



# *Aureobasidium* spp.: Diversity, Versatility, and Agricultural Utility

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**Abstract:** The black yeast-like fungi *Aureobasidium* spp. are ubiquitous microorganisms found in a wide variety of extreme and benign environments as saprophytes, endophytes, and pathogens. Since this diverse genus includes species with potential uses in agriculture and the food industry, it is important that we explore their evolution and spread in the context of climate change. *Aureobasidium* spp. are known to be capable of producing a plethora of various metabolites, many of which find applications in the field in the control of plant pathogens. The present review aims to explain how these microorganisms can provide ecological and safe strategies that might be adopted in agricultural production systems and food processing. The versatility and potential of the *Aureobasidium* genus lie perfectly within the Sustainable Development Goals Agenda 2021–2030 by opening new horizons that are respectful to the environment and human health.

**Keywords:** agriculture; environment; metabolites; species; yeasts

## 1. Introduction

Fungi represent one of the most assorted forms of life with about 100,000 species already identified, and a vast number of species yet to be catalogued [1]. They are equipped with versatile metabolic pathways that allow them to fill important roles in ecological processes providing services for ecosystem functionality and human well-being [2].

Their crucial roles in ecosystems around the globe are obvious from their involvement in nutrient cycling, decomposition (e.g., nitrogen fixation, the mobilization of phosphorous and other micronutrients, carbon cycle) [3] and bioremediation (e.g., degradation of persistent organic pollutants, petroleum, polyaromatic hydrocarbons, pharmaceuticals pollutants, toxins, pesticides) [4]. Moreover, they are often directly beneficial to humanity by producing pharmaceuticals, antibiotics, and immune system boosters [5]. Fungi can be a protein-rich food as well as a source of enzymes. Being producers of various compounds, fungi are involved in many food transformation processes (e.g., fermentation and bioconversion) and have many industrial applications [6]. Finally, they can also play important roles in agriculture as promoters of plant growth and as biocontrol agents in pest control [7]. However, some species are also important pathogens of animals (including humans), but especially of plants, leading to major economic losses in the agricultural sector. The above-mentioned ecological roles are all found among species in the yeast-like fungal genus *Aureobasidium* (*Ascomycota*, *Dothideomycetes*, *Dothideales*), which we discuss in the present review with particular focus on their beneficial roles in agriculture.

The new European Plant Health Regulation (EU 2016/2031) [8] jointly with the European Green Deal policy aims to accelerate the transition to more sustainable systems of food production, with a 50% reduction in the use of pesticides, and an incremental increase of the land area used for organic farming to 25% by 2030. Within this framework, beneficial fungi could contribute towards an alternative and safe strategy in the agricultural sector. While some species are already commercially exploited, the versatility of other potentially effective species is enormous and underexplored. Among the most interesting groups of



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antagonistic microorganisms, *Aureobasidium* spp. hold great promise as one of the most useful in future agricultural practices [9–13].

Among *Aureobasidium* spp., *Aureobasidium pullulans* (*sensu lato*) has been the most widely studied and is now regarded as both effective and safe for various applications in agriculture [14]. In fact, its ability to produce a wide range of natural compounds such as melanin [15], pullulan,  $\beta$ -glucan, aureobasidin [16,17], siderophores [18], glycerol-liamocin [19], exophilins [20], and volatile organic compounds (VOCs) [21,22] render it of particular interest for applications in agriculture. For this reason, the present review aims to thoroughly examine the current potential and future perspectives of the *Aureobasidium* genus for sustainable applications relevant to the European Green Deal policy, by also focusing attention on the diversity of species and habitats.

## 2. Different Environments Support High Diversity of *Aureobasidium* spp.

*Aureobasidium* is a ubiquitous and widespread genus, and it can be found in forest soil, fresh and hypersaline water, ice, aerial portions, on plant leaves and fruit surfaces [23]. The ability of many of its species to produce a large quantity of propagules, and their pronounced intra-specific diversity has allowed it to populate a wide variety of environments, some of which are classed as harsh or extreme [24]. *Aureobasidium* species also exhibit a wide range of lifestyles, including as saprophytes, endophytes, and as plant or human pathogens [25].

Its most closely studied habitats have been the phyllosphere and the carposphere of various fruits and vegetables [26]; most of the studied biocontrol agents (BCAs), belonging to the species *A. pullulans* have so far been isolated from these dynamic plant environments, where physiological changes linked to ripening and ageing, and nutrition availability all happen in the presence of a large microbial community [27]. In fact, plant morphology, different levels of nutrients (carbohydrates, calcium, and phenolic compounds), and environmental factors (e.g., temperature, rainfall, wind, solar radiation) have been found to significantly influence microbial community composition [28].

Aquatic environments such as concentrated seawater in salterns, sea sediments, mud of sea salterns, have also been found to be favorable habitats for those *Aureobasidium* spp. that are highly tolerant to hypersaline conditions [29–31] and which possess cellulolytic, pectinolytic, and ligninolytic enzymes for the rapid decomposition of organic materials [32]. Other *Aureobasidium* spp. in marine habitats with low iron availability have been found to secrete siderophores that allow iron to be taken up in a siderophore-iron complex [18,33]. Aquatic environments seem to be preferred more by *A. melanogenum* than by other species of the genus [34]. Polyextremotolerant species like *A. melanogenum* are often extremely adaptable and able to colonize unusual environments such as human indoor habitats [35] including hospitals [36].

*Aureobasidium subglaciale* is unique for its psychrotolerant nature as it is almost exclusively found in glacial habitats in Svalbard (Norway) [37]. Given the adaptation of this species to low temperatures, its application as a biocontrol agent of produce stored under cool conditions appears particularly relevant [38].

Another species, *A. namibiae*, is tolerant to the extreme temperature changes from day to night, and is so named from a single isolate found on Namib Desert marble [23].

Di Francesco et al. [11,22] searching for new and effective antagonists, have demonstrated the wide potential of *Aureobasidium* spp. isolated from all sorts of uncommon places to tolerate a range of different non-plant environments.

## 3. The Taxonomy and Novel Species of the Genus *Aureobasidium*

The *Aureobasidium* genus is characterized by a hyaline terminal, lateral or intercalary conidiogenous cells that synchronously produce single-celled conidia of variable shapes and sizes [39–41] distinguishing *Aureobasidium* from other related genera. This conidiation is also known in sporodochial *Kabatiella* species, which makes identification sometimes difficult, thus requiring molecular analysis [42].

The morphological characters of *Aureobasidium* cannot be exclusively used as species identification features. The species belonging to the genus *Aureobasidium* are phenotypically extremely plastic: they can switch from hyphal to yeast morphology and they express various degrees of melanisation even when grown repeatedly under the same conditions [43]. The phenotypic plasticity is not only reflected among various species but also within the same species; this leads to the dead-end of classical morphology-based taxonomy [44]. However, even multilocus DNA sequence analyses were not able to resolve the phylogenetic relationship of the *Aureobasidium*-like isolates. For instance, as mentioned above, *A. pullulans* was considered to be a species-complex of four varieties, namely, var. *pullulans*, var. *subglaciale*, var. *melanogenum* and var. *namibiae*, based on their overlapping morphological and physiological features, supported by multi-locus molecular analysis [23]. Later, the large genomic distance between the varieties, together with distinguishable traits in their ecology, stress resistance, and degree of melanisation, elevated the taxonomic status of the varieties to the level of separate and well-defined species. Furthermore, a recent population genomics study has revealed that several species initially recognized as *A. subglaciale* are most probably members of a new species, yet to be described [38]. Bearing in mind the pathogenic traits recognized for the species *A. melanogenum*, the taxonomic identification of *Aureobasidium* spp. is not simply a trivial issue undertaken in order to exploit their biotechnological and biocontrol potential safely [45]. The analysis of the genomic data combined with ecophysiological traits seems to be the right path to resolve the complex taxonomy of this genus. The *Aureobasidium* genus comprises over 50 taxa (species and varieties) according to the *Index Fungorum* database and literature mining; novel species are also regularly being described [46]. Among the *Aureobasidium* species, *A. pullulans* is by far the most studied. However, nowadays interest in other species is increasing due to the versatile and applicable properties they possess. The diversity of species has also increased in recent years due to the numbers of newly described *Aureobasidium* spp. (Table 1). Among the new species, *Aureobasidium vineae*, *Aureobasidium mustum*, *Aureobasidium uvarum* [47], *Aureobasidium castaneae* [48], *Aureobasidium khasianum* [49], *Aureobasidium thailandense* sp. nov. [40] and *Aureobasidium iranianum* [50] were detected and noted through a phylogenetic and morphological analysis. For example, *A. thailandense* sp. nov. possesses an approx. 500 bp type I intron in the 18S rRNA that is missing in *A. pullulans* [40]. By contrast, *A. iranianum*, was detected as an endophytic black yeast isolated from healthy bamboo stems, easily distinguished from *A. melanogenum* by its far larger conidial dimensions. In 2019, from needles of *Pinus tabuliformis* in China, a new species *Aureobasidium pini* sp. nov. was identified and phylogenetically recognized as a close species of *A. namibiae* [24]. One of the most recent species, *Aureobasidium acericola* sp. nov. was discovered in 2021 during a survey of a deciduous forest of *Acer pseudosieboldianum* in Korea [25]. Another new species, *A. aerium*, was described after being found during the survey of air microbiome in Beijing, China [51]. However, only two species of *Aureobasidium* spp. have been recognized so far in the context of biological control, namely *A. pullulans* and *A. subglaciale* with the first being by far the more studied [11,38]. Conversely, several species are pathogenic to plants or humans. For instance, two species *Aureobasidium proteae* comb. nov. and *Aureobasidium leucospermi* sp. nov. have been found to cause leaf spot symptoms on *Protea* spp. and *Leucospermum* spp. plants, respectively [52], whereas *A. melanogenum* is an opportunistic human pathogen [53]. The ecological relevance of many other species of the genus *Aureobasidium* remains unexplained, as does their potential for possible exploitation.

**Table 1.** Known and novel *Aureobasidium* spp. and the relative habitats.

<i>Aureobasidium</i> spp.	Habitat
<i>A. pullulans</i>	Fruits carposphere [21]
<i>A. namibiae</i>	Extreme environments [23]
<i>A. pini</i>	Needles of <i>Pinus tabulaeformis</i> [24]
<i>A. acericola</i>	Leaves of <i>Acer pseudosieboldianum</i> [25]
<i>A. melanogenum</i>	Aquatic and hypersaline environments, human indoor habitats [34–36]
<i>A. subglaciale</i>	Glacial habitats [37,38]
<i>A. vineae</i>	Grape juice [47]
<i>A. mustum</i>	Grape juice [47]
<i>A. uvarum</i>	Grape juice [47]
<i>A. castaneae</i>	Leaves of <i>Castanea henryi</i> [48]
<i>A. khasianum</i>	Leaves of <i>Wightia speciosissima</i> [49]
<i>A. iranianum</i>	Plant endophyte [50]
<i>A. aerium</i>	Air [51]
<i>A. proteae</i> ,	<i>Protea</i> spp. plants [52]
<i>A. leucospermi</i>	<i>Leucospermum</i> spp. plants [52]

#### 4. Genomic Traits Linked to Biotechnological and Biocontrol Potential of *Aureobasidium*

Few studies have addressed the genome analysis of *Aureobasidium* spp. not only for the purpose of phylogenomic analysis, but also to reveal their biotechnological and biocontrol potential, exceptional stress tolerance and possible virulence traits, that might help to promote its exploitation in various fields.

The de novo sequencing and analysis of the genomes of four *A. pullulans* varieties was first performed by Gostinčar et al. [37]. This study supported the redefinition of the varieties to four separate species, *A. pullulans*, *A. subglaciale*, *A. melanogenum*, and *A. namibiae*, based on their large genomic differences. The four genomes were reported to be from 25.4 Mbp to 29.6 Mbp and to encode between 10,000 and almost 12,000 predicted proteins. Most of the protein families are shared among the four species, with many of them being of biotechnological or biocontrol interest [37]. The predicted secretome of the genomic data confirmed the broad spectrum of extracellular enzymatic activities previously observed in *Aureobasidium* spp. [54–56]. Some of the observed enzymes such as amylases, lipases, xylanases, laccases, etc. have biotechnological potential [56]; others, such as alkaline serine proteases, chitinases and glucanases, might have roles in antagonistic behaviour against other fungal competitors. The redundancy of these gene families could be associated both to oligotrophisms and general nutritional versatility [57].

The largest group of predicted secretory proteins were CAZs (carbohydrate active enzymes), of which more than half were glycoside hydrolases. The genomes encoded a rich repertoire of glycoside hydrolase families involved in the degradation of plant materials, such as cellulose, hemicellulose, and pectin, which were especially enriched in plants associated with *A. pullulans*, albeit not exhibiting any plant pathogenic characters [58]. In the predicted secretome the number of genes or gene families of proteases were less than 10%; the number of lipases were lower. However, some lipases, phospholipases, proteases and  $\beta$ -lactamases are virulence factors that need careful consideration before application *in planta* [37,59].

That study also revealed there to be a significant enrichment of sugar transporters in all four species and the presence of putative synthases of siderophores. The latter are iron-chelating compounds that have a role in fungal-host interactions and resistance to oxidative

stress. They also act as antimicrobials and are major factors of competitive advantage in the microbial community [33,37].

Gostinčar et al. [37] also showed that none of the four sequenced *Aureobasidium* species contained homologues of the genes involved in aureobasidin A (ABA1 gene) biosynthesis. This suggests that the existence of ABA1 homologues and the production of this antifungal cyclic peptide is not a universal trait among *A. pullulans* strains.

In line with their exceptional stress tolerance, several stress-tolerance linked protein coding genes were recognised in *A. pullulans* such as those coding for high numbers of various alkali-metal cation transporters, aquaporins and aquaglyceroporins, proteins of the high-osmolarity glycerol pathway, and proteins involved in the synthesis of compatible solutes and melanin [37,60].

The production of pullulan (a neutral polysaccharide of maltotriose units) has a wide range of potential applications in the food-industry and medicine. Although it is a common trait in *A. pullulans*, different strains produce differing amounts of pullulan under the same conditions. The genome mining of all four sequenced species revealed all the putative pullulan-biosynthesis genes [61], indicating that this trait is not limited to *A. pullulans* (*sensu stricto*). One of the functions of pullulan is the adhesion of fungal cells to a surface and the formation of a biofilm, which is a desirable characteristic for biocontrol applications [57]. Biofilm formation often results in the efficient antagonism of a biocontrol agent (BCA) against plant pathogens by niche exclusion mainly due to competition for space [12]. Additionally, the biofilm communities seem to be more durable to stress compared to planktonic lifestyle. *A. pullulans* thrives *in vitro* in its biofilm form [57] as well as on plant phyllosphere and root surfaces [12,62,63].

Interesting conclusions have emerged from recent studies that focused on the population genomics of numerous isolates of *A. pullulans* and *A. subglaciale* [38,64]. The analysis of 50 genomes of *A. pullulans* from different environments in various parts of the world revealed the homogenous population genetics structure of the strains and the high level of recombination. This confirmed the generalistic behaviour of *A. pullulans* that can thrive in various, including extreme, environments, without specialization to these habitats at the genomic level [64]. The opposite was revealed in a genomic population study of *A. subglaciale* [38], for which population structure of the species clearly corresponded to the habitat and geographic location of the strains. A linkage disequilibrium analysis also indicated *A. subglaciale* to be strictly clonal. This confers an important advantage in its biocontrol applications because such clonal strains will most likely sustain their efficient genomic configuration for longer periods of usage and would not be expected to recombine with wild strains of the same species [38]. The genome data and population genomic analysis of the species reveal important features, both beneficial and problematic, relevant to its intended exploitation that need to be carefully considered before actual application. The next level of investigation to increase our understanding of *Aureobasidium* spp. behaviour should employ a transcriptomic approach in order to reveal which genes are activated under particular conditions and applications.

## 5. Use of *Aureobasidium* spp. in Agriculture

In organic production systems, the most commonly used plant protection products are copper fungicides, of which the maximum allowable quantity applicable has been restricted in Europe over recent decades and is currently limited by European plant-protection legislation (EU Regulation 2018/1981) [8,65]. Microorganisms, plant extracts, or essential oils could be deployed as alternative means for plant protection.

Although several potential BCAs against fungal pathogens of crop plants have been studied, only a few have been developed as bio-fungicides [13] compared with the conspicuous number of synthetic ones. For example, the commercial bio-fungicides (Botector<sup>®</sup>, Blossom protect<sup>®</sup>), containing two *A. pullulans* strains (DSM 14940 and DSM 14941) are allowed and recommended as treatments against fungal and bacterial diseases of grape, strawberry, and pome fruit [13,66]. In fact, *A. pullulans* represents an effective alternative

to agrochemical treatments both in the field and in storage. Its efficacy is attributed to different modes of action such as competition for nutrients and space, antibiosis, parasitism, and induction of fruit/plant resistance [67], the objective being to prevent or at least significantly slow down the build-up of fungicide-resistant populations. An efficient strategy needs to take into account the BCAs' modes of action in relation to the specific epidemiology and pathogenesis of each disease.

### 5.1. Field Treatments

Because of the economic and environmental impact of agriculture, several microbial BCAs and alternative products have been used in the field to combat different diseases. However, the market uptake of microbial biofungicides has been limited, partly due to their variable efficacy in comparison to synthetic agrochemicals. Nevertheless, BCAs used against field pathogens can have higher efficacy, especially when used when the level of disease is relatively low to medium, when they are integrated with other agronomic practices, and when the timing of treatment is optimised [13].

Field applications can reduce pre-harvest rates of infection and allow beneficial microbes to colonize the fruit surface before harvest, so reducing levels of infection during cold storage [68]. To reduce brown rot of cherries, both in field and in storage, applications of *A. pullulans* strain Y126 closer to harvest was effective in controlling *Monilinia laxa* [68]. In the case of grey mould disease, the efficacy of *A. pullulans* was first demonstrated by Bhatt and Vaughan [69,70] who showed that spraying strawberry plants at petal fall or early green fruit stage with the BCA suspension reduced the fungal infection on fruits by 31%. More recent studies of *A. pullulans* being applied against grey mould have clearly demonstrated its efficacy in vineyards [13,71], and in greenhouse conditions on cucumbers, tomatoes, and strawberries [9,72]. Furthermore, for controlling fungal diseases such as grey mould, entomovectoring by using pollinating insect vectors is an ecofriendly and efficient strategy for delivering BCA both in the field and greenhouse [10,72]. In fact, Iqbal et al. [10] demonstrated that by using bumblebees (*Bombus terrestris*) *A. pullulans* strain AP-SLU6 can be delivered directly to the flowers, which are known as the focal point of infection soon after flower opening. This provides immediate protection and does not affect the insect vector. Moreover, by eliminating the water that accompanies usual spray applications of BCA, the relative humidity (R.H.) remains unchanged and the pathogen, which would otherwise benefit from damper conditions, is disfavored.

In wheat plants, Wachowska and Głowacka [73] reported that the survival rates of applied *A. pullulans* on kernels were very high, thus rendering the antagonist effective in protecting the plant from damage by *Fusarium* spp. In fact, during a greenhouse experiment, Schisler et al. [74] reported that *A. pullulans* strain AS 55 reduced the severity of *Fusarium graminearum* on wheat by 84% probably by the biodegradation of choline, a compound that stimulates the growth of the pathogen [75]. Dressing *Sida hermaphrodita* seeds with *A. pullulans* as a treatment against *Alternaria alternata* in the greenhouse also resulted in a higher number of healthy seedlings than non-dressed seeds [76].

Despite these successes, the efficacy of one or more BCAs in field could be improved further by including other alternative strategies, such as plant extracts, physical methods, agronomical techniques, bio-fumigation with biocidal plants [77], although such strategies may cause farmers higher costs or more labour. Nevertheless, combining different strategies offers many advantages: the different modes of action that each strategy employs against a targeted pathogen (e.g., direct fungicidal or bactericidal activity and induced defence responses) can delay the development of resistance, and also help control other pathogens in a given crop. For example, in addition to controlling pathogenic fungi, *A. pullulans* has also been shown to control oomycetes, such as *Phytophthora cactorum* which causes crown rot, leather rot, and root rot in a number of crops and wild plants [9]. Moreover, the ability of *A. pullulans* L1 and L8 strains to stimulate growth of bean and soybean plant roots, stems, and leaves has been demonstrated by Di Francesco et al. [12], suggesting that these yeasts could have applications not only as BCAs but also as plant growth biostimulators.

Currently, very little has been published concerning hazard evaluation regarding the eco-toxicology and persistence of BCAs in the field. This knowledge is necessary in order to apply treatments promptly and time applications more effectively. For this reason, further detailed research is required to optimize their effectiveness and improve our understanding of the environmental fate of BCAs, the ecological niches they occupy, and their precise modes of action.

### 5.2. Postharvest Applications

The two main objectives when using microbial antagonists during the postharvest phase are the reduction of food waste, and reducing the usage of agrochemical products, the latter particularly as consumers are ever more seeking safer and healthier foods free of pesticide residues [78]. The postharvest phase has always been considered the best environment for the successful application of BCAs [64]. The first work published on the biological control management of stone fruit brown rot using bacterial strains during cold storage was reported by Pusey and Wilson [79]. Cold storage provides all the right conditions that can increase the efficacy of antagonists against fungal pathogens. Each antagonistic BCA acts according to a particular strategy dependent on the pathogen and host involved and how the prevailing environmental conditions affect them both. Thus, knowing their precise mechanisms of action and biology is necessary in order to obtain good results in fruit and vegetable management. Many authors have identified *A. pullulans* to be a good candidate for controlling different fruit and vegetable postharvest diseases under storage conditions [80–83]. For example, different isolates of *A. pullulans* have been shown to be effective in protecting pome fruit [21,80,83–85], stone fruits [82,86,87], grape [88,89], and citrus fruit [21,51] during the postharvest storage by exerting different mechanisms of action in their respective situations. Interesting new perspectives are emerging from the use of *A. subglaciale* as biocontrol agent for long periods of storage mainly motivated by its cold tolerance being so much greater than that of *A. pullulans* [54]. In two recent studies, Di Francesco et al. [11,22] have demonstrated that *A. subglaciale* is highly effective in reducing pathogen growth both through its soluble metabolites and its volatile organic compounds.

As far as we know, the potential of using *A. namibie* in postharvest control has not yet been verified; this thus represents a new area of research to develop in the field of biological control.

## 6. Use of *Aureobasidium* spp. in Food Industry

In addition to the above-mentioned sectors, *A. pullulans* has significant potential as a biotechnological tool for use in the food industry. *Aureobasidium* spp. strains are known to produce many important enzymes, such as amylase, protease, lipase, cellulase, xylanase, mannanase, and transferases, consequently, becoming an important organism in food technology [42]. In particular, endo-1,4- $\beta$ -xylanase,  $\beta$ -xylosidase, polygalacturonase, and pectin lyase for clarification of fruit pulp and juices [42]. One of the most interesting uses is in the vitivinicultural sector. *A. pullulans* is the most abundant microorganism in most grapevine environments [26] and has been observed as the most abundant genus in grape juice at the earliest stages of spontaneous fermentation [90,91]. Many studies have been conducted in order to verify the effect of this species on wine composition and fermentation. From the large spectrum of possible enzymatic activities, only pectinolytic activity has been reported in grape juice in which it has a positive effect on the colour and aroma of the wines produced from it [92]. *A. pullulans* may also affect the concentrations of volatile compounds in wines, especially terpenes [93]. Furthermore, glucoamylase and  $\alpha$ -amylase enzymes produced by *Aureobasidium* spp. have been used for starch saccharification, bread and baking processing [42].

One of the many characteristics of *A. pullulans* is its ability to reduce asparagine content in potato and wheat flour [94]. Di Francesco et al. [95] demonstrated that in fried potato chips, *A. pullulans* strain L1 reduced the acrylamide content by 83% through the consumption of free amino acids (asparagine), without having any significant effect on quality

parameters or otherwise damaging the product. The same strain has also been shown to be able to control green mould, *Trichoderma pleuroti* and *Trichoderma pleuroticola*, of the oyster mushroom, *Pleurotus ostreatus*, without affecting mushroom growth or quality [96].

Another interesting aspect strictly connected to *A. pullulans* involvement in the food industry is the production of the polysaccharide pullulan. Pullulan has many uses such as the formation of edible films for food ingredients [97], as coating of fruits and vegetables [97,98] and packaging materials [99]. It can also be used as texture stabilizer, and to intensify certain food properties [16,100]. It can also be introduced as a GRAS (Generally Recognized as Safe) ingredient in the production of low-calorie foods [100].

## 7. Future Perspectives

Although not yet fully exploited, yeasts have a great potential to be used in a number of ways in various sectors of agricultural and industrial production, and in environmental remediation. Due to its ubiquitous occurrence encompassing diverse habitats over most of the planet, *A. pullulans* probably retains the potential of a diverse array of an enormous number of as yet unexploited activities [14]. In fact, the strains adapted to extreme environmental conditions could be potential candidates for applications in various production processes undertaken in specialized extreme conditions. Moreover, we need to find resilient solutions in an attempt to resolve some of problems associated with climate change and the increasingly frequent extreme environmental conditions, particularly in the agriculture sector.

As well as discovering interesting and effective new isolates of *Aureobasidium* spp., future perspectives on this versatile microorganism should aim to verify the possibilities for its genetic recombination and diversification by sexual reproduction, in order to provide a bank of recombinant progeny, well-adapted to changing environments and conditions. In fact, crossbreeding with other yeasts provides an attractive approach that might allow sexual reproduction to generate novel yeast strains that could exhibit combinations of desirable characteristics suitable for various practical applications [101].

There remain many gaps in our knowledge of *Aureobasidium* that need to be filled. For example, many of the mechanisms underlying biocontrol and the promotion of plant growth are still unexplored. Similarly, environmental association analyses remain to be done for most, if not all, adaptive traits. Increasing our knowledge of the variation and distribution of these traits on a global scale would make it possible to target isolates and optimise crossbreeding in order to develop the diverse range of uses described in this review.

## 8. Conclusions

The present review highlights the versatility of the *Aureobasidium* genus and some of the known and unknown potential and consequent benefits that this microorganism might offer to mankind and the environment. All the potentialities of this yeast that have so far emerged are perfectly in line with the United Nations Environment Programme 2021–2030 [1]. In fact, the use of *Aureobasidium* spp. in the agricultural sector (field and postharvest) and food industry opens up new horizons in respect of the environment and human health. However, although research is travelling in the right direction, knowledge of the real potential of *Aureobasidium* spp. requires further assessment and analysis. Addressing the remaining gaps in our knowledge is of crucial importance because *Aureobasidium* spp. has the potential to become a central beneficial agent that might contribute significantly to our ambition to transition to sustainable agriculture and food production as envisioned in the European Green Deal and similar policy initiatives around the world.

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