophytic microorganisms also play an important role in plant defense against pathogens, which is also critical from an agricultural point of view. They can reduce or neutralize the harmful effects of fungi, viruses, bacteria, insects and nematodes [84]. Many endophytes produce chelators, antimicrobial metabolites, lytic enzymes and hydrogen cyanide, inhibiting the growth of phytopathogens. Furthermore, they compete with pathogenic microorganisms for available nutrients and space, thereby excluding them from the plant's ecological niche. They also have the potential to induce systemic resistance [84]. One of the most powerful and thoroughly studied mechanisms is the production of antibacterial, antifungal and antiviral antibiotics. Many compounds produced by endophytic bacteria have been identified, e.g., phenazine, pyrolnitrin, 2,4-diacetylphloroglucinol (DAPG), pyoluteorin, oomycin A produced by *Pseudomonas* sp., or oligomycin A, canozamine, zwittermycin A and xanthobaccin synthesized by bacteria of the genera *Bacillus*, *Streptomyces* and *Stenotrophomonas* [36]. Hydrolytic enzymes such as chitinases, cellulases, 1,3-glucanases, proteases and lipases cause cell lysis of fungal pathogens, while biosurfactants can act as antimicrobial compounds [78,84]. Bacteria belonging to the genera *Pseudomonas* and *Bacillus*, were reported to produce hydrogen cyanide, which has a deleterious effect on weeds, thus enabling plants to compete with them [85]. Bacterial endophytes also make low molecular weight bioactive compounds that are active at low concentrations and act antagonistically against a range of plant pathogens [85].

An indirect antagonism mechanism occurs when bacteria reduce or prevent harmful effects of pathogens on plants by producing inhibitory substances or inducing induced systemic resistance (ISR) [86]. There are many examples of endophytes that reduce the susceptibility of plants to pathogens. Furthermore, endophytic microorganisms are characterized by a faster and more intense induction of defense mechanisms in host plants, against various pathogens, compared to rhizospheric microorganisms [84]. Studies conducted on endophytes isolated from mulberry, among which bacteria from the genera *Pantoea*, *Bacillus*, *Pseudomonas*, *Curtobacterium* and *Sphingomonas* predominated, showed that the isolates had high activity against the fungal pathogens *Sclerotinia sclerotiorum*, *Botrytis cinerea* and *Colletotrichum gloeosporioide* [87]. Islam et al. [88] demonstrated that *Pseudomonas tremae* and *Curtobacterium herbarum* strains were sources of bioactive compounds providing resistance to phytopathogens. A *Nicotiana benthamiana* plant grown from seed inoculated with the aforementioned bacteria showed several times higher concentrations of endogenous salicylic acid and increased resistance to a disease caused by *Pseudomonas syringae* pv. *tabaci*. Some fungal species, such as *T. harzianum* and *T. longibrachiatum*, are also known for their beneficial interactions with plants [88]. Various studies also report the extensive capabilities of this beneficial fungus in alleviating plant stress when conditions are unfavorable for plant growth [89]. Also of interest is the genus *Fusarium*, which includes species described as both endophytes and plant pathogens. This is due to its ability to colonize and produce various mycotoxins, in addition non-pathogenic *Fusarium* species show biocontrol effects against potential pathogens [89].

The use of a stress-tolerant consortium of endophytic bacterial strains can be used to improve plant growth under abiotic and biotic stress conditions by regulating plant hormones, improving nutrition, producing siderophores and enhancing the antioxidant system [90,91]. It has been suggested that endophytes 'sense' physiological changes in plants and adjust gene expression to adapt to the new environment, and can therefore be used as protective agents in agricultural systems under extreme climatic conditions [12].

2.2.5. Endophytes of the Most Common Crops

Cereal products are the basis of human nutrition. They provide the body with essential nutrients in amounts that meet its daily requirements [92]. Currently, global food production is dominated by the cultivation of three crops: maize, wheat and rice [92]. In the EU, wheat production is by far the most important, in terms of area, volume and revenue.

This is due, among other reasons, to the fact that it is better adapted than other cereals to grow under suboptimal conditions [93].

Maize (*Zea mays* L.) is grown on all continents except Antarctica, and its global importance extends to agriculture, the food industry and biofuels [94]. Global maize cultivation is rapidly growing, driven by increasing demand for food, feed, biofuels and industrial products. Major maize producers such as the US, China, Brazil and Argentina play a key role in the global trade and development of the sector [94].

Various groups of endophytes can be found in maize that affect its health and yield [91]. Wallace [95] reported that bacteria of the maize seed are dominated by Proteobacteria, Actinobacteria and Firmicutes, with the majority of fungi placed in the Ascomycota phylum. Among endophytic bacteria, the following are common for maize [96]: *Azospirillum* spp.; these nitrogenous bacteria support maize by improving N assimilation. *Rhizobium* spp. and *Pseudomonas* spp. can promote plant growth and protection against pathogens [91]. Various species of *Bacillus*, *Paenibacillus*, *Sphingomonas*, *Staphylococcus*, *Enterococcus*, *Pantoea* and *Pseudomonas* were found in maize tissues as well [96,97]. Also, some of the most common fungal endophytes in maize were identified [96]: *Fusarium* spp.—although some species are pathogenic, others can act as endophytes, supporting the plant against disease; *Aspergillus* spp.—can promote plant growth and improve stress resistance, and *Penicillium* spp.—often found in maize tissues, can promote plant health. Fungal endophytes isolated from maize seeds also include representatives of *Chaetomium cochliodes*, *Chaetomium subaffine*, *Cladosporium cladosporioides*, *Alternaria alternata* and *Rhizopus oryzae* [98]. Seed endophytes are found to promote maize growth, which is usually expressed by increasing the size of roots, shoots and leaves [96,98]. Other identified benefits include better germination [98], drought tolerance [99] and ion uptake [100]. Studies on endophytes in maize are still in progress, and their full potential as plant growth-promoting agents and disease protection are promising research areas.

Also wheat (i.e., Triticum *aestivum* L., *T. durum* L.) cultivation is one of the key crops worldwide, as wheat is one of the most important grains and a primary source of food for billions of people [101]. China and India are the world's largest wheat producers. However, wheat is a primary source of income for farmers and is a key export commodity for many countries. Makar et al. [102] isolated bacterial endophytes from grains of emmer wheat *T. turgidum* subsp. *dicoccum* and identified the genera *Staphylococcus*, *Pantoea*, *Sphingobium*, *Bacillus*, *Kosakonia* and *Micrococcus* as common endophytes. What is more, the indole-related compounds (auxins) that were produced by the endophytic *Pantoea* spp. and *Bacillus* spp. isolated from Oksamyt myronivs'kyi and Holikovs'ka grains may be regarded as one of the determinants of the wheat yield and its nutritional characteristics [102]. A large number of endophytic bacteria belonging to *Achromobacter*, *Acinetobacter*, *Arthrobacter*, *Chitinophaga*, *Enterobacter*, *Erwinia*, *Flavobacterium*, *Klebsiella*, *Leifsonia*, *Microbispora*, *Micrococcus*, *Micromonospora*, *Mycobacterium*, *Paenibacillus*, *Pseudomonas*, *Roseomonas*, *Staphylococcus*, *Streptomyces* and *Xanthomonas* genera have been isolated and identified from wheat [27,103]. It was also found that inoculation of endophytic microbes (*Acinetobacter*, *Bacillus subtilis*, *Azospirillum brasilense*, *Klebsiella* sp., *Streptomyces coelicolor*, *Herbaspirillum hiltneri*, *Pantoea alhagi* and *Paenibacillus* sp.) decreased chlorophyll degradation and enhanced the accumulation of soluble sugars, resulting in higher grain yield [27].

The occurrence of endophytic fungi has also been detected in the tissues of wheat plants. It has been evidenced that endophytic fungi can reduce the susceptibility of wheat to pest attacks and pathogens, enhance resistance to drought or high temperatures, and induce plant growth and development [104]. However, the study conducted so far related to the distribution and ecological role of fungal endophytes in wheat plants, and has focused mainly on the Clavicipitaceae family, or rather was limited to the model system of fungi of the genera *Neotyphodiumi Epichloë* [105]. The ITS region as a DNA barcode was used by Nilsson et al. [106] in the identification of many fungi important for agriculture, such as genera *Colletotrichum*, *Fusarium*, *Alternaria*, *Puccinia* and *Rhizoctonia*.

Rice (*Oryza sativa* L.) is the most important cereal crop for more than 50% of the world's population [107]. Endophytes are crucial for growth and stress tolerance of rice and can be used to increase its yield [107]. The beneficial effects of endophytes on rice growth are mediated by several functional traits such as phytohormones and siderophores production, N fixation and metal detoxification [108]. Kumar et al. [108] successfully isolated more than 60 bacterial endophytes from the roots, leaves, stems and grains of rice. The highest number of bacterial endophytes were isolated from the root, followed by the stem, leaf and grains [108]. Two phyla (Proteobacteria and Firmicutes) and five genera *Bacillus*, *Enterobacter*, *Klebsiella*, *Leclercia* and *Xanthomonas* were identified in the majority of rice tissues [107,108]. Other most documented rice endophytes are representatives of the genera *Micrococcus*, *Pantoea*, *Lysinibacillus* [109], *Burkholderia* and *Pseudomonas* [110]. Walitang et al. [111] reported that the cultivable seed endophytes were dominated by Proteobacteria and mostly class Gammaproteobacteria. They also confirmed the presence of *Flavobacterium* sp., *Microbacterium* sp. and *Xanthomonas* sp. in the rice seeds [111]. Seed bacterial endophytes were also mentioned as promising PGP activities, including hormone modulation, nitrogen fixation, siderophore production and phosphate solubilization [112].

A summary of the benefits of plant endophytes is illustrated in Figure 2.

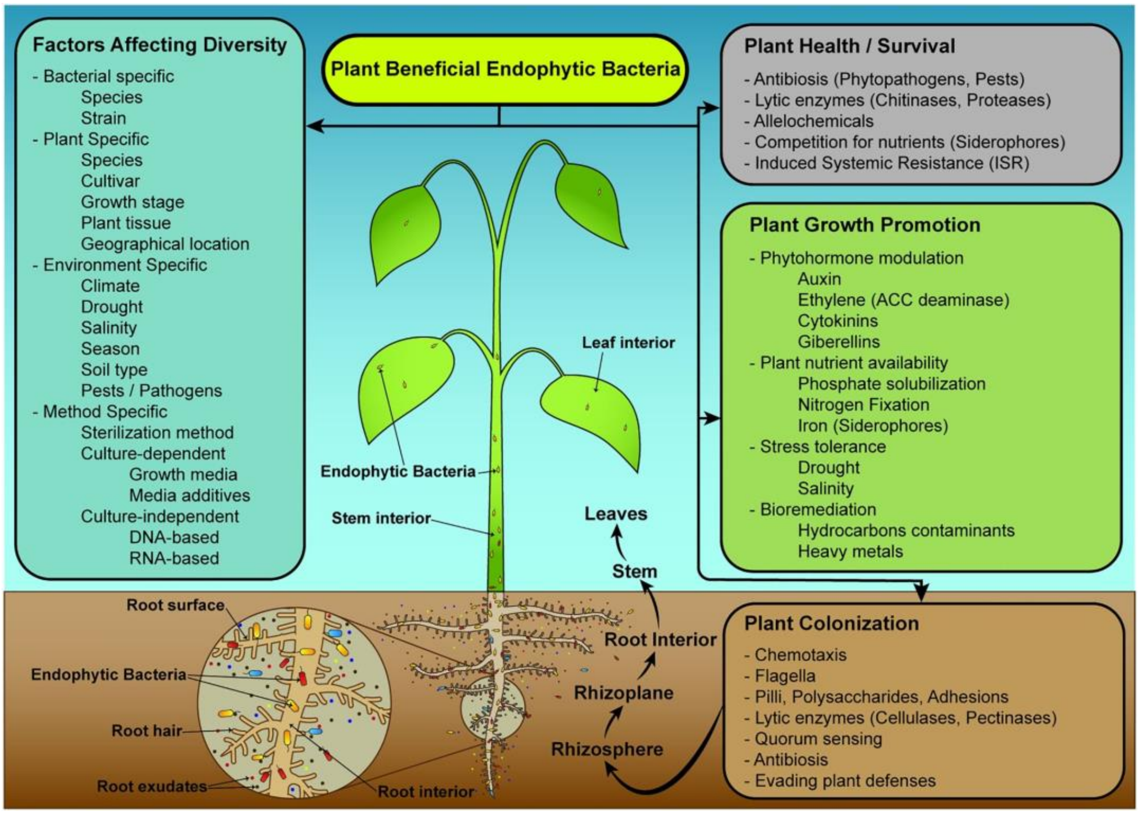

Figure 2. Factors impacting plant endophytes and beneficials of their presence in plant tissues, according to Afzal et al. [28].

2.3. Endophytes as a Feeding Niche for Animals

Endophytes have shown potential to influence various aspects of animal health and performance. Their effects on animals are often indirect, mediated through the plants that host them.

NGS has provided new insights into the importance of host genetics on the bovine microbiota sustainable development [113,114]. Also, aspects connected to how the microbiome is influenced by diets/dietary additives has been studied [115,116]. Microbiota and metabolites that are significantly influenced by human diet were also identified [117].

Plants are complex food sources, and contain many diverse nutrients, some of which are already known to interact with the microbiome [117]. When animals graze on more productive plants, they benefit from higher nutrient intake. For example, endophytic fungi produce secondary metabolites that increase N availability, improving the quality of the plants that animals consume, which in turn boosts their growth rates [118]. Endophyte-infected plants may have a higher protein content or improved digestibility, further supporting the growth of herbivores like cattle, sheep, and horses [119]. What is more, endophytes help plants resist various forms of stress, which in turn benefits animals feeding on those plants. It has been reported that endophyte-infected plants are often more resistant to drought conditions due to improved water-use efficiency and root structure [118]. This ensures more consistent forage availability for animals during dry seasons. Similarly, endophytes can help plants grow in soils containing increased concentrations of salts or trace elements [119]. This allows animals access to forage in otherwise suboptimal environments, reducing the risk of malnutrition or stress.

Moreover, some endophytes produce secondary metabolites (e.g., alkaloids) that deter insects and herbivores from damaging plants. Such protection can improve the yield and quality of forage crops, reducing the impact of pests on the feed supply [118]. Endophytes can also act as biocontrol agents by producing antimicrobial compounds or inducing systemic resistance in plants [119]. Healthier, disease-resistant plants offer more reliable nutrition, which supports better animal health. The metabolites of endophytes may also explain the effect of medicinal plants in improving immunity of mammals [120]. Saponins and secondary extracts derived from endophyte fungal have the potential to be immunostimulant, and they can be implicated as medicine for improving immune diseases [120]. Also, the lipoproteins of endophytic bacteria can stimulate receptors associated with their recognition and immunity, and could consequently regulate the immune responses [121]. Thus, the endophytes with specific metabolic compositions were the potential reason for explaining the mechanisms of medical plants in improving human immunity [120].

Endophytes can have a direct or indirect role in enhancing the resistance of animals to pathogens [118]. Some endophytes produce compounds with antimicrobial properties that can help reduce the presence of harmful pathogens in plants and, potentially, in the digestive tracts of animals [5]. For example, fungal endophytes in grasses have been shown to produce alkaloids that deter fungal pathogens, insects and even parasitic nematodes [118,119]. Symbiotic relationships between the host and the microbiome, and optimal functioning of the holobiont, are dependent on the environment [122]. Endophyte-enriched plants can influence the gut microbiome of animals, promoting beneficial microbes and limiting harmful ones [119]. A balanced gut microbiome is crucial for healthy digestion and immune function, which helps animals in resisting infections and diseases [5]. Finally, what the animal is exposed to, as a result of toxic tall fescue grazing, will influence host physiology, and what that animal excretes [52]. Consequently, grazing animal excrements and grazing stresses will affect the tall fescue plant/endophyte physiology [52].

It should also be pointed out that while endophytes can provide various benefits, certain strains can also produce compounds that are toxic to animals [5]. For example, *Neotyphodium* sp. endophytes in ryegrass and tall fescue produce alkaloids like ergovaline and lolitrem B, which can cause toxicity in grazing animals [52]. This condition, known as fescue toxicosis or ryegrass staggers, leads to issues like poor weight gain, reduced fertility, and heat stress in cattle, sheep and horses [52]. Endophyte-enriched plants can influence the gut microbiome of animals, promoting beneficial microbes and limiting harmful ones [118]. A balanced gut microbiome is crucial for healthy digestion and immune function, which helps animals to resist infections and diseases [5]. In turn, ergot alkaloids produced by endophytes can cause vasoconstriction, leading to circulation problems in livestock, especially during hot weather.

Relatively little is known about the immunological implications of endophyte exposure in cattle [123]. For example, ergovaline is an ergot alkaloid found in some endophyte-infected ryegrasses and it has been implicated in the expression of ergotism-like symptoms of grazing livestock, as well as in the protection of the plant against invertebrate predation and abiotic stresses [124]. Ergovaline is produced by an endophyte (*Neotyphodium coenophialum*) in tall fescue (*Lolium arundinaceum)* commonly found in south-eastern USA. Animals consuming ergovaline-containing feedstuffs appear to have a reduced capacity to maintain a thermoneutral body temperature with rapid changes in ambient temperature [124]. Although there are mechanisms that protect the animal from ergovaline exposure, tissues are very sensitive to ergovaline, indicating that ergovaline is very potent and that small quantities have the potential to cause noticeable physiological effects; decreased circulating prolactin, vasoconstriction and increased susceptibility to heat stress are all linked to the interaction of ergovaline with biogenic amine receptors found throughout the body [124].

In conclusion, endophytes have a dual role in influencing animals, particularly through their effects on plant hosts. While they can offer benefits like growth stimulation and enhanced stress resistance, the potential for toxicity means that their use, especially in forage crops, needs to be managed carefully to avoid adverse effects on animal health [5]. Mentioned interactions evidenced that endophytes are valuable not only for plant health but also for animal productivity and overall health in agricultural settings.

Persistence-Perishable of Endophytes in the Gut Microbiome of Animals

It should be emphasized that endophytic microbes can be short- or long-lived. What is more, they possess a huge diversity of metabolic pathways, which, together with their horizontal gene transfer systems, enable rapid evolution and environmental responses [125]. McFall-Ngai et al. [126] suggested that these metabolic add ons of microorganisms allow the animal to thrive by adapting to otherwise noncompetitive lifestyles (e.g., feeding on nutrient-poor diets) or environments (e.g., oligotrophic habitats). There is some acceptance that the animal gut microbiome is inherited largely from our mothers at birth, as well as environmental microorganisms with which we come in contact via the food we eat through life [126]. It should be emphasized that this information is important especially for herbivores or those for whom the food mainly consists of plants [125]. It was also suggested that among the various parts of the animal body, the gut is likely the site of the most dynamic and consequential bacterial-signaling benefiting animal hosts. This is due to the sheer number and diversity of its microbes, as well as the inherent permeability and sensitivity of the gut epithelium [127]. Pandey et al. [128] indicated that there are conspicuous similarities among animals and plants related to microbial associations. This phenomenon distinctly points towards the importance of endophytes as probiotics for a plant similar to probiotics in animals. Based on literature reports and our own observations, they indicate that the gut microbiota of herbivores consists of specific microbes that are common plant-associated microbes [129]. What is more, there is some acceptance that plant-associated microbes play an important role in maintaining human gut flora as plant-based diets feed beneficial bacteria (diet-borne bacteria) in the human digestive tract [130–132]. The evidence documented shows that the largest microbial diversity was exhibited by herbivores. This phenomenon might be due to the persistence of plant-associated endophytic bacteria in animals, as these bacteria are present inside plant tissues during digestion in the stomach [130–132]

The gut microbiome plays a crucial role in the health and well-being of animals. It is especially critical for animals that depend on this bacterial community for digesting their food. One of the key components of diets are plants used as a vegetable diet, providing not only fibers, vitamins, minerals, essential amino acids and metabolites but also the important microbes maintaining animal gut flora. It has been observed that the gut microbiota of herbivores consists of specific microbes that are common plant-associated microbes [127]. Therefore, it is important to analyze the endophytes as potential probiotics that benefit animals. It should be emphasized that animals benefit from a healthy gut, but not all microorganisms are beneficial for the host. Inside the gut, the available space for anchoring to the mucosa is limited, and bacteria and other microorganisms are in a constant struggle, competing with newcomers in the search for a niche in which to settle [133]. Herbivores exhibit the largest diversity, including probably plant-associated bacteria, especially endophytes, that, by being inside plant tissues, may survive digestion in the stomach.

In Table 2, we indicated some microorganisms that can colonize the intestines of animals and can also have the characteristics of endophytism.

Table 2. Specified animal microbiota potentially of endophytic origin. Selected microorganisms based on the literature and own studies combined with sharing of common taxa between endophytic microorganisms and the gut microbiota.

Microorganism	Animal	Literature
Bacillus spp.	*Oreochromis niloticus*	[134]
Pseudomonas mosselii, *Trichocladium asperum*, *Titata maxilliformis*, *Clonostachys epichloe*, and *Rhodotorula babjevae*	Mouse	[135]
Lactobacillus plantarum	Intestinal tract of different animals	[127]
Latilactobacillus, *Syntrophococcus*, *Streptococcus*	*Capreolus capreolus*	[136]
Flavobacteriaceae.	*Cervus elaphus*	[137]
Pseudomonadaceae	*Cervus elaphus*	[137]
Clostridia	*Amur tiger*	[135]

Dighiesh et al. [134] showed the symbiotic effects of dietary multi-strain *Bacillus* probiotics (MSB) (*Bacillus licheniformis*, *B. pumilus*, and *B. subtilis*) in Nile tilapia (*Oreochromis niloticus*) exposed to *Aspergillus flavus* infection. These authors indicated that the dietary intervention of multi-strain *Bacillus* spp. is symbiotic and enhances the benefits for the maintenance of O. niloticus' health, growth and digestion. This is achieved by supporting growth genes, reducing inflammatory genes and enhancing immune-antioxidant resistance to combat *A. flavus* infection [134]. It is emphasized that these bacteria can be transferred from plants.

D. officinale endophytes decrease their interference on the gut microbiome. *D. officinale* juice could increase beneficial gut microbiota and metabolites including short-chain fatty acids. *D. officinale* endophytes *Pseudomonas mosselii*, *Trichocladium asperum*, *Titata maxilliformis*, *Clonostachys epichloe* and *Rhodotorula babjevae* could colonize the intestinal tract of mice and modulate the gut microbiome after oral administration of the juice for 28 days [135].

One of the microorganisms may also be *Lactobacillus plantarum*, which is present in plants, intestinal tracts of animals and fermented food. These plant microbes may have specific features like the ability to degrade plant fibers, production of specific metabolites and enzymes having health-beneficial activities [127]. Another microorganism that can be proposed is *Clostridium* sp., which is an endophyte also present in the animal gut; it has cellulose degradation capabilities due to having cellulosomes [128]. Dahl et al. [136] have determined that the core microbiome of *Capreolus capreolus* is composed of the following genera, such as *Fretibacterium*, *Latilactobacillus*, *Syntrophococcus*, *Streptococcus*, *Lentilactobacillus*, *Ralstonia*, *Tyzzerella*, *Catenisphaera*, *Enterococcus* and *Leuconostoc*. What is more, it highlighted the key microorganisms responsible for converting naturally available nutrients of different botanical origins [136]. Víquez et al. [137] studied the bacterial microbiota composition in animals experiencing semi-captive and captive management conditions, compared with free-living red deer. The bacterial microbiota of winter-gated and all-year-gated were mainly composed of Firmicutes (60.1–67.1%), followed by Bacteroidota (24.6–31.2%). The authors reported that the free-living individuals also had a bacterial microbiome firmly founded on Firmicutes (61.4%) and Bacteroidota (18.5%) but additionally harbored a substantial contribution from Proteobacteria (15.3%) [137]. What is more, they indicated that free-living individuals had a substantially higher representation of the Pseudomonadaceae family (10.8%), which may suggest an endophytic origin of these microorganisms [136].

Other microorganisms identified in the microbiome of *Cervus elaphus* are the bacterial families such as Lachnospiraceae, Rikenelleaceae, Flavobacteriaceae and Eggertheliaceae, which were also significantly more abundant in free-living individuals. We would also like to point out that among the above-mentioned components of microbiomes, there are microbes that are also potentially endophytic microorganisms and potentially probiotics for plants, especially strains belonging to the Flavobacteriaceae.

Positive correlations were reported between Firmicutes and the intake of plant fiber and carbohydrate. They were key microbes that helped red deer deal with wild plant resources [138]. These authors suggested that the combinations of Firmicutes were represented by Eubacteriales and Clostridia. This study indicates that high abundance of Firmicutes is an important guarantee for red deer to adapt to the wild feeding environment. We emphasize that microorganisms belonging to Clostridia can also occur as endophytic partners of plants. New data from our labs [139] indicated that invertebrate animals are also involved in the processing/persistance of endophytes. Our results suggested that trophic activity of the earthworm increases the reservoir of plant endophytes. It should be emphasized that the activity of the *Aporrectodea caliginosa* earthworm in the soil led to the emergence of 11.66% of all bacteria [139].

It is worth emphasizing that human health is not isolated but connected to the health of animals, plants and environments. As a summary, Figure 3 shows how various soil microbes are also in plant's leaves, human guts, and the guts of other animals.

Soil microbes have also been proven to perform beneficial roles for animals [140]. The soil environment can be a source of animal microbiomes. Similarly, the current paper presents that endophytic microorganisms can be a source of animal microbiomes as another component of the ecosystem. The microorganisms that animals consume through food are often derived from soil or plant endophytes [140]. It was also suggested that endophytic microorganisms can be a source of animal microbiomes according to the hypothesis "one health" [141]. In analyzing the one health framework, jointly considering humans, animals and their shared environment, it is important to analyze the possible sources of the microbiota that drive the metabolic potential of herbivores [142]. It is worth pointing out that analysis of the different effects of plant and animal proteins on human health suggest that an important influence on the microbiota is the diet of animals [143]. Considering first the exposure to microorganisms at global human–animal–environment interfaces and its potential implications for human and animal health, the environmental factors that drive microbial variation in human and animal populations were analyzed [142].

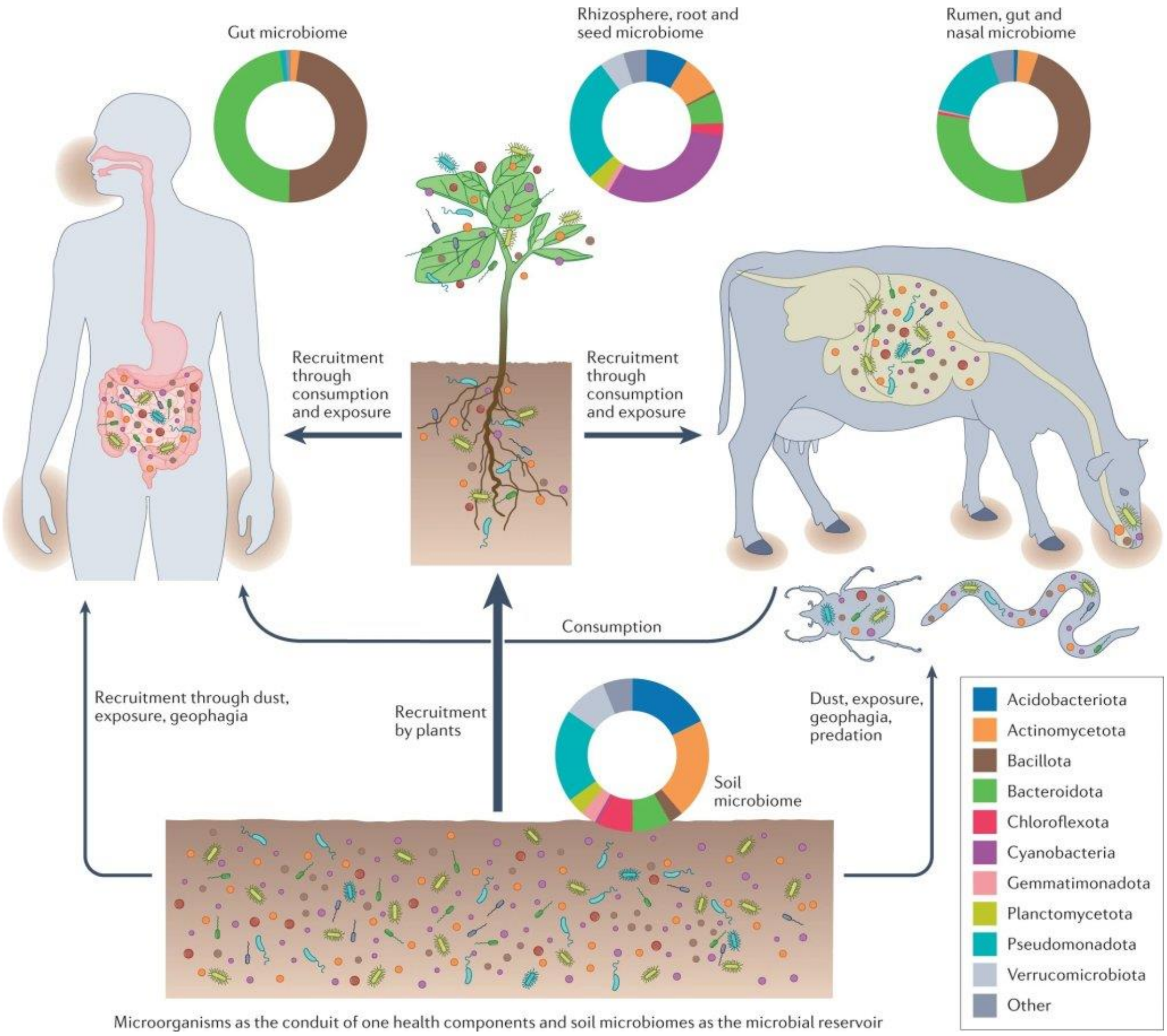

Figure 3. The link between soil, plant, animal and human microbiomes, according to Banerjee et al. [140].

Microorganisms that animals consume through food are often derived from soil or plant endophytes. It has been shown that each component of poultry feed carries a rich microbial community including both beneficial and pathogenic types that can seed birds continuously [144]. Other examples have been described, such as transfer of the microbiome in soil–plant–host–plant food webs can be common [145]. The gut microbiome plays a key role in many aspects of host life, and the composition of the microbial community is highly dependent on the prevailing conditions in the gut environment. As an example, the soil microbiome can even influence the health and social behavior of soil-dwelling macroorganisms [140].

Endophytes can contribute to the degradation of plant fibers or antimetabolites and the synthesis of metabolites due to the multitude of enzymatic activities they exhibit. Gellman and co-workers [146] provided evidence that *Prevotella* sp. requires carbohydrates available to the microbiota from the diet to survive in mice. *Prevotella* sp. was isolated and sequenced from fecal samples. *Prevotella* colonization required vegetable fiber in the mouse diet [146]. The role of bacterial endophytes in host starch metabolism is well studied in humans. *Prevotella*, an anaerobic Gram-negative bacterium belonging to Bacteroidetes, is a supergeneralist genus and is considered a commensal bacterium in humans [147]. Other endophytic-intestinal bacteria may have cellulases, pectinases, xylanases, tannases, proteases, nitrogenases and other enzymatic abilities that may be attractive for biotechnological development, in fact, many endophytes are used to promote plant growth.

Further research is needed to examine the relationship between one health environmental microbial diversity and human and animal health by habitat or species composition, and various relationships may emerge, including microbial facilitation, alternative stable states, and no relationship.

2.4. Possibilities of Using Endophytes in Agriculture-Bioproducts and Strains Used in Biofertilizers

By 2050, the global population is estimated to grow to 9.7 billion [148]. This will be associated with an increased demand for agricultural products, making it a priority to find solutions to increase the production efficiency of particularly important crops such as wheat, rice, maize and sugar beet [12]. In addition, unsustainable agricultural systems, a decreasing area for cultivation, climate change, a trend of increasing soil salinity and poor land management practices have led to an enhanced use of chemical fertilizers, pesticides and herbicides in agriculture, resulting in groundwater pollution, eutrophication, greenhouse gas production, soil nutrient imbalance and loss of soil microbial diversity [149–152]. It is therefore necessary and justified to disseminate more sustainable and environmentally friendly agricultural production techniques that ensure food security. One such method is the use of endophytic organisms [153]. This is an ecological alternative to conventional agricultural practices as it relies less on the use of chemicals. What is more, endophytic bacteria and fungi can provide a wide range of benefits, from plant growth stimulation to plant protection against stress factors [154].

In recent years, the use of bioproducts based on microorganisms, including endophytic microorganisms, has become increasingly popular in agriculture [148,154]. Bioproducts used in agriculture containing endophytic bacteria and fungi can include biopreparations, biofertilizers, biopesticides, biostimulants, vaccines and biocontrol agents [148,155].

Biopreparations are substances containing living organisms or suitably prepared products of their metabolism [154–157]. Considering the composition, we distinguish between bacterial, fungal, bacterial-fungal, enzymatic and bacterial/fungal-enzymatic biopreparations [158]. Biopreparations are mainly dedicated to the inhibition of pathogenic fungi and bacteria [159,160]. Numerous researchers claim that applying biopreparations to plant residues not only stimulates the mineralization process, but also accelerates the release of nutrients [161,162]. Microorganisms often used as components of biopreparations are fungi of the genus *Trichodema* [162,163]. They produce compounds that inhibit pathogen development and mycoparasitism. Moreover, they induce systemic immunity and stimulate plant growth [161]. They are also known for their very rapid growth and compete with parasitic fungal species such as *Fusarium* sp. [161]. *Trichoderma* sp. is characterized by its ability to produce enzymes that efficiently decompose dead organic matter and thus contribute to improving the physical and chemical properties of the soil [162].

One of the best ways to increase or maintain the current rate of food production while ensuring environmental stability is to use biofertilizers [76,150]. The main difference between biopreparations and biofertilizers concerns their composition. Biofertilizers contain organic matter and one or more organic active compounds in addition to selected microorganisms [156]. They enable microorganisms to adapt to new conditions, increase their activity and stimulate growth and development of crop plants [156]. Atmospheric nitrogen-fixing endophytes are commonly used in biofertilizers [57,153]. Replacing chemical nitrogen fertilizers with biofertilizers is an efficient and environmentally friendly solution [150,164,165]. Due to their greater ecological benefits, direct contact with the plant, and delivery of nitrogen directly to the host, endophytic microorganisms are more often used as components of biological fertilizers compared to rhizospheric or epiphytic microorganisms [150,166]. Endophytes commonly used in biofertilizers include bacteria from the genera *Azospirillum*, *Acetobacter*, *Azotobacter*, *Pseudomonas* and *Bacillus* [10].

It is also worth emphasizing that several rhizobacteria have the potential to fix atmospheric N using the nitrogenase enzyme-mediated reduction of nitrogen into ammonia that is accessible for plants [167]. This feature resulted in the common application of rhizobacteria (especially *Rhizobium* and *Bradyrhizobium*) as components of biofertilizers. Some rhizobacteria are also able to produce siderophores and therefore are useful in enhancing plant Fe nutrition [167]. All aforementioned features make rhizobacteria important candidates for improving soil fertility and plant health [167]. To summarize, the use of rhizobacterial biofertilizers reduces the environmental pollution caused by chemical fertilizers and protects plants against many soil-borne pathogens [167,168].

Another type of biological products are biostimulants, which support plant growth already in small amounts. Their main purpose is to increase crop yields in organic farming as a result of increased solubility of nutrients in the soil [169]. They are also used to stimulate natural processes that increase abiotic stress tolerance and yield quality, the effect of which is not dependent on nutrient content [57]. According to the European Biostimulant Industry Council (EBIC), the major aim of biostimulant application is "to stimulate natural processes to benefit nutrient uptake, nutrient efficiency, tolerance to abiotic stress, and/or crop quality, independently of its nutrient content" [170]. It was suggested that biostimulants may be an alternative to the auxin-based rooting enhancers because they contain active substances, which, during application to plants, stimulate their life processes, i.e., photosynthesis [171]. Also, biostimulants can increase the microbial and enzymatic activities of soil and change the solubility of micronutrients [169,172]. Some of the most common plant biostimulants are humic substances that stimulate root growth and consequently increase nutrient uptake together with soil pH neutralization [169].

Preparations that can provide an alternative to chemical pesticides in many crops are also biopesticides [156]. In Europe, the increased interest in such products is linked to the increased demand for environmentally safe products and the expansion of areas of organic farming [173]. Endophytic microorganisms that are the active ingredients of biopesticides are bacteria from the genera *Pseudomonas* and *Bacillus* and fungi from the genera *Trichoderma*, *Coniothyrium*, and *Beauveria* [174]. It is worth clarifying that biopesticides include not only preparations based on living organisms, but also products containing chemicals of natural origin, plant growth regulators, or pheromone traps [161].

Bacterial and fungal vaccines are also frequently used in agricultural practice [52]. Vaccines containing endophytic microorganisms, e.g., nitrogen-fixing bacteria in symbiosis with legume roots, and fungi (e.g., of the genus *Trichoderma*) that protect plants by producing antibiotics and enzymes that degrade the cell walls of pathogens are available on the market [163]. It is worth mentioning that vaccines are approved for marketing after fulfilling the requirements of the registration procedure. Therefore, they are classified as products of proven quality and efficacy [156].

The use of different types of bioproducts mentioned above is associated with many advantages. Treating seeds and plants with preparations based on endophytic microorganisms increases yield quality and promotes plant growth and development [72,175]. Through their biological activity, endophytes supply the soil with nutrients and improve their availability [96]. The use of bioproducts also has a positive effect on the soil structure.

It has been evidenced that the use of biopreparations can increase soil organic carbon and soil porosity [175]. Use of biological products is also characterized by high yields even when applied in small quantities and this in turn affects the lower costs of plant cultivation [12]. It is important to remember that the efficacy of bioproducts is highly dependent on a number of factors, such as weather conditions, soil moisture, and storage, which can affect the germination rate of conidia in fungal-based bioproducts [170]. The form of the preparation also has a great influence on its performance [148].

Microbial endophytes are found in every plant species known to date. Within the host plant the entire microbial community lives non-invasively in active internal tissues, causing no harm to the plant [6].

Endophytes interact with the host plant through metabolic communication, which enables them to generate signaling molecules. It is noted that plant endophyte communities are structurally and functionally heterogeneous for many reasons. There are various factors such as host plant, growth stage, plant organ, environmental factors, soil and management practices and the presence of plant pathogens that are responsible for the distribution of endophytes. Key research areas include the study of phytobiome components, interactions (plants, animals, other microorganisms), dynamics and functions. Also relevant in the application of endophytes as components of bioproducts is the generation of integrated system models for the analysis and prediction of the phytobiome. Most significant, however, is the development of practical crop management strategies based on the phytobiome and the establishment of global collaboration platforms for open communication between breeders, researchers, industry, agricultural advisors and consumers [6].

Currently the most important fact for agricultural producers is to be able to manage phytobiomes rather than individual components of the phytobiomes [26,176]. This paradigm shift in agriculture and ecosystem ecology could result in a solution to potential risks associated with environmental issues:

- Increased resilience of our cropping systems to water and nutrients
- limitation and heat stress;
- Increased resistance to the continued emergence of new pests and pathogens;
- Reduced yield losses due to pathogens and pests through the management of
- practices other than pesticides as the primary means of protection;
- Full integration of biological substances into site-specific crop management (precision agriculture);
- Effective rehabilitation of marginal, degraded and depleted land
- worldwide;
- Increased possibilities to identify crops suitable for biomass, including
- shifting cultivation systems due to climate change and data-driven
- selection of crop species for a given location;
- Reduced negative impact of crop production on the environment;
- Increased safety, quality and nutritional value of our food supply;
- Reduced reliance on external inputs to maintain crop productivity;
- Increased capacity for effective crop management to support long-term soil and ecosystem health;
- Adaptive, data-driven on-farm phytobiomes management systems for optim-al productivity;
- Increased profitability of sustainable food, feed and fiber production to enable farmers to meet demand [177].

Regulation and Commercialization of Use of Endophyte–Plant Symbiosis

Today, countries with modern agriculture have numerous rules and regulations. Their purpose is to reduce the use of chemicals and limit the side effects of their use. In 2009, plant protection acts were adopted in the European Union (EU). They are designed to protect human health and protect the environment from the risks associated with the use of pesticides. EU regulations apply in all member states and override national laws. Although uniform EU criteria guide the registration of plant protection products, the decision to place a product on the market is made for each member state separately [178]. The accession of individual countries to the EU and compliance with EU requirements is closely linked to a decline in the number of chemical plant protection products approved for marketing. Products that were not thoroughly tested and did not meet strict safety criteria are withdrawn from use throughout the EU [178].

EU countries have an agrochemical regulation (1107/2009) [179] and bioproducts are subject to registration according to its rules. Unfortunately, this is a rigorous process and very expensive. The dossiers submitted to the relevant European institutions must contain a detailed description of the results of tests of physicochemical and biological properties [180]. It is necessary to prepare a dossier containing information on ecotoxicology, toxicology and environmental behavior of the product [180]. In addition, the application should include information on the agronomic efficiency of the bioproduct [180]. It is essential to provide data on the microorganisms used, such as information on the collection, from which the pure culture was deposited, as well as the active form of the microorganism, its content and the presence of other components, such as carriers [178]. The documentation must also include a characterization of the analytical method used to determine the active substance(s), both in the bioproduct and in the plants and environment [178,180]. This is why, in practice, preparation of such documentation for bioproducts is not easy [156]. This is due to the difficulty, and sometimes even impossibility, of isolating and identifying the active substance(s). Another problem is also the difficulty in developing analytical methods. It is also difficult to determine the stability of the bioproduct and prepare the formulation. This is particularly important because the product should be safe, not clog applicators or precipitate. In addition, the preparation of the working solution should be easy, and the formulation should not lose its effect [156,181]. Any registration application should also include such basic information as the storage period of the bioproduct and its shelf life, as well as the scope and rules of use. Despite the fact that the registration process for bioproducts is quite cumbersome all the time, it certainly ensures safety, both for people and the environment, and is a guarantee of quality. It should also be added that bioproducts may also contain the endophytic microbes, which we dedicate this review to. It should be taken into account that there are also pathogenic microbes; therefore, a concern for their pathogenicity and risk for environmental safety also exists. What is more, Pandey et al. [128] rightly state that the presence of a high-cell number of particular endophytic strains in a formulation makes safety also a very important concern. Therefore, it is important that the consequences of the application of bioproducts is considered at different ecological levels, taking into account both comparing and contrasting the animal–bacterial, plant–animal and also soil–plant–animal [128].

On 1 September 2022, the European Union introduced four new regulations aimed at revising the approval process for microorganisms used in plant protection products (PPPs). These changes modify the criteria for evaluating microorganisms to make them more suitable for biological substances. The amended regulations address the approval of microorganisms as active substances, update the data requirements for their approval, and revise the evaluation and authorization principles applied by member states. The goal is to simplify the risk assessment process for microorganisms and accelerate the market entry of biopesticides, aligning with the EU's objectives under the Farm to Fork Strategy and the Green Deal to reduce reliance on chemical PPPs [181].

The updates to Regulation (EC) No 1107/2009 introduce new criteria tailored to the biological and ecological properties of microorganisms, replacing those previously modeled on chemical substances. Before this change, requirements for microorganisms were similar to those for chemical active substances. The Commission Regulation (EU) 2022/1438 eliminates criteria irrelevant to microorganisms, such as data on isomers, and changes the approach to residue evaluation, as microorganisms themselves are not considered hazardous in this context. It also focuses on specific risks, such as toxic metabolites from certain fungi and bacteria, and clearly differentiates between chemical and biological active substances [181].

The updated rules introduce precise requirements for defining microorganism compositions, including (1) unique accession number in a recognized culture collection; (2) scientific identification at species and strain levels; and (3) information on whether the microorganism is a wild type, mutant or genetically modified [181].

Additionally, the manufacturing and analytical methods for microorganisms differ from those for chemicals. The new guidelines mandate validated analysis techniques to identify and quantify active microorganisms, detect contaminants and evaluate metabolites and impurities [181].

Regulation 2022/1438 further establishes that microorganisms must meet safety standards, demonstrating that (1) the strain is non-pathogenic; (2) any isolated virus is not infectious to humans; and (3) bacterial strains lack transferable genes for antimicrobial resistance [181].

New criteria for determining low-risk microorganisms expand the category to include additional virus species beyond baculoviruses. Substances approved as low-risk are granted a 15-year approval period instead of the standard 10 years, incentivizing the use of these safer alternatives [181].

Three related regulations refine other aspects of the approval process: (1) Regulation 2022/1439 updates data requirements for approving microorganisms as active substances; (2) Regulation 2022/1440 specifies data submission needs for PPPs containing microorganisms; and (3) Regulation 2022/1441 adjusts principles for member states' evaluation and authorization of such PPPs [181].

This regulatory overhaul supports the EU's push to reduce chemical pesticide use, promote biopesticides compatible with organic farming, and advance integrated pest management (IPM). By streamlining authorization and tailoring risk assessments to the unique nature of biopesticides, the EU aims to foster their development and market availability [181].

In summary, endophytes are environmentally friendly, non-toxic, easy to apply and cost-effective in nature, so farmers can use them as a fertilizer substitute for sustainable agriculture. The issues that influence successful commercialisation should be listed:

- Detailed studies about the biochemical, molecular and genetic mechanisms of endophytes determining stress resistance in different crops;
- Stability of strains/consortia;
- To obtain diligent research on both the positive and negative effects of endophytes in order to gain a true understanding of their potential for use in field trials of at least three years;
- Documented biosafety of bioproducts (especially containing live strains) in agroecosystems;
- An easy way to commercially produce bioproducts.

3. Conclusions

Recent years have brought great scientific interest in the study of endophytic microorganisms. This situation may be due to easier isolation and identification methods and current next-generation sequencing tools. Essentially, we face the same challenges of understanding relationships on a very different level (animal–plant; animal–plant–soil) under the assumption that these levels of research simultaneously use the same techniques and methods. The comparison of plant and gut microbiomes of animals help to guide research toward the understanding of such complex phenomena. We and other researchers indicated that now one must consider microbiome studies across multiple spatial, temporal and trophic scales in order to better understand and predict community change. What is more, identifying sources of degradation in these endophytic communities, and implementing changes to restore them, will be crucial if we are to make use of the knowledge gained from studying our microbial partners to improve human and animal health, agricultural productivity, and maintenance of healthy ecosystems. One of the key theories that the researchers highlight is the approach of using endophytes in bioproducts as probiotics, which benefit both plants and animals. We believe that if the study is precisely designed and constructed to investigate endophytic microbiota, achieving targeted and reliable progress of research approaches in the environment is not a very far-off dream.

We would like to present future directions and specific research priorities for advancing the field of endophyte-based agricultural applications, particularly on the following topics:

- The study of individual phytobiome components and their interactions;
- The integration of knowledge, resources and tools based on phytobiomes systems,
- The optimization of site-specific phytobiome-based solutions;
- The application of phytobiome-based solutions in next-generation precision agriculture to sustain increased food and feed production worldwide;
- The education and engagement of scientists and the public;
- The use of advanced technologies to monitor the application of biological components of fertilizers and preparations in the agroecosystem.

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