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## EDITED BY

Akram Sadeghi,  
Agricultural Biotechnology Research Institute  
of Iran, Iran

## REVIEWED BY

Saira Ali,  
SGS (Canada), Canada  
Malek Marian,  
Agriculture, University of Trento, Italy

## \*CORRESPONDENCE

Yedir Ouhdouch  
✉ youhdouch@gmail.com

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# The potential of facultative predatory *Actinomycetota* spp. and prospects in agricultural sustainability

Manar Ibrahimi<sup>1,2</sup>, Souad Loqman<sup>3</sup>, Martin Jemo<sup>4</sup>,  
Mohamed Hafidi<sup>4,5</sup>, Laurent Lemee<sup>6</sup> and Yedir Ouhdouch<sup>4,5\*</sup>

<sup>1</sup>Laboratory of Molecular Chemistry, Materials and Catalysis, Faculty of Sciences and Technics, Sultan Moulay Slimane University, Beni-Mellal, Morocco, <sup>2</sup>Higher School of Technology Fkih Ben Salah, Sultan Moulay Slimane University, Fkih Ben Salah, Morocco, <sup>3</sup>Laboratory of Microbiology and Virology, Faculty of Medicine and Pharmacy, Cadi Ayyad University, Marrakesh, Morocco, <sup>4</sup>AgroBiosciences Program, Mohammed VI Polytechnic University (UM6P), Ben Guerir, Morocco, <sup>5</sup>Labelled Research Unit N°4 CNRST, Laboratory of Microbial Biotechnologies, Agrosociences and Environment (BioMAGe), Faculty of Sciences Semlalia, Cadi Ayyad University, Marrakesh, Morocco, <sup>6</sup>Institut de Chimie des Milieux et Matériaux de Poitiers (IC2MP–CNRS UMR 7285), Université de Poitiers, Poitiers, France

*Actinomycetota* in the phylum of bacteria has been explored extensively as a source of antibiotics and secondary metabolites. In addition to acting as plant growth-promoting agents, they also possess the potential to control various plant pathogens; however, there are limited studies that report the facultative predatory ability of *Actinomycetota* spp. Furthermore, the mechanisms that underline predation are poorly understood. We assessed the diversity of strategies employed by predatory bacteria to attack and subsequently induce the cell lysing of their prey. We revisited the diversity and abundance of secondary metabolite molecules linked to the different predation strategies by bacteria species. We analyzed the pros and cons of the distinctive predation mechanisms and explored their potential for the development of new biocontrol agents. The facultative predatory behaviors diverge from group attack “wolfpack,” cell-to-cell proximity “epibiotic,” periplasmic penetration, and endobiotic invasion to degrade host-cellular content. The epibiotic represents the dominant facultative mode of predation, irrespective of the habitat origins. The wolfpack is the second-used approach among the *Actinomycetota* harboring predatory traits. The secondary molecules as chemical weapons engaged in the respective attacks were reviewed. We finally explored the use of predatory *Actinomycetota* as a new cost-effective and sustainable biocontrol agent against plant pathogens.

## KEYWORDS

bacteria, interactions, diversity, ecology, survival mechanism, prokaryotic predation

## 1. Introduction

Cellular tropism also referred to as “cellular predation,” is a regular interspecific antagonistic that occurs in diverse living habitats. It also defines an act of a predatory organism to kill and devour a prey organism for its nutritional requirements (Pérez et al., 2016). Predation behavior expands from primitive prokaryotic microbes to highly evolved mammals in the

animal kingdom (Sinclair et al., 2003; Ripple and Beschta, 2004). Among the microorganisms, a family member of the virus, bacteria have developed predatory behaviors that are well investigated under *in vivo* and *ex vivo* conditions (Curds, 1982; Gonzalez et al., 1990; Parry, 2004). Myxobacteria and *Bdellovibrio* are  $\delta$ -*Proteobacteria* in the *bacteria* phyla with well-known bacteriophagic nature (Stolp and Starr, 1963; Casida, 1982; Berleman et al., 2006; Martins et al., 2022). Through predation attitude, *Myxobacteria*, and *Bdellovibrio* contribute to community structuring and carbon recycling in the soil food web systems and play an important ecosystem function are well-known keystone taxa (Bratanis et al., 2020; Cavallo et al., 2021; Mookherjee and Jurkevitch, 2022; Ogundero et al., 2022; Whitworth, 2022; Wu et al., 2022). Thus, bacteria species in the actinomycetes species are gram-positive and mostly studied for secondary metabolites production and were recently discovered to exert a facultative predatory role (Zeph and Casida, 1986; Hoshino et al., 2015; Ait Barka et al., 2016; Katz and Baltz, 2016; Baltz, 2019; Ouchari et al., 2019; Ibrahimi et al., 2020; Korichi et al., 2021). Studies deciphering or investigating the facultative predation role of *Actinomycetota* are gaining growing research attention (Kumbhar et al., 2014; Ibrahimi et al., 2019, 2020; Baig et al., 2021) owing to their lifestyles adjustment to adapt to complex limited resources (Ibrahimi et al., 2019, 2020) and importantly potential application to design bio-pesticides molecules/products alternatives to heavy toxic pesticides inorganic molecules (Palaniyandi et al., 2013). The approach is driven by increasing consumer demands for safe, healthy, and organically produced foods globally (Alvarez et al., 2017; Sathya et al., 2017; AbdElgawad et al., 2020). However, in the context of *Actinomycetota* species, the mechanisms that underline opportunistic predation behaviors are under-investigated (Ibrahimi et al., 2019, 2020).

Predation is a bacteria co-evolutional trait in the *Actinomycetota*, owing to adjustments in lifestyles among the species, possible geographical local adaptations, and habitat change (Jousset, 2012; Ibrahimi et al., 2020). For a long time, *Actinomycetota* were only viewed as competitive, rather than predatory organisms (Kumbhar and Watve, 2013; Kumbhar et al., 2014; Ibrahimi et al., 2020; Pérez et al., 2020). As a consequence, despite their widespread ecological importance in the environment, there are very few investigations on *Actinomycetota* predation (Bentley et al., 2002; Mawang et al., 2021; Boubekri et al., 2022; Santos-Aberturas and Vior, 2022). The first evidence of the *Actinomycetota* opportunistic predation behaviors is described in the *Streptomyces* and *Agromyces* genera (Waksman and Woodruff, 1941; Casida, 1980). The author examined the utilization of *Micrococcus luteus* as prey by *Streptomyces* species. As versatile-opportunistic *Actinomycetota*, *Streptomyces* is also a non-obligate epibiotic predator of various microorganisms, specifically, *Staphylococcus aureus*, *Escherichia coli*, *Bacillus* sp., *Pseudomonas aeruginosa*, and *Klebsiella* sp. (Kumbhar et al., 2014). In addition, It was reported in the literature that under *in vivo* conditions, *Streptomyces* isolates exhibited the predatory ability on various prey bacteria cells (Gram+, Gram-) and multidrug-resistant strains (Ibrahimi et al., 2020). The latest supportive evidence of good predatory behavior by *Streptomyces* against various types of prey is reported by Baig et al. (2021). However, studies examining the mechanisms that underline predator-prey relationships and the diversity or identity of small signal molecules are lacking (Ibrahimi et al., 2020).

Increasing plant diseases due to pathogenic microbes represent an important global constraint for agricultural production

and economic losses (Collinge and Sarrocco, 2022). Current interventions are toward the use of synthetic heavy toxic molecules pesticides for crop protection that negatively poses acute risks to human health and the environment (Rani et al., 2021). It is imperative to find alternative solutions for a sustainable crop yield (Collinge and Sarrocco, 2022). The increasing knowledge and understanding of plant-microbe interactions, in particular the predatory capability of *Actinomycetota* to design as a biopesticide product to combat plant-associated pathogenic microbes (Shivlata and Satyanarayana, 2017). The objective of the present study was to:

- a) critically review the facultative predatory mechanisms of bacteria and *Actinomycetota*;
- b) discuss the various small molecules synthesized from bacteria and *Actinomycetota* species during their opportunistic predatory lifestyle stage; and
- c) explore the potential beneficial use of *Actinomycetota* synthesized small molecules during the predation stages in the development of biocontrol agents for plant disease suppression and protection.

## 2. Mechanisms of predation by bacteria and *Actinomycetota* species

Predation by bacteria has traditionally attracted lower attention than their multicellular development or their production of bioactive compounds (Furness et al., 2020). In recent years, many aspects of bacterial predation are starting to be explored through research (Table 1). Since the purpose of a predatory bacteria is to kill and digest its prey, it remains necessary to understand the hunting and killing behavior of the predator. Most authors propose to classify bacterial hunting strategies into four general categories: epibiotic, group attack, or wolfpack, periplasmic penetration, and endobiotic predation or direct invasion (Martin, 2002; Jurkevitch, 2007; Berleman and Kirby, 2009; Pasternak et al., 2014; Pérez et al., 2016). Epibiotic is a tactic that requires close cell-to-cell proximity (Shi et al., 1993). When the predation is extracellular, the predator attached to the prey from outside does not invade either the periplasm or the cytoplasm of the prey, degrades and assimilates host molecules through specialized structures, but without penetrating the prey (Martin, 2002; Pérez et al., 2016), consuming it from the exterior before dividing into the daughter cells via binary division (Koval et al., 2013; Figure 1). *Ensifer adhaerens* (Druga et al., 2011), *Myxococcus xanthus* (Nair, 2016; Thiery and Kaimer, 2020), and *Streptomyces* (Casida, 1988; Ibrahimi et al., 2020) are some examples of epibiotic strategy. The cell-to-cell contact between the epibiotic predator and its prey is crucial for the transfer of compounds between their cells (Castelle and Banfield, 2018; Yakimov et al., 2022). As a consequence of the limited literature on culture-based investigations, our current state of understanding of the behavior of epibiotic lifestyles is relatively poor (Bor et al., 2020; Batinovic et al., 2021; Yakimov et al., 2022). However, Cross et al. (2019) suggested that to clearly demonstrate cell-to-cell contact, conditions that could enhance predator abundance to the degree that allows detailed microscopic characterization must be evaluated.

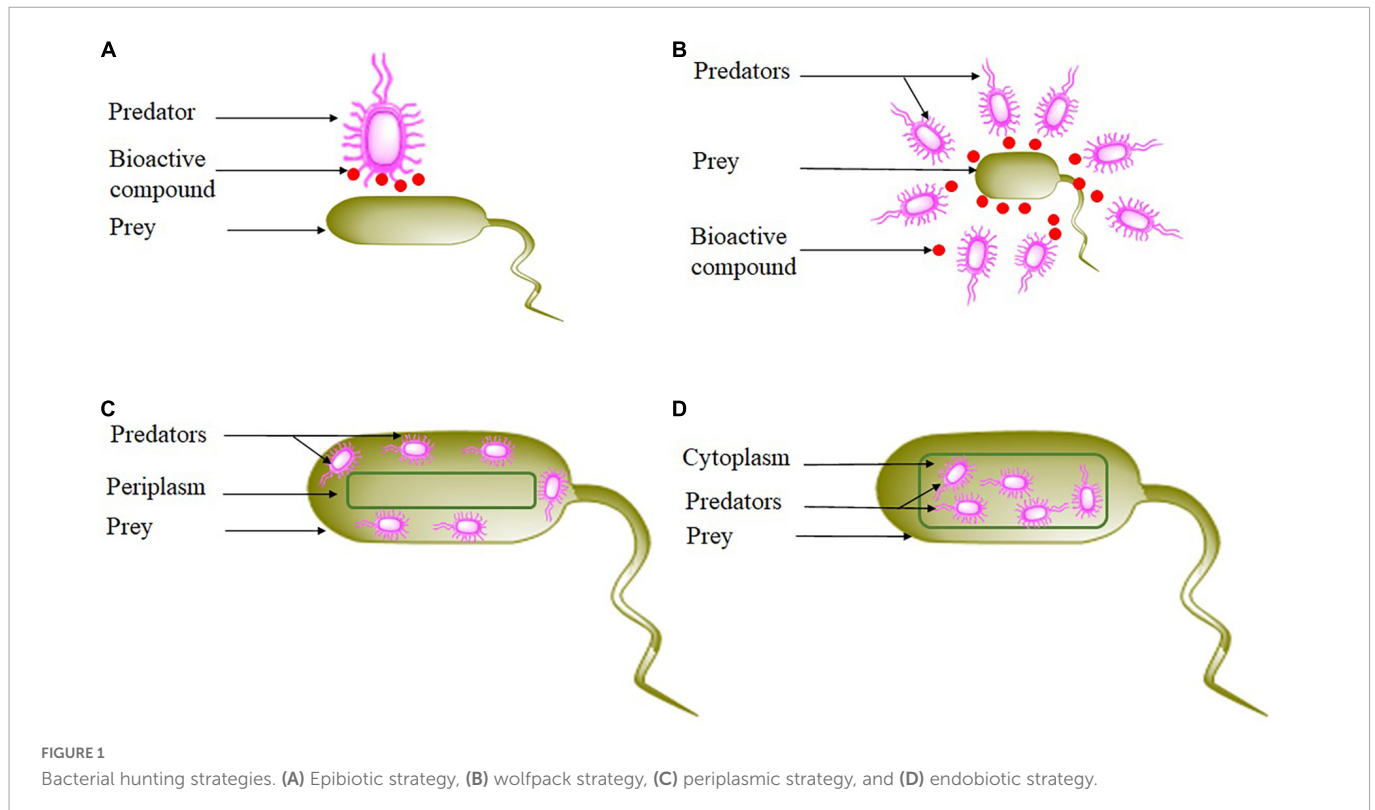
TABLE 1 Predatory bacteria and their biological activity.

Group	Known habitat	Prey Gram+	Gram–	Predatory strategy	Antibiotic production	Predation type	References
<b>α-Proteobacteria</b>							
<i>Ensifer adhaerens</i>	Soil	+		Epibiotic	Yes	Facultative	Casida, 1982; Germida and Casida, 1983; Druga et al., 2011
<i>Micavibrio</i> sp.	Soil		+	Epibiotic	No	Obligate	Davidov et al., 2006; Kadouri et al., 2007
<b>β-Proteobacteria</b>							
<i>Cupriavidus necator</i>	Soil	+	+	Epibiotic	Yes	Facultative	Makkar and Casida, 1987; Kreutzer et al., 2012
<i>Aristabacter necator</i>	Soil	+	+	Epibiotic	Yes	Facultative	Casida, 1992; Cain et al., 2003
<b>γ-Proteobacteria</b>							
<i>Lysobacter</i> sp.	Soil	+	+	Wolfpack	Yes	Facultative	Li et al., 2008; Seccareccia et al., 2015
<i>Stenotrophomonas maltophilia</i>	Soil	+	+	Epibiotic	Yes	Facultative	Ryan et al., 2009; Kumbhar and Watve, 2013
<i>Pseudomonas</i>	Soil	+	+	Epibiotic	Yes	Facultative	Casida, 1992
<b>δ-Proteobacteria</b>							
<i>Bdellovibrionales</i> (d-BALOs) <i>Bdellovibrionaceae</i> <i>Bdellovibrio</i> spp.	Soil, freshwater, sewage, marine sediments perialpine lakes, marine waters, river, estuaries, terrestrial plants, gut of animals and humans		+	Periplasmic Epibiotic	Not characterized	Obligate	Cotter and Thomashow, 1992; Fratamico and Cooke, 1996; Jurkevitch and Ramati, 2000; Jurkevitch et al., 2000; Schwudke et al., 2001; Davidov et al., 2006; Jurkevitch, 2007; Sockett, 2009; Hobley et al., 2012; Ezzedine et al., 2020
<i>Bacteriovoracaceae</i> <i>Bacteriovorax</i> sp. <i>Peredibacter</i> sp.				Periplasmic	No		
Myxobacteria	Cell contact, Soil, dung, bark, Sediments	+	+	Wolfpack	Yes	Facultative	Reichenbach and Höfle, 1993; McBride and Zusman, 1996
<b>Chloroflexi</b>							
<i>Herpetosiphon</i> sp.	Cell contact freshwater	+	+	Wolfpack	Yes	Facultative	Quinn and Skerman, 1980; Trick and Lingens, 1984; Nett et al., 2006; Kiss et al., 2011
<b>Bacteroidetes</b>							
<i>Saprospira</i> sp.	Coastal sediment Sea water	+	+	Wolfpack Epibiotic	Yes	Facultative	Furusawa et al., 2003; Saw et al., 2012
<i>Flavobacterium</i>	Marine Fresh Water	+	+		Yes	Facultative	McBride et al., 2009; Banning, 2010
<b>Actinomycetota</b>							
<i>Streptomyces</i>	Soil, marine water, marine sponge Marine water	+	+	Epibiotic Wolfpack Epibiotic	Yes	Facultative	Waksman and Woodruff, 1941; Casida, 1988; Kumbhar et al., 2014; Ibrahimi et al., 2020; Baig et al., 2021
<i>Agromyces ramosus</i>	Soil		+		Yes	Facultative	Casida, 1983; Arcamone et al., 2000; Chernyakovskaya et al., 2004
<i>Brevibacterium</i> , <i>Glutamicibacter</i> , <i>Micromonospora</i> , <i>Nocardiopsis</i> , <i>Rhodococcus</i> <i>Rothia</i>	Marine sponge	+		Epibiotic	Yes	Facultative	Baig et al., 2021

(Continued)

TABLE 1 (Continued)

Group	Known habitat	Prey Gram+	Prey Gram–	Predatory strategy	Antibiotic production	Predation type	References
<b>Bacillales</b>							
<i>Bacillus</i>	Soil		+	Epibiotic	Yes	Facultative	Gumbo et al., 2010
<i>Paenibacillus</i>	Soil Water Rhizosphere Veg. matter		+	Epibiotic	Yes	Facultative	Raza et al., 2008; Be'Er et al., 2009



The second strategy is wolfpack or group attack or group predation, predatory bacteria in this kind of predation work as a group (Marshall and Whitworth, 2019), they are assumed to hunt collectively to attack prey (Figure 1). They assemble and collectively secrete a diversity of diffusible compounds like hydrolytic enzymes and extracellular antibiotics that degrade and kill nearby bacteria. Wolfpack strategy lyse prey cells from the exterior through concerted action (Martin, 2002). Furthermore, the aim of the process of lysis is to produce small molecules that are easily assimilated by the predator (Xiao et al., 2011). Moreover, higher predatory cell densities suggest higher diffusible compounds (Keane and Berleman, 2016). The most important property of wolfpack is the lysed prey will be consumed by the predatory bacteria secreting and non-secreting (Mendes-Soares and Velicer, 2013). *Lysobacter* sp. (Hashizume et al., 2004; Li et al., 2008), *Myxobacteria* (McBride and Zusman, 1996; Thiery and Kaimer, 2020), and *Herpetosiphon* sp. (Nett et al., 2006) are examples of predatory bacteria using this strategy.

The third approach is when cells enter the prey periplasm (Figure 1). The predator invades and develops in the periplasm of gram-negative bacteria (Hobot et al., 1984; Ferguson, 1990; Ferguson et al., 1992). Predator produces hydrolytic enzymes that promote penetration and damage the prey cell wall (Lerner et al., 2012). In parallel, the infected prey is destroyed once

respiration comes to a halt and the outer membrane is damaged (Thomashow and Rittenberg, 1978). The invading predator attaches to the prey's cytoplasmic membrane and initiates growth using the cytoplasm of the prey as a nutrient supply. The predator grows like a polynucleotide filament, the length of which is dependent on the prey size (Kessel and Shilo, 1976). In the end, filaments septate into individual attack-phase cells that grow a flagellum, induce the formation of pores in the cell wall and burst into the external medium to engage in another cycle (Fenton et al., 2010). Therefore, the predator kills the prey by ingesting its cytoplasm. *Bdellovibrionales* (Jurkevitch and Davidov, 2006), *Bdellovibrio bacteriovorus*, *Bacteriovorax marinus*, *Bacteriolyticum stolpii*, and *Peredibacter starrii*, use periplasmic predation (Socket and Lambert, 2004; Pasternak et al., 2014). However, the mechanism used by predators to release their intracellular contents to achieve their original cell cycle is poorly described (Laloux, 2020).

Moreover, some predatory bacteria can utilize more than one hunting strategy, like *Bdellovibrio*, which employs the periplasmic and epibiotic strategy; also, *Myxobacteria* can use both epibiotic and wolfpack strategies.

The last category of predation includes all predators that penetrate the host cytoplasm (Figure 1). This approach is also

known as the invasion of cytoplasm or diacytotic strategy (Moulder, 1985). After the penetration, the predator grows and divides inside the cytoplasm. *Daptobacter* is the only bacteria that employ this strategy (Guerrero et al., 1986), but no other study has been reported about this group. Among predatory *Actinomycetota*, a few investigations have highlighted strategies used in predation because they have not received the level of attention of competitors (Ibrahimi, 2020). Pérez et al. (2016) suggest that bacteria secreting secondary metabolites, including *Actinomycetota*, can attack their prey in groups, which is supported by the fact that they are social prokaryotes that form and develop in multicellular structures. Correspondingly, Kumbhar and Watve (2013) reported that antibiotic producers such as *Actinomycetota* are unable to use an endobiotic strategy and direct contact with the prey is not required. Kumbhar et al. (2014) showed that *Actinomycetota* are non-obligate epibiotic predators of diverse prey such as *S. aureus*, *E. coli*, *Bacillus* spp., *Pseudomonas aeruginosa*, and *Klebsiella* spp. Recently, a study by Zeng et al. (2021) demonstrated that *Streptomyces globisporus*, a predatory *Actinomycetota*, preyed on *Microcystis* through an epibiotic mode of predation. Overall, among the phylum *Actinomycetota*, only two genera, *Agromyces* and *Streptomyces*, are known to have an epibiotic predatory behavior against other bacterial species (Casida, 1983; Arcamone et al., 2000; Ibrahimi et al., 2020). All this information allows us to believe that the predatory *Actinomycetota* can hunt their prey through wolfpack and epibiotic strategies. Therefore, our understanding of *Actinomycetota* predation is still very fragmentary, including gaps in their mechanisms of predation. Understanding these mechanisms by *Actinomycetota* species is required for better knowledge and understanding of their effect on prey structure to develop a new strategy to control plant disease and multidrug-resistant pathogens.

### 3. Identity and diversity of small molecules produced from bacteria and *Actinomycetota* during predation lifestyles

Predatory bacteria represent a diversified collection of prokaryotic organisms that have the ability to consume other bacteria (Jurkevitch, 2007). While some of these bacteria act as solitary hunters, others are known to hunt in groups in a wide mixture before they attack their prey (Martin, 2002). This predatory strategy generally implicates the production of lytic enzymes and small bioactive compounds as predatory weapons (Rosenberg and Varon, 1984; Reichenbach and Höfle, 1993; Berleman and Kirby, 2009), while genome sequencing programs of these microorganisms have revealed the presence of very broad and varied secondary metabolites (Kiss et al., 2011). Therefore, extraction and purification of antimicrobial molecules from predatory bacteria have yielded the discovery of numerous novel molecules, as illustrated by jahnellamides (Plaza et al., 2013), salimyoxins (Felder et al., 2013), cystomanamides (Etzbach et al., 2014), and precorallopyronin (Schäberle et al., 2015). It is confirmed by Xiao et al. (2011) that this variety of secondary metabolites is supposed to be involved in the death of the prey. It has been found that a defect in the production of these substances significantly affects predatory activity. In this

section, all research relative to the results of chemical studies of compounds produced by predatory bacteria will be reviewed and critically analyzed in Table 2.

Traditionally, *Actinomycetota* species are renowned for their excellent potential to produce secondary metabolites and antibiotics compounds (Hoshino et al., 2015; Ait Barka et al., 2016; Ouchari et al., 2019; Ibrahimi et al., 2020; Korichi et al., 2021). These molecules are produced to antagonize the growth of surrounding microbes (Ortiz-Ortiz et al., 2013). To date, up to 33 new secondary metabolites have been successfully isolated from 12 *Actinomycetota* through the co-culture (Hoshino et al., 2019). With their novel roles as predatory microbes, the diversity and identity of molecules produced during predation strategies should be considered an untapped source of biomolecules. A further co-culturing of predator and prey monitored for 15 days induced an increase in the total amount of methylated fatty acids biomarker of the predatory *Actinomycetota* responsible for the predation process (Ibrahimi et al., 2019). Therefore, secondary metabolites engaged in the facultative predation and antagonistic mechanism are likely to differ, from the *Actinomycetota* strain, the origin of habitat, or the ecology of isolated strains (McBride and Zusman, 1996; Jurkevitch, 2007; Octaviana, 2021).

Predatory *Actinomycetota* are mostly isolated from marine and soil environments (Kumbhar et al., 2014; Ibrahimi et al., 2020; Baig et al., 2021). They exhibit a wide range of predatory activities against diverse bacteria (Kumbhar et al., 2014; Ibrahimi et al., 2020; Baig et al., 2021). This is explained by the bioactive compound that they produce, which possess a range of antimicrobial activities. These molecules are used as a weapon by predatory *Actinomycetota* to kill their prey (Kumbhar and Watve, 2013). Recently, Baig et al. (2021) demonstrated a strong correlation between predation and enzyme inhibition, particularly trypsin and chymotrypsin inhibition, in which predatory *Actinomycetota* were found to release more enzymes in the presence of prey. On this basis, it has become apparent that *Actinomycetota* can exhibit the great potential to produce antibiotics and enzymes during predation. Also, it should be noted that, to date, no compounds produced by predatory *Actinomycetota* during predation behavior have been elucidated. Therefore, it will be interesting to conduct further studies to isolate new predatory *Actinomycetota* as well as the extraction and identification of their molecules involved in predation lifestyle.

## 4. Predatory *Actinomycetota* as an eco-friendly and promising tool in agricultural and environmental sustainability

### 4.1. Plant pathogens

Recent years have been marked by an expanding array of virulent infectious diseases caused by pests which are increasingly recognized as presenting a worldwide threat to food security (Olsen et al., 2011; Bosso et al., 2015; Hartmann, 2022). In addition, the extensive use of agrochemicals molecules has led to the development of bacterial resistance, causing significant risks to the environment and human health (Ebele Mbachu et al., 2022). Consequently, providing food for the world's population without disrupting the

environmental balance is becoming eminent (Pandit et al., 2022). It is highly recommended to provide sustainable solutions for agriculture (Jamiołkowska, 2020). Microbes are an alternative to agrochemical molecules like synthetic pesticides for controlling plant pathogens (Elnahal et al., 2022). Different microorganisms are used as biocontrol agents, such as bacteria, fungi, and *Actinomycetota* (Table 3). Direct antagonism and predation are the possible modes of action of biocontrol agents to eliminate plant parasites (Ebele Mbachu et al., 2022).

Predatory bacteria can be used as alternative applications in biological control (Olanya and Lakshman, 2015; Swain et al., 2017). Most of the *Bacillus* strains can control the plant pathogen as *Fusarium* fungi (Ongena and Jacques, 2008). *Bdellovibrio* also attacks a large variety of different plant pathogens (Baer et al., 2000;

Jurkevitch et al., 2000; Dwidar et al., 2012). In addition, a very promising result in the control by *Bdellovibrio* of *Pseudomonas glycinea* blight of soybean was demonstrated by Scherff (1973). Recently, Ye et al. (2020) demonstrated the use of the *Myxobacterium Corallococcus coralloides* to control cucumber *Fusarium* wilt by migrating to the plant root and regulating the soil microbial community.

In the case of *Actinomycetota*, several investigations showed their successful ability to function as biocontrol agents against plant pathogens (Goudjal et al., 2014; Braga et al., 2016; Ebrahimi-Zarandi et al., 2022). The co-cultivation of *Actinomycetota* with other microorganisms generates several new secondary metabolites, which are not present during pure culture conditions (Scherlach and Hertweck, 2009; Sung et al., 2017;

TABLE 2 Secondary metabolites from different predatory bacteria and their biological activity.

Predatory Bacteria	Product	Chemical Formula	Biological activity	References
<i>Aristabacter necator</i>	<i>Banegasine</i>	C <sub>11</sub> H <sub>12</sub> N <sub>2</sub> O <sub>2</sub>	Potentiate the antimicrobial activity of pyrrolnitrin	Cain et al., 2003
	Pyrrolnitrin	C <sub>10</sub> H <sub>6</sub> Cl <sub>2</sub> N <sub>2</sub> O <sub>2</sub>	Anti-fungal, anti-bacterial	
	<i>Maculosin</i>	C <sub>14</sub> H <sub>16</sub> N <sub>2</sub> O <sub>3</sub>	Potentiate the antimicrobial activity of pyrrolnitrin	
<i>Herpetosiphon</i> sp.	(+)-O-methylkolavelool	C <sub>20</sub> H <sub>34</sub> O	Anti-bacterial	Nakano et al., 2015
	Auriculamide	C <sub>17</sub> H <sub>24</sub> ClNO <sub>4</sub>	Antibiotic properties are still open	Schieferdecker et al., 2015
	Siphonazole	C <sub>25</sub> H <sub>25</sub> N <sub>3</sub> O <sub>6</sub>	Not reported	Nett et al., 2006
<i>M. xanthus</i> DK1622	Myxalimid B	C <sub>25</sub> H <sub>40</sub> NO <sub>3</sub>	Yeasts and Gram-positive bacteria	Gerth et al., 1983
	Myxochelin A	C <sub>20</sub> H <sub>25</sub> N <sub>2</sub> O <sub>7</sub>	Anti-bacterial and antitumoral activity	Kunze et al., 1989; Miyana et al., 2006; Krug et al., 2008
	Myxovirescin A1	C <sub>34</sub> H <sub>60</sub> NO <sub>8</sub>	Bactericidal	Gerth et al., 1982; Xiao et al., 2012
	Myxochromide A3	C <sub>45</sub> H <sub>64</sub> N <sub>7</sub> O <sub>9</sub>	Not reported	Korp et al., 2016
	DKxanthene-534	C <sub>29</sub> H <sub>34</sub> N <sub>4</sub> O <sub>6</sub>	Antioxidative activity	Meiser et al., 2006; Wenzel and Müller, 2009
	Myxoprincomide	C <sub>45</sub> H <sub>76</sub> N <sub>10</sub> O <sub>16</sub>	Not reported	Cortina et al., 2012
<i>Myxococcus fulvus</i> Mxf50	Myxopyronins A	C <sub>23</sub> H <sub>31</sub> NO <sub>6</sub>	Anti-bacterial activity	Kohl et al., 1983
	Myxopyronins B	C <sub>24</sub> H <sub>33</sub> NO <sub>6</sub>		
<i>Streptomyces althioticus</i> <i>Myxococcus Virescens</i> <i>M. xanthus</i> <i>Cystobacter fuscus</i>	Althiomycin	C <sub>16</sub> H <sub>17</sub> N <sub>5</sub> O <sub>6</sub> S <sub>2</sub>	Anti-bacterial activity	Fujimoto et al., 1970; Kunze et al., 1982
<i>Myxobacterium</i>	Gulmirecin B	C <sub>22</sub> H <sub>34</sub> O <sub>9</sub>	Anti-bacterial activity	Schieferdecker et al., 2014
<i>Myxobacterium Pyxidicoccus fallax</i> HKI 727	Gulmirecin A	C <sub>27</sub> H <sub>42</sub> O <sub>1</sub>	Anti-bacterial activity	Schieferdecker et al., 2014
<i>Cystobacter</i> sp.	Cystobactamids 919-2	C <sub>25</sub> H <sub>29</sub> N <sub>3</sub> O <sub>7</sub>	Anti-bacterial activity	Baumann et al., 2014
	Cystobactamids 919-1	C <sub>46</sub> H <sub>45</sub> N <sub>7</sub> O <sub>14</sub>	Anti-bacterial activity	Baumann et al., 2014
<i>Coralloccoccus coralloides</i>	Precorallopyronin A	C <sub>29</sub> H <sub>39</sub> NO <sub>7</sub>	Not reported	Korp et al., 2016
	Corallopyronins A	C <sub>30</sub> H <sub>41</sub> NO <sub>7</sub>	Block specifically eubacterial RNA polymerase	Irschik et al., 1985
	Corallopyronins C	C <sub>30</sub> H <sub>41</sub> NO <sub>7</sub>		
	Corallopyronins B	C <sub>31</sub> H <sub>43</sub> NO <sub>7</sub>		
<i>Lysobacter</i> spp.	Lysobactin	C <sub>58</sub> H <sub>97</sub> N <sub>15</sub> O <sub>17</sub>		
<i>Myxobacterium Enhygromyxa salina</i>	Salimyxin A	C <sub>21</sub> H <sub>30</sub> O	Anti-bacterial activity	Felder et al., 2013
	Salimyxin B	C <sub>21</sub> H <sub>32</sub> O		

Wakefield et al., 2017; Shin et al., 2018; Vikeli et al., 2019; Yu M. et al., 2019). Indeed, the production of secondary metabolites in co-culture is enhanced by competitive or antagonistic interactions (Ibrahimi et al., 2020). For example, the co-cultivation of the *Streptomyces coelicolor* with the agricultural pathogen *Aspergillus niger* has activated the actinorhodin silent pathway in *Actinomycetota* (Wu et al., 2015).

Prior research suggests that *Actinomycetota* in co-culture can inhibit pathogens' growth, decrease, and degrade toxins. For example, a recent investigation demonstrated that coculturing *Streptomyces roseolus* with the phytopathogen *Aspergillus flavus* could reduce the

contamination generated by the mycotoxin aflatoxin B1, which is produced by *A. flavus* (Caceres et al., 2018). In addition, several *Streptomyces* strains showed the ability to inhibit *Aspergillus flavus* growth and decrease and degrade mycotoxin (Verheecke et al., 2015; Campos-Avelar et al., 2021). Another field that seems promising for the use of *Actinomycetota* in agriculture is their function as eco-friendly biofertilizers since they are involved in nutrient management, soil quality, decomposing of organic matter, enhancing plant growth promoting, recycling organic residues, and activating plant immune responses (Shivlata and Satyanarayana, 2017; Boubekri et al., 2022; Ebrahimi-Zarandi et al., 2022).

TABLE 3 Predatory bacteria application.

Predatory bacteria	Pathogen	Application	References
<i>Bacillus</i>	Bacteria, fungi and oomycetes	Biocontrol against phytopathogens, including bacteria, fungi and oomycetes	Ongena and Jacques, 2008
	<i>Fusarium fungi</i>	Biocontrol agent of <i>Fusarium</i> head blight of wheat	Schisler et al., 2002
	Phytophthora species such as <i>P. capsica</i>	Biocontrol agent for <i>P. capsica</i> pathogenic fungi	Douillet, 2003
<i>Bacteriovorax</i> spp.	<i>Vibrio vulnificus</i> and <i>Vibrio parahaemolyticus</i>	Reduced <i>Vibrio</i> sp. populations	Richards et al., 2012, 2013
<i>Bdellovibrio bacteriovorus</i>	<i>Pseudomonas aeruginosa</i> and <i>Staphylococcus aureus</i>	Reduced <i>S. aureus</i> (periplasmic on Gram-negative and epibiotic on Gram-positive).	Iebba et al., 2014
	<i>Staphylococcus aureus</i>	Reduced biofilm formation	Monnappa et al., 2014
	Multidrug resistant Gram-negative bacteria	Reduced biofilm formation	Kadouri et al., 2013
	Gram-negative foodborne pathogens and spoilage bacteria	Lysed foodborne and spoilage bacteria	Fratamico and Whiting, 1995
	<i>Salmonella enterica</i> <i>Klebsiella pneumoniae</i> <i>Escherichia coli</i> <i>Enterobacter</i>	Biocontrol agent to treat urban wastewater treatment	Jafarian et al., 2020
	Microbial biomass in sludge	Alteration of the microbial community composition of activated sludge flocs and granules	Feng et al., 2017
<i>Bdellovibrio bacteriovorus</i>	<i>Pseudomonas tolaasii</i>	Reduced bacterial cells <i>in vitro</i> and blotch severity on pile of mushroom at post-harvest	Saxon et al., 2014
	Shrimp pathogens <i>V. cholerae</i>	Biocontrol agent in freshwater farming industry as a biological control	Cao et al., 2015, 2019
	<i>Alcaligenes</i> , <i>campylobacter</i> , <i>Erwinia</i> , <i>Escherichia</i> , <i>Helicobacter</i> , <i>Pseudomonas</i> , <i>Legionella</i> , and <i>Shigella</i>	Biocontrol agent	Markelova, 2010
	<i>Escherichia coli</i>	Lyse gram-negative foodborne pathogenic and spoilage bacteria Novel antibody-modulating tools	Fratamico and Whiting, 1995; Bratanis et al., 2017; Bratanis and Lood, 2019
<i>Lysobacter enzymogenes</i>	<i>Bipolaris sorokiniana</i>	Role in fungal plant disease control	Li et al., 2008
<i>Myxobacteria</i>	<i>Cylindrocarpon</i> spp., <i>Fusarium oxysporum</i> sp. <i>apii</i> , <i>Phytophthora capsici</i> , <i>Pythium ultimum</i> , <i>Rhizoctonia</i> spp., <i>Sclerotinia minor</i> . .	Plant pathogenic fungi	Bull et al., 2002
<i>Pseudomonas fluorescens</i>	<i>Tobacco necrosis virus</i>	Biocontrol agent against phytopathogens	Maurhofer et al., 1998
<i>Micavibrio aeruginosavorus</i> and <i>B. bacteriovorus</i>	Gram-negative bacteria: <i>Pseudomonas aeruginosa</i> and <i>Escherichia coli</i>	Biocontrol agent against phylogenetic bacteria	Dashiff et al., 2011
<i>Streptomyces griseoflavus</i> EMM111 <i>Streptomyces coelicoflavus</i> EMM112 <i>Streptomyces mutabilis</i> EMM183 <i>Streptomyces champavatii</i> EMM184	<i>Micrococcus luteus</i> , <i>Staphylococcus aureus</i> (native and methicillin-resistant) <i>Escherichia coli</i> (native and ampicillin-resistant)	Biocontrol agent against multidrug-resistant bacteria	Ibrahimi et al., 2019, 2020
<i>Brevibacterium</i> , <i>Glutamicibacter</i> , <i>Micromonospora</i> , <i>Nocardioopsis</i> , <i>Rhodococcus</i> and <i>Rothia</i>	<i>Acetobacter pasteurianus</i> <i>Alcaligenes fecalis</i> <i>Bacillus subtilis</i> <i>Enterobacter fecalis</i> , <i>Escherichia coli</i> <i>Klebsiella pneumoniae</i> <i>Micrococcus luteus</i> <i>Mycobacterium smegmatis</i> <i>Proteus vulgaris</i> <i>Pseudomonas aeruginosa</i> <i>Salinicoccus roseus</i> <i>Salmonella enterica</i> <i>Serratia marcescens</i> <i>Staphylococcus aureus</i>	Biocontrol agent against pathogenic bacteria	Baig et al., 2021

Using predatory *Actinomycetota* in co-culture may be a potential biocontrol agent and biofertilizer used in agriculture. Indeed, the plant can benefit on several different levels. It was reported in the literature that the co-cultivation of *Streptomyces* with the phytopathogenic fungus *Sclerotinia sclerotiorum* induces the deformation and fragmentation of the fungal mycelium through the production of hydrolytic enzymes and secondary metabolites (Liu et al., 2019). In parallel, the same study linked the promotion of plant growth through the solubilization of inorganic phosphate and the production of 1-aminocyclopropane-1-carboxylate deaminase and indole acetic acid by the *Actinomycetota* (Liu et al., 2019).

The predation of gram-negative and gram-positive bacteria by *Actinomycetota* may enhance their potential application for the biocontrol of foodborne and plant pathogens (Ibrahimi et al., 2019, 2020). Thus, predatory *Actinomycetota* can provide an ecologically sustainable solution for agricultural farming. This is explained by the fact that they will not increase the accumulation of antibiotics in the environment, which may generate antibiotic resistance (Pérez et al., 2020).

## 4.2. Cyanobacterial bloom

Cyanobacterial bloom can produce toxic molecules called cyanotoxins in freshwater (Saraf et al., 2018). The presence of such molecules can affect the functionality of ecosystems and water quality for recreation, drinking water, fisheries, and agriculture (O'Neil et al., 2012; Corbel et al., 2014). In the agriculture field, several publications have appeared in recent years documenting the bioaccumulation of cyanotoxins in plants used for human and animal food (Corbel et al., 2014; Machado et al., 2017; Ai et al., 2020; Melaram et al., 2022). Consequently, several physical, chemical, and biological strategies were deployed to control cyanobacterial bloom (Jia et al., 2018; Sun et al., 2018; Yu Y. et al., 2019; El Amrani Zerrifi et al., 2020). Although the physic-chemical techniques represent a high cost, the risk of contamination and toxicity to humans has limited their general use (Moreira et al., 2014). Whereas biological techniques involving microorganisms have attracted researchers for their promising eco-friendly tools and high potential (Yu Y. et al., 2019).

One of the most promising aspects is the use of microbes of predatory bacteria as a control agent of cyanobacterial blooms. However, despite some initial promising discoveries, this field has been almost completely ignored. The first predatory bacteria able to lyse various species of cyanobacteria was first reported in 1967 (Shilo, 1967). Since then, numerous strains of lytic gliding bacteria, mainly members of the *Myxobacteria* and *Cytophaga* groups, have been isolated (Daft and Stewart, 1971; Granhall and Berg, 1972; Gumbo et al., 2008) and lysed cyanobacteria cells by attachment and secretion of diffusible lytic substances. These bacteria produce a variety of different exoenzymes capable of hydrolyzing the cyanobacterial cell wall (Sudo and Dworkin, 1972; Gnosspeilius, 1978). Subsequently, Rashidan and Bird (2001) isolated two strains of *Cytophaga* sp., with lytic activity on different cyanobacteria with a restricted host range. The same study showed that the lysis of cyanobacteria by predatory bacteria may be an important factor in their population dynamics in lakes and may contribute to the prevention or the sudden disappearance of cyanobacteria blooms and draw attention to the possibilities of using host-specific lytic bacteria in biological

control of harmful cyanobacterial blooms (Rashidan and Bird, 2001).

Furthermore, *Bdellovibrio* and *Myxococcus* have received a lot of investigation as predators of cyanobacterial bloom (Bauer and Forchhammer, 2021). In contrast, the use of *Actinomycetota* as a predator is still broadly uncharacterized. However, recently Zeng et al. (2021) demonstrated the use of a predatory *Actinomycetota* to face harmful cyanobacterial algal blooms. The research demonstrated that *Streptomyces globisporus* could predate *Microcystis aeruginosa* via cell-to-cell contact with high algicidal activity (Zeng et al., 2021). The present findings confirm the use of predatory *Actinomycetota* as promising eco-friendly tools to combat harmful cyanobacteria blooms. Also, further investigations are highly recommended to assess the predation toward cyanobacteria. In addition, it is necessary to recognize the predatory *Actinomycetota*-cyanobacteria ratio due to their important role as a key to achieving effective lysis of cyanobacteria.

## 5. Future perspectives and conclusion

Nowadays, one of the most alarming world wild problems is the increase of plant diseases caused by pathogenic bacteria, which causes great economic, environmental, and human health damage. Therefore, finding alternative and sustainable solutions to confront these pathogens represent one of the biggest challenges. In this review, we suggest the use of predatory *Actinomycetota* as an effective biocontrol agent. Predation is an important cause of mortality and determines the structure and activity of microbial communities in both terrestrial and aquatic ecosystems, with a complex process involving several components such as prey finding, recognition, consumption, and digestion. The literature has concentrated largely on the presence of predatory *Actinomycetota* and their effective activity against a panel of pathogenic microorganisms but has not examined the mechanisms of the prey lysis. Indeed, a good knowledge of the predation mechanism used by predatory *Actinomycetota* is essential to improve the efficiency of the lysis of the prey cells and predation performance. The application of predatory *Actinomycetota* in large-scale systems and field experiments must be examined to determine if there will be ecological consequences. Furthermore, it is suggested that research evaluating predators' efficiency should include molecular viability assays, such as EMAqPCR and EMA-Illumina, to determine the efficacy of treatment. Finally, during this review, we noticed that antibiotics produced during the process of predation by predatory *Actinomycetota* are demonstrated but have not yet been identified. Consequently, it seems advisable to discover such compounds. In the future, actinobacterial predation could be a new approach to control plant pathogen, cyanobacterial blooms; however, intensive research efforts are required to pursue this aim.

## Author contributions

MI wrote the manuscript. YO and MJ refining and critical reading of the manuscript. LL, SL, and MH revised the manuscript. All



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## Conflict of interest

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