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Genome Analysis Reveals Diversity and Functional Potential of Novel *Janthinobacterium* Species From Subarctic Soils

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ABSTRACT

The Arctic tundra and boreal forest regions are affected by ongoing climate change, leading to increased warming, increased plant production, and heightened microbial activity. Microbes play a key role in carbon release from stored soil organic matter, and characterizing their diversity and function in high-latitude soils is thus of significant interest. The Pseudomonadota are abundant and diverse members of high-latitude soils. Here, we describe two novel species of the genus *Janthinobacterium*, of the order *Burkholderiales*, isolated from tundra heath and northern boreal forest soils. The isolates are aerobic, chemoorganotrophic psychrophiles and are well-adapted to the subarctic climate conditions. Phylogenomic analyses and ANI values confirmed the novelty of the strains, designated as *Janthinobacterium silvisoli* sp. nov. K2Li3 and *Janthinobacterium saanense* sp. nov. S3T4. Genome analysis revealed that the new species have the metabolic potential for degradation of complex carbon and polyphenols, which are abundant in tundra heath and lichen-dominated, nutrient-poor forest soils. The strains are well-adapted to nitrogen-limited soil ecosystems and can scavenge nitrogen from both organic and inorganic sources. Additionally, the strains harbor secondary metabolite gene clusters that encode antimicrobial compound production, potentially enhancing their competitiveness in the subarctic environment. The comparative pangenome analysis indicated that the strains have unique gene clusters for carbohydrate transport and metabolism, and energy generation and conservation. The genome-based functional exploration enhances our understanding of this genus and how environmental conditions may shape the functionality and interactions of *Janthinobacterium* species in subarctic soil ecosystems.

1 | Introduction

The Arctic is warming at a rapid rate due to global climate change, which increases the air temperature considerably, and it is expected that the warming rate will be up to four times more than the global mean temperature in the coming years (Stroeve et al. 2025). In many regions, such as Fennoscandia, the climate is warming, especially during winter months (Mikkonen et al. 2015), and in general, precipitation in the form of rain instead of snow is expected to increase (Mikkonen et al. 2015; Bintanja and Andry 2017). The Fennoscandian part of the Arctic region, which includes the Scandinavian Peninsula (Norway and Sweden) and Finland, is experiencing climate change-driven alteration in the vegetation structure and nutrient dynamics. The rise in temperatures, increased rainfall, and a longer growing season are facilitating the northward extension of shrubs and tree species, leading to changes in ecosystem composition and functioning (Elmendorf et al. 2012; Bjorkman

et al. 2018; Stark et al. 2023; Maliniemi et al. 2025). Changes in vegetation can affect both the quality and amount of organic matter that enters soils, leading to subsequent impacts on the diversity and abundance of microbial communities, carbon cycling processes, and the availability of nutrients (Vozzo et al. 2025). Moreover, variations in snow cover and the soil freeze–thaw dynamics are affecting microbial activity and the rates of nutrient mineralization (Sorensen et al. 2018; L. Liu et al. 2023). The ecological responses of microbial communities in this area appear to be strongly connected to the evolving interactions among plants, soil, and microbes. Therefore, understanding the behavioral and ecological roles of microbial species in the climate-changing Fennoscandian environment is of utmost importance.

The Arctic tundra and forest soils are composed of diverse bacterial communities primarily from the phyla Pseudomonadota, Actinomycetota, Bacteroidota, Acidobacteriota, and Verrucomicrobiota (Malard et al. 2019). Within these phyla, Pseudomonadota comprises approximately 25%–30% of the overall bacterial abundance (Wong et al. 2023; Männistö et al. 2024). Members of the Pseudomonadota include phototrophs, heterotrophs, and lithotrophs, and they play vital roles in nutrient cycling, carbon and nitrogen fixation, and the breakdown of organic matter (Kersters et al. 2001; Degli Esposti 2018). The genus *Janthinobacterium* of the family Oxalobacteraceae within the Pseudomonadota, consists of aerobic, motile, rod-shaped, chemoorganotrophic, and psychrotolerant organisms. The genus currently comprises 26 species, of which 23 have validly published names (Parte et al. 2020; https://lpsn.dsmz.de/). *Janthinobacterium* species have been isolated and described from various locations, including glacier ice, aquatic habitats (Ambrožič Avguštin et al. 2013; Gong et al. 2017; Lu et al. 2020; Inan et al. 2023; Park et al. 2023; Yang et al. 2026), trout (Jung et al. 2021), diseased mushrooms (Lincoln et al. 1999), soils (Shoemaker et al. 2015; Wu et al. 2017), and sediments (McTaggart et al. 2015), indicating a diverse distribution.

Janthinobacterium spp. are mostly chemoorganotrophic, which suggests that they are actively involved in the degradation of organic matter (Gillis and De Ley 2006). Most of these strains also synthesize violacein and other pigments that have antiparasitic, antimicrobial, and antioxidant properties (Wu et al. 2021). Moreover, they are psychrotolerant organisms and are commonly found in cold environments (Ambrožič Avguštin et al. 2013; Kumar et al. 2018; Rajawat et al. 2019; Yang et al. 2026). Despite their chemoorganotrophic and psychrotolerant nature, they are understudied in Fennoscandian soils, and little is known about their ecological function and diversity. The current study reports on five new *Janthinobacterium* strains belonging to two new species of the genus that were isolated from Fennoscandian tundra heath and forest soils. Genome-based functional analysis was done to examine the metabolic potential and ecological functions of these strains. Moreover, to gain insight into the ecological significance of the Fennoscandian strains, a pangenome comparative analysis was performed with other *Janthinobacterium* strains isolated from different habitats. The study aims to extend the knowledge about the diversity and functional differences of *Janthinobacterium* strains in subarctic tundra heath and boreal forest soils.

2 | Materials and Methods

2.1 | Strain Isolation

Janthinobacterium strains were isolated from soil samples obtained from two ecosystem types: Arctic–alpine tundra soils from Mt. Saana, Kilpisjärvi (69°01′ N, 20°50′ E), and forest soil from an oligotrophic lichen-dominated Scots pine forest located in Kätkäsuvanto (68°08′ N, 23°21′ E) in Finnish Lapland. Sample collection and isolation are described in more detail by Männistö and Häggblom (2006). Strains K2Li3, K2E3, and K2C7 originated from the Scots pine forest. Soil was sampled in September 2001 from fenced enclosures that have prevented reindeer grazing, and the ground vegetation is dominated almost exclusively by a dense mat of *Cladonia stellaris* lichen (Stark et al. 2010). Strains S3M3 and S3T4 were isolated from tundra soil samples collected in August 2001 from an altitude of 960 m on Mt. Saana, Kilpisjärvi (Männistö and Häggblom 2006). As the aim was to isolate a diverse collection of bacterial strains, several media were used for isolation. Strains K2Li3, K2C7, and S3T4 were isolated on media containing lichenin, cellulose, or starch as carbon sources, respectively, while strains S3M3 and K2E3 were isolated on media containing moss extract or a combination of soil, moss, and lichen extracts, respectively. The media are described in detail in Männistö and Häggblom (2006). After isolation, the strains were maintained on R2A agar (pH 7.0).

2.2 | Phenotypic and Fatty Acid Methyl Ester Analysis

The utilization of different carbon sources by the novel *Janthinobacterium* spp. was tested using Biolog PM1 plates (Biolog Inc., Hayward, CA). After inoculation, the Biolog plates were incubated at 20°C for 7 days, and growth was determined by measuring optical density at 600 nm and by observing the dye color change. The temperature growth profile was determined by growing the isolates on R2A (Dfico) agar plates (pH 6) for 2 weeks at 4°C–34°C. The pH growth profile was determined by growing the isolates in GY (50 gL^{-1} glucose, 10 gL^{-1} yeast extract) medium broth at a pH range of 4–10 (in 0.5 pH unit increments) in 96-well plates.

The total fatty acids were extracted and methylated from the bacterial isolates grown on R2A agar plates (pH 6) at 20°C using a previously described method (Männistö and Häggblom 2006). The fatty acid methyl esters were separated by an Agilent 6890 Series Gas Chromatography System equipped with an HP-5MS column with helium as the carrier gas and analyzed using a 5973 Mass Selective Detector (Santa Clara, CA). Fatty acid methyl esters were identified by their retention times (Equivalent chain length, ECL, values) and mass spectra.

2.3 | Genome Sequencing and Assembly Generation

The genomes of the five *Janthinobacterium* strains from the subarctic soils (K2Li3, S3T4, K2C7, K2E3, and S3M3) were previously sequenced by the US Department of Energy Joint Genome Institute (Genomic Sequencing of Core and Pangenomes of Soil and Plant-associated Prokaryotes) using an

Illumina NovaSeq S4 sequencer, and assembled using SPAdes v3.13.0 assembler, with the draft genomes available in the JGI Genome Portal (Table S1). Strains S3T4 and K2Li3 were re-sequenced to close the genome assemblies. The DNA from the bacterial isolates was extracted using the DNeasy UltraClean Microbial Kit (Qiagen) following the manufacturer's protocol. The genomic library for strains S3T4 and K2Li3 was prepared using the MinION Rapid Sequencing Kit (SQK-RAD004) and sequenced on a MinION-Mk1C with an R9.4 flow cell. The raw pod5 reads generated from the MinION sequencer were base-called and demultiplexed in high accuracy mode using Dorado basecaller v0.4.3. The genome assembly using MinION reads for strains K2Li3 and S3T4 was constructed using the Trycycler tool v0.5.4 (Wick et al. 2021) by employing Flye v2.9.3 (Kolmogorov et al. 2019), Minipolish v0.1.3 (Wick and Holt 2021), and Raven v1.8.3 (Vaser and Šikić 2021) assemblers at default settings. The assemblies were further polished using Medaka v1.11.1, Polypolish v0.5.0 (Wick and Holt 2022), and POLCA tool v4.1.0 (Zimin and Salzberg 2020) using Illumina short-read sequences of the isolate genomes available via the JGI Genome Portal (Table S1). The assembly quality was determined by using CheckM v1.2.2 (Parks et al. 2015) and QUAST tools v5.2.0 (Gurevich et al. 2013).

2.4 | Genome Analysis

The genome assemblies of the tundra and forest soil *Janthinobacterium* strains were analyzed using the DRAM v1.5 tool (Shaffer et al. 2020) to gain insight into the metabolic functions carried out by the strains. Further, the secondary metabolites encoded by the strains were predicted using the antiSMASH v7 (Blin et al. 2023), and the polyphenol degradation ability was assessed using the CAMPER tool (McGivern et al. 2024). The nitrogen and sulfur cycling genes in the genome were predicted by the NCycDB (Tu et al. 2019) and SCycDB (Yu et al. 2021) databases, respectively. Further, the additional annotation of the subarctic *Janthinobacterium* genomes was performed using the Bacterial and Viral Bioinformatics Resource Center (BV-BRC) online platform (Olson et al. 2023). The carbohydrate degradation potential of the *Janthinobacterium* strains was evaluated by employing the dbCAN3 server (Zheng et al. 2023).

2.5 | Phylogenetic, Phylogenomic, and Pangenome Analysis

The 16S ribosomal RNA (rRNA) gene sequence was extracted from the genome assemblies of the strains using the Barrnap v0.9 tool, aligned with other *Janthinobacterium* species, and a maximum likelihood phylogenetic tree was constructed using MEGA-11 (Tamura et al. 2021) with 1000 bootstrap replications. The Phylogenomics tree was prepared using UBCG v3 (Na et al. 2018) and the RAxML tools (Stamatakis 2014). The average nucleotide identity (ANI) values were calculated using the OrthoANI tool (Yoon et al. 2017).

The pangenome analysis of the subarctic isolates was performed by comparing them with other publicly available *Janthinobacterium* strains (complete or contig-level) from different environments using the anvi'o v8 tool (Eren et al. 2021), following a previous method (Delmont and Eren 2018). A contig database of all the strains was constructed and annotated with COGs, KEGG, tRNA-scan, and single-copy core gene (SCG)-taxonomy databases. The pangenome was calculated by employing NCBI-BLAST and Markov Cluster algorithm (Van Dongen and Abreu-Goodger 2012) at an inflation value of 6. Further, the core and unique genes in the strains were evaluated using the anvi-compute-functional-enrichment-in-pan command.

3 | Results and Discussion

3.1 | Novel *Janthinobacterium* Species From Tundra and High-Latitude Forest Soil

Janthinobacterium strains were isolated from tundra heath and boreal forest soil samples using different carbon substrate combinations (Männistö and Häggblom 2006). Initial analysis of partial 16S rRNA sequences indicated that these were members of the genus *Janthinobacterium* (Figure S1). The genomes of the subarctic *Janthinobacterium* strains (K2Li3, S3T4, K2C7, K2E3, and S3M3) were sequenced previously using an Illumina NovaSeq S4 sequencer and assembled using SPAdes v3.13.0 assembler. The Illumina-based assemblies were not complete (assembly quality and statistics are given in Table S2). Following the phylogenetic analysis, one representative strain from each group (K2Li3 and S3T4) was resequenced using the Oxford Minion, and the complete closed genomes of both strains were assembled (Table S2). The nanopore-based genome sequences enabled complete circular genome assembly of the *Janthinobacterium* strains S3T4 and K2Li3, with completeness of 98.73% and 98.45% and contamination of 5.01% and 3.32% at the genus level, respectively.

A phylogenomic tree comparing the subarctic strains with other members of the *Janthinobacterium* genus is presented in Figure 1. The tree shows the separation of the subarctic strains into two new groups, separate from other described species of the genus *Janthinobacterium*. Strains K2Li3, K2C7, and K2E3 from forest soil form one cluster, while strains S3T4 and S3M3 from tundra soil form the other. A phylogenomic tree of the subarctic strains and all strains of the *Janthinobacterium* genus with available genomes is shown in Figure S2. The calculated ANI values between the described *Janthinobacterium* species and strains K2Li3 and S3T4 were below the threshold value used for species delineation (Figure S3). The combined phylogenomic and ANI analysis clearly indicates that strains K2Li3, K2C7 and K2E3, and S3T4 and S3M3, respectively, represent two novel species of the *Janthinobacterium* genus. Here we describe two novel species of the genus *Janthinobacterium* with their respective type strains, for which we propose the names *Janthinobacterium silvisoli* sp. nov. (strains K2Li3^T, K2E7, and K2C7) and *Janthinobacterium saanense* sp. nov. (strains S3T4^T and S3M3).

3.2 | Phenotypic Characteristics of *Janthinobacterium* Isolates

The different carbon sources utilized by the novel *Janthinobacterium* isolates are listed in Table S3. The strains were able to utilize L-arabinose, D-galactose, D-trehalose, D-xylose, D-ribose, D-fructose, α-D-glucose, maltose, sucrose, maltotriose, L-galactonic, acid-γ-lactone, and D-galacturonic acid. The

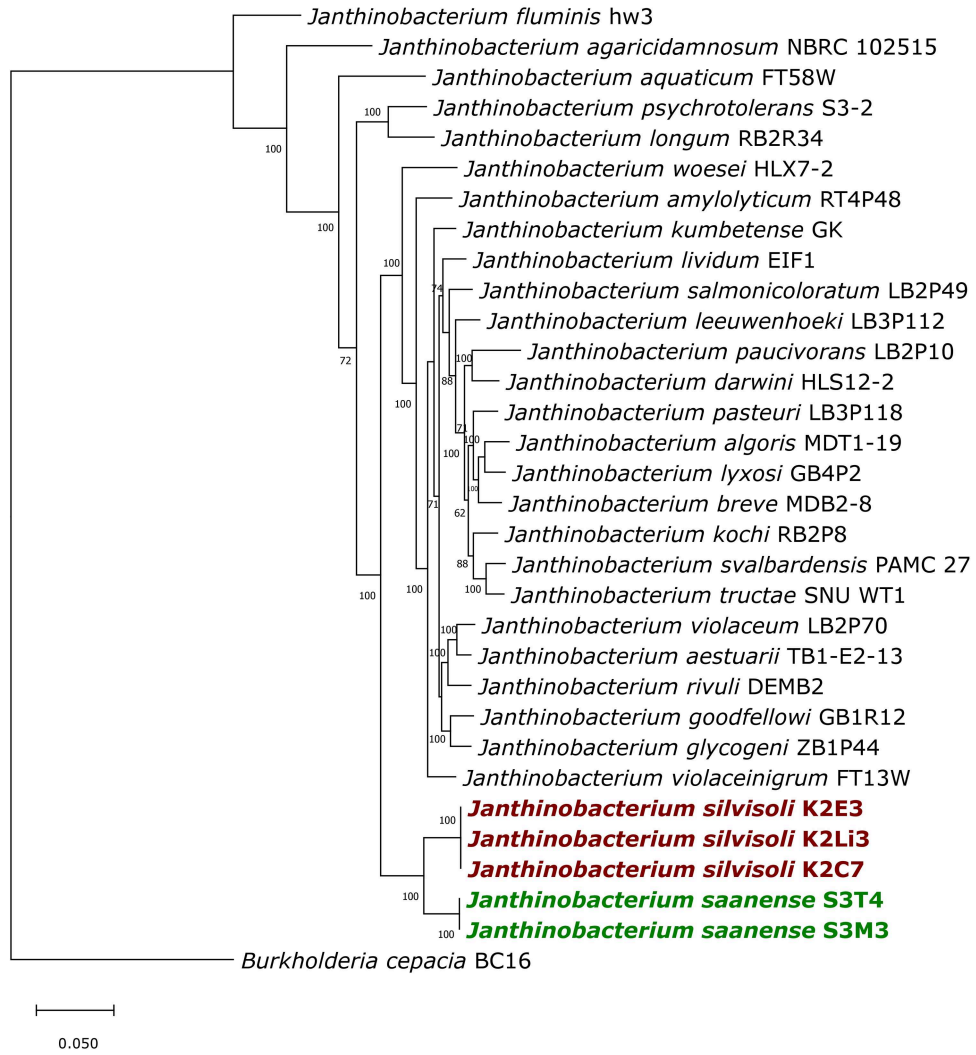

FIGURE 1 | Maximum likelihood phylogenomics tree of the subarctic isolates and type strains of described *Janthinobacterium* species. The tree was prepared with the UBCG v3 tool (by taking 92 core genes) employing RAxML with bootstrap values of 1000 replications, shown at the branch point. Values below 50 are not shown. *Burkholderia cepacia* BC16 was used as an outgroup. The scale bar corresponds to the number of nucleotide substitutions per site.

isolates grew at a pH range of 6–9 and a temperature range of 4°C–35°C. Cellular fatty acid composition analysis after growth on R2A agar at 20°C indicated that C16:0, C17:1 ω10c, C16:1 ω7c, C12:0, and C10:0 3-OH were the main fatty acids present in the K2Li3 and S3T4 strains, which were also observed in the other described *Janthinobacterium* species (Table S4).

3.3 | Novel *Janthinobacterium* Strains Are Complex Carbon and Polyphenol Degraders

The novel *Janthinobacterium* isolates were evaluated for their carbohydrate degradation ability using the dbCAN3 tool. The analysis of the genomes showed that tundra and forest *Janthinobacterium* species have the potential for degradation of a wide range of complex carbohydrates, such as exopolysaccharides, lignin, peptidoglycan, starch, xylan, cellulose, chitin, chitosan, and pectin (Figure 2A). Subarctic Fennoscandian soils contain a vast pool of organic carbon that is composed of carbohydrates, phenols, carboxylic acids, and peptides (Frossard et al. 2021). Most of this carbon pool originates from plant litter in the form of cellulose, hemicellulose, and pectin (Pushkareva et al. 2020). Previously, the psychrotolerant heterotrophic *Janthinobacterium* strains isolated from the subarctic sites showed cellulose hydrolytic ability (Männistö and Häggblom 2006). In another study, members of the phylum Pseudomonadota were found active in the degradation of complex carbon, such as cellulose, pectin, chitin, and lignin, in alpine peatland (Yan et al. 2022). The novel *Janthinobacterium* isolates show the potential for breakdown of these complex carbohydrates, which may account for their distribution in these soils and their role in carbon cycling. Moreover, there was a difference in the abundance/distribution of CAZymes between the *Janthinobacterium* strains based on their source of isolation, suggesting a link between microbial functional potential and environmental origin. Strains isolated from forest soils exhibited a greater number of pectin-degrading enzymes compared with those from tundra soils, likely reflecting adaptation to the differing input of organics in these environments. The higher pectinase content in forest-derived strains is consistent with the greater abundance of pectin-rich plant material in forest ecosystems, whereas the relatively sparse vegetation in tundra soils may result in lower

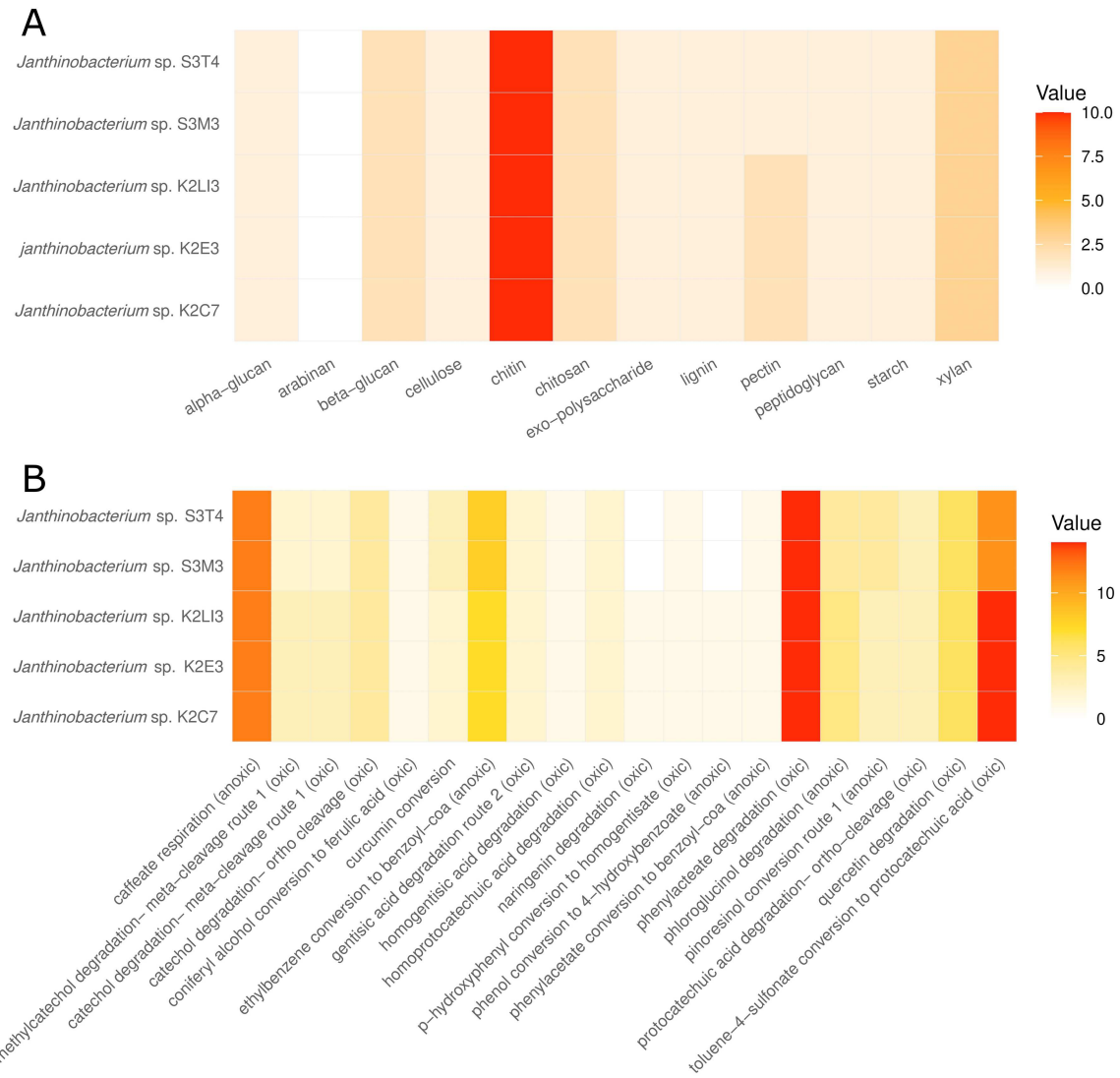

FIGURE 2 | Carbohydrate degradation (A) and polyphenol degradation (B) potential of novel *Janthinobacterium* isolates. The carbohydrate degradation potential of the isolates was determined using the dbCAN3 server, while the polyphenol degradation ability was predicted using the CAMPER tool. The heatmap's gradient values indicate gene copy number.

selective pressure for pectin degradation. These findings suggest that local vegetation and soil composition play an important role in shaping the enzymatic repertoire of soil-dwelling microorganisms.

The subarctic tundra and forest ecosystems are dominated by ericaceous shrubs and other vegetation that are a rich source of phenolic compounds (Eskelinen et al. 2009). The understory vegetation in the coniferous forest site was dominated by the ericaceous shrub *Empetrum nigrum* and *C. stellaris* lichen, which produce polyphenol-rich litter and secondary metabolites (Tybirk et al. 2000; Stark et al. 2007), which may either support or inhibit the soil microbiota. Therefore, *Janthinobacterium* species were evaluated for polyphenol degradation ability. The analysis shows that the *Janthinobacterium* strains have the potential for hydrolysis of a variety of polyphenols, such as phenylacetic acid, caffeic acid, ethylbenzene, toluene, naringenin, quercetin, curcumin, catechol, phloroglucinol, and homoprotocatechuic acid (Figure 2B). Earlier studies suggest that the subarctic shrubs *Betula nana*, *E. nigrum*, and *Salix arctica* synthesize phenolic compounds, including catechin, naringenin, quercetin, and catechol (Hansen et al. 2006; Deslippe and Simard 2011; Väisänen et al. 2013; Curtasu and Nørskov 2024). The abundance of polyphenols in the subarctic heath soils likely drives the prevalence of genes encoding polyphenol degradation in *Janthinobacterium* species. There were differences in the abundance of different polyphenol-degrading enzymes between the forest and tundra *Janthinobacterium* strains (Figure 2B). *Janthinobacterium* strains from forest sites (K2Li3, K2E7, and K2C7) showed higher abundance/distribution of toluene, phloroglucinol, naringenin, catechol, and 4-methylcatechol-degrading enzymes. In contrast, the tundra strains (S3T4 and S3M3) showed a higher occurrence of curcumin and pinoresinol-degrading enzymes. Polyphenols such as catechol and 4-methylcatechol have been reported in previous studies where they were synthesized and released into soil by native plant communities found in boreal forests (Komenda and Koppmann 2002; Hakola et al. 2017; Purser et al. 2021). The differential abundance of polyphenol-degrading enzymes among *Janthinobacterium* strains isolated from forest and tundra environments suggests a strong

influence of local environmental conditions and available organic substrates on microbial functional potential. This discrepancy highlights potential unknown metabolic pathways or substrate analogs in subarctic environments and underscores the need for further chemical and ecological characterization of soil organic matter. Overall, these findings suggest that the habitat-specific chemical landscapes shape the selection of particular strains/species and emphasize the importance of integrating microbial and environmental data in ecosystem studies.

3.4 | Novel *Janthinobacterium* Isolates Harbor Stress Response Proteins and Varied Energy-Generation Strategies

The cold, harsh subarctic ecosystem affects the growth and survival of organisms. Microbes adopt several ways to endure and survive in such conditions. The *Janthinobacterium* strains in the current study harbor genes for cold, heat, osmotic, and oxidative-stress responses (Figure 3A). Genes for cold and heat-shock proteins protect bacterial cells from temperature fluctuations (Zhang and Gross 2021). Moreover, choline uptake, betaine synthesis clusters, and EnvZ and OmpR regulons were observed, which can protect cells from osmotic stress (Sleator and Hill 2002). The potential for biosynthesis of glutathione and other proteins that protect cells from reactive oxygen species was also observed. In addition to stress response proteins, the isolates harbor genes for proteins and enzymes required for DNA damage repair (Figure 3A). The *Janthinobacterium* isolates possess response proteins that suggest they can survive in the subarctic ecosystem, characterized by nutrient-limited and cold conditions with periodic temperature fluctuations.

The novel *Janthinobacterium* isolates appear to adopt several strategies for energy generation in the extreme subarctic habitat. In addition to the central carbon metabolism pathways including glycolysis, TCA cycle, and pentose phosphate pathways, alternative pathways like an anaerobic module of the TCA, Entner–Doudoroff pathway, glycolate, glyoxylate interconversions, gluconeogenesis, and so forth, were present in the genome (Figure 3B). The fermentation routes for energy generation, such as acetoin, butanediol metabolism, lactate, and mixed acid fermentation, were observed in the genomes. The presence of diverse energy-generating pathways in the genomes suggests that the strains do not depend solely on central carbon metabolism pathways for energy for growth and survival. In a previous study, examining the effect of freeze–thaw cycles on tundra soil bacteria (Männistö et al. 2009) *Janthinobacterium*/*Herbaspirillum* spp. were found in high relative abundance in the rRNA-derived community profiles. These declined in relative abundance during laboratory microcosm incubation and appear to be quite transient. From these data, we concluded that *Janthinobacterium* spp. represent copiotrophic bacteria with fast turnover of their biomass/ribosomes. Combined, these data further underscore the adaptability and growth strategies of *Janthinobacterium* species in the subarctic ecosystem.

3.5 | *Janthinobacterium* Isolates Show Potential for Growth in Nitrogen and Sulfur-Deficient Tundra and Forest Soil

Subarctic soils have low nitrogen content, which limits microbial growth (X. Y. Liu et al. 2018; Stark et al. 2023). Microbes adapt in different ways to nitrogen-limited conditions, such as increasing inorganic nitrogen uptake and utilization efficiency or using alternative nitrogen sources (Geisseler et al. 2010). Hence, the nitrogen metabolism pathways in the novel *Janthinobacterium* isolates were explored. The NCyc database analysis showed diverse nitrogen uptake and metabolism mechanisms in the subarctic isolates (Table 1). The strains showed the potential to scavenge nitrogen from organic matter through degradation or from inorganic compounds, such as nitrates. The *Janthinobacterium* strains harbored genes responsible for

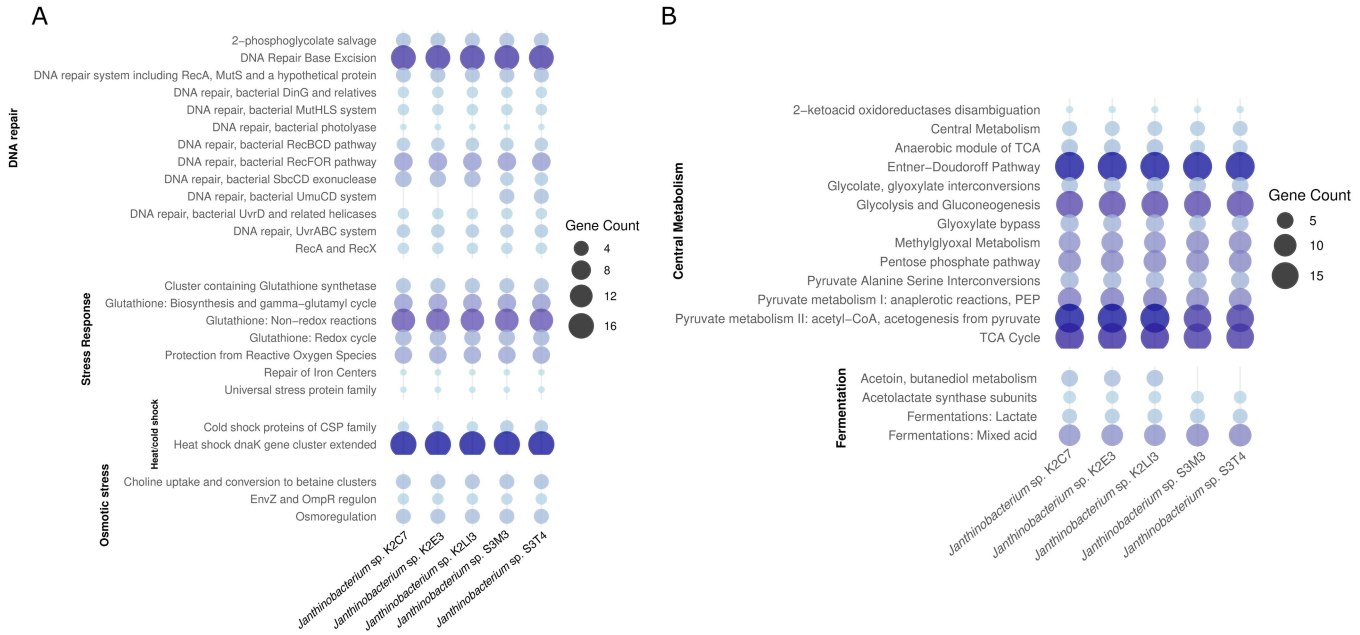

FIGURE 3 | Stress response proteins (A) and energy generation pathways (B) identified in *Janthinobacterium* strains.

TABLE 1 | Marker genes identified for nitrogen metabolism across subarctic *Janthinobacterium* strains utilizing the NCyc database.

Strains						
Marker genes and functions		***Janthinobacterium saanense* S3T4**	***J. saanense* S3M3**	***Janthinobacterium silvisoli* K2Li3**	***J. silvisoli* K2E3**	***J. silvisoli* K2C7**
Organic degradation and synthesis						
ansB	Glutamin-(asparagin-)ase	1	2	2	2	2
asnB	Glutamin-(asparagin-)ase	2	2	2	2	2
gdh_K00261	Glutamate dehydrogenase (NAD(P)+)	2	2	2	2	2
gdh_K00262	Glutamate dehydrogenase (NADP +)	1	1	2	2	2
gdh_K15371	Glutamate dehydrogenase	2	2	2	2	2
glnA	Glutamine synthetase	7	7	10	10	9
glsA	Glutaminase	2	2	2	2	2
gs_K00265	Glutamate synthase (NADPH/NADH) large chain	1	1	1	1	1
gs_K00266	Glutamate synthase (NADPH/NADH) small chain	3	3	3	3	3
nmo	Nitronate monooxygenase	6	5	5	4	5
ureA	Urease subunit gamma	1	1	1	1	1
ureB	Urease subunit beta	1	1	1	1	1
ureC	Urease subunit alpha	2	0	2	2	2
Denitrification						
napA	Periplasmic nitrate reductase NapA	1	1	0	0	0
narJ	Nitrate reductase molybdenum cofactor assembly chaperone	2	2	2	1	2
nirB	Nitrite reductase (NADH) large subunit	2	2	3	3	3
nirD	Nitrite reductase (NADH) small subunit	2	2	2	2	2
nirK	Nitrite reductase (NO-forming)	2	1	1	1	1
nosZ	Nitrous-oxide reductase	0	1	1	1	0
nrfC	Protein NrfC	1	1	1	1	1
Assimilatory nitrate reduction						
narB	Assimilatory nitrate reductase	1	1	1	1	1

(Continues)

TABLE 1 | (Continued)

Strains						
Marker genes and functions		***Janthinobacterium saanense* S3T4**	***J. saanense* S3M3**	***Janthinobacterium silvisoli* K2Li3**	***J. silvisoli* K2E3**	***J. silvisoli* K2C7**
nasA	Assimilatory nitrate reductase catalytic subunit	2	2	2	2	2
NR	Nitrate reductase (NAD(P)H)	3	3	4	4	4

Note: The genes for nitrification (amoA, amoB, amoC, hao, nxrA, and nxrB), denitrification (napB, napC, narG, narH, narI, nirS, norB, norC, narZ, narY, narV, and narW), assimilatory nitrate reduction (nasB, nirA, and narC), nitrogen fixation (anfG, nifD, nifH, nifK, and nifW), and anammox (hzo, hzsA, hzsB, hzsC, and hdh) were not found in the strains.

organic nitrogen degradation (a*nsB*, *asnB*, *gdh*, *glnA*, *glsA, gs_K00265*, and *gs_K00266*), indicating that nitrogen can be assimilated through the breakdown of organic compounds. Moreover, genes for urea metabolism (*ureA*, *ureB*, and *ureC*) were present, releasing nitrogen as ammonia, which can be utilized by microbes. Further, the assimilatory nitrate reduction genes (*narB*, *nasA*, and NAD(P)H nitrate reductase) were detected, suggesting inorganic nitrogen utilization by the *Janthinobacterium* isolates. The denitrification pathways were incomplete, suggesting *Janthinobacterium* species are not actively involved in releasing nitrogen from the tundra and forest soils. Nitrogen fixation genes were not observed in the strains, suggesting the strains were not involved in nitrogen fixation in the subarctic soils. The analysis suggests that *Janthinobacterium* isolates can obtain nitrogen from both organic and inorganic sources, supporting their growth in nitrogen-poor subarctic soils.

The subarctic tundra and forest soils remain frozen for most of the year, limiting nutrient availability in the soil; therefore, the sulfur assimilation pathways were also explored. The SCyc database analysis suggested diverse pathways for sulfur uptake and usage in *Janthinobacterium* isolates (Table S5). The genes for the assimilatory sulfate reduction pathway were prominent in the *Janthinobacterium* isolates, suggesting efficient sulfate utilization for biosynthesis and supporting growth in sulfur-limited environments. The dissimilatory sulfur reduction and oxidation pathway was incomplete, suggesting that the isolates do not use sulfur for energy generation. The isolates have the potential to utilize inorganic and organic forms of sulfur and have transporters for sulfur acquisition. In summary, the isolates possess a variety of mechanisms for sulfur acquisition, enabling them to thrive in environments where sulfur is limited.

3.6 | Genome Analysis of *Janthinobacterium* Strains Shows Their Potential for Bioactive Compound Synthesis and Antimicrobial Resistance

Microbes can synthesize secondary bioactive molecules that help them survive and grow in their natural environment (Davies and Ryan 2012). These metabolites can have antimicrobial activity, which inhibits the growth of other microbes, or may have some defense properties (Keswani et al. 2020). The *Janthinobacterium* isolates were explored for the presence of bioactive secondary metabolites using antiSMASH v7. The results showed that they have gene clusters for the synthesis of metabolites like Linear azole-containing peptides (LAP), non-alpha poly-amino acids like e-Polylysin (NAPAA), ribosomally synthesized and post-translationally modified peptides (RiPP), Lanthipeptide-class-iv and terpene (Figure 4A). LAPs, NAPAA, and RiPP are a group of peptides with antimicrobial activity (Travin et al. 2019; Ongpipattanakul et al. 2022; Zhu et al. 2023). Most *Janthinobacterium* species are violet due to the production of violacein, an indole that has antimicrobial and antioxidative activities (Wu et al. 2021). The indole biosynthetic gene cluster was absent in subarctic *Janthinobacterium* isolates, so their colonies are not violet, but they do harbor gene clusters with potential for the synthesis of other secondary metabolites with potential antimicrobial activity. Gene clusters for the synthesis of antimicrobial compounds in the novel *Janthinobacterium*

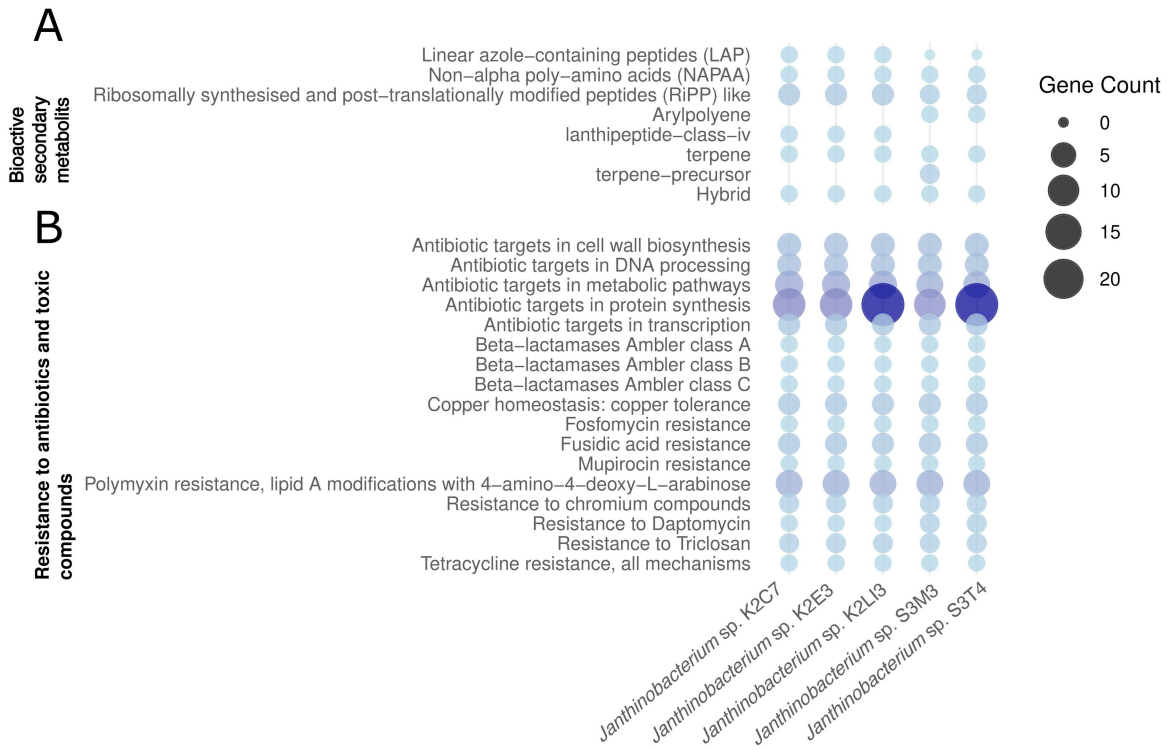

FIGURE 4 | Secondary metabolite gene clusters (A) and genes for antibiotic and toxic compound resistance (B) in subarctic tundra and forest *Janthinobacterium* strains.

isolates suggest a role in their competitiveness with other organisms in the subarctic soils.

Soil is the habitat for a diverse group of microbes that interact and compete for their survival and growth. Many microbes synthesize antimicrobial/antibiotic compounds to resist or inhibit other microbes in their habitat (Spagnolo et al. 2021). A range of antibiotics and resistance traits among Arctic microorganisms have been revealed (McCann et al. 2019; Fang et al. 2024). Therefore, the *Janthinobacterium* strains were examined for the presence of antimicrobial/antibiotic resistance genes in their genomes. The BV-BRC annotation of the isolates shows potential resistance of the *Janthinobacterium* strains to diverse antimicrobial compounds (Figure 4B) that target vital cellular functions, such as cell wall and protein synthesis and transcription. The strains were also predicted to be resistant to antimicrobial/antibiotic compounds, such as fosfomycin, fusidic acid, mupirocin, daptomycin, triclosan, and tetracycline. These antimicrobial resistance traits may contribute to the proliferation and prevalence of the *Janthinobacterium* strain in subarctic environments.

3.7 | Pangenome Comparison of *Janthinobacterium* Isolates Highlights Both Shared and Unique Genetic Traits

The tundra and forest soil *Janthinobacterium* strains were compared with other published and public genomes using Anvio. The pangenome analysis of the five subarctic isolates compared with 39 other *Janthinobacterium* species and strains revealed 27,228 gene clusters with 232,909 genes (Figure 5). There were 701 SCG clusters with 32,169 genes present in all genomes. The unique gene clusters in the *Janthinobacterium* isolates were explored to determine any differential functions performed by the isolates from subarctic soils. The evaluation of the unique gene clusters based on the COG category shows that they are involved in post-translational modification, protein turnover, chaperones, energy production and conversion, signal transduction mechanisms, intracellular trafficking, secretion, and vesicular transport (Table 2). The COG functions for the unique gene clusters revealed proteins, such as carbohydrate-selective porin, which facilitates the transport of carbohydrates across the cell membrane (Wylie and Worobec 1995), as well as thiol-disulfide isomerase/thioredoxin that help in proper protein folding and maintain intracellular redox homeostasis (Anjou et al. 2024). Thioredoxin also helps in oxidative and nitrosative stress response, signal transduction, and regulating metabolism (Anjou et al. 2024). The unique gene cluster also encodes the cytochrome c biogenesis protein that helps in respiratory electron transport and metabolic pathways (Stevens et al. 2011). The AraC-containing cupin protein superfamily was observed in the subarctic isolates that function in carbon metabolism and stress responses (Dunwell et al. 2000). Additionally, the unique gene clusters also encode adenylate cyclase that synthesizes cyclic AMP, which further controls cellular activities like carbon source utilization and stress responses (Donovan et al. 2013). The KOfam-based functional annotation of the unique gene cluster revealed differential functions of the subarctic strains, such as a suppressor for copper-sensitivity, polyamine oxidase, and high-affinity Mn^{2+} porin. Previously, it has been shown that Arctic and subarctic regions have an abundance of copper ions (Skierszkan et al. 2024), and higher metal abundance causes slow litter degradation because of lower microbial growth due to metal toxicity (Sarneel et al. 2020). The presence of copper ion transporters in the novel *Janthinobacterium* strains would make them resistant to copper

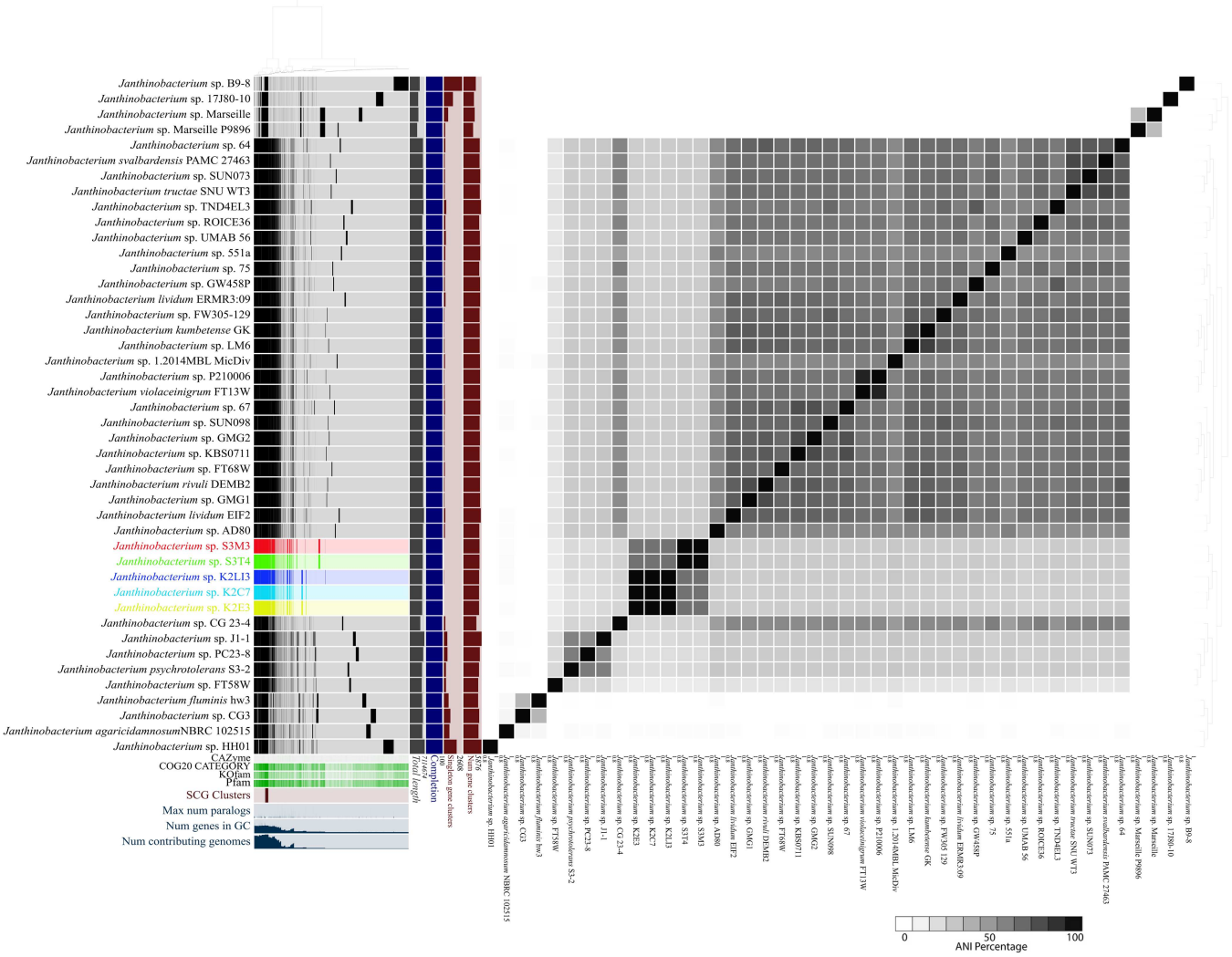

FIGURE 5 | Pangenome analysis of subarctic *Janthinobacterium* strains alongside other selected members of the genus isolated from various habitats. Comparison of gene clusters between the assembled subarctic soil isolate genomes and known *Janthinbacterium* spp. Each row designating a *Janthinobacterium* strain starts with information on the presence of gene clusters (gene clusters are marked by the darker-colored regions within the row). This is followed by the columns indicating levels of genome total length, completion, singleton gene clusters, and number of gene clusters. The heatmap illustrates the average nucleotide identity (ANI) among the strains.

toxicity and which further supports their growth in these soils. Additionally, KEGG module-based annotation of the unique gene clusters shows the presence of ceramide and sphingosine biosynthesis in *Janthinobacterium* strains. Ceramide and sphingosine have diverse physiological functions in bacteria, like inducing sporulation, bacteriophage protection, and predation (Stankeviciute et al. 2022). In summary, the novel *Janthinobacterium* isolates have unique gene clusters that may help in stress response, carbohydrate transport and metabolism, predation, as well as energy generation and conservation.

The core and shared gene clusters and their functions were also explored among the *Janthinobacterium* strains. The shared gene functions include central carbon metabolism pathways, such as the TCA cycle, glycolysis, glyoxylate cycle, pentose phosphate pathway, Entner–Doudoroff pathway, and electron transport complexes (Figure S4). The genes for essential and aromatic amino acids biosynthesis, nucleotide biosynthesis, beta-lactam and multidrug resistance, as well as NAD synthesis, were present in all the genomes. Additionally, the genes to synthesize compounds such as biotin, heme, isoprenoid, cobalamin, molybdenum cofactor, tetrahydrofolate, and ubiquinone were observed in all the *Janthinobacterium* strains. The necessary genes required for growth and metabolism, like carbon, nucleotide, and amino acid metabolism, coenzyme biosynthesis, were observed in the core genomes of *Janthinobacterium* strains, specifying their adaptability and abundance in different sites.

4 | Conclusions

Climate change-driven alteration in the vegetation structure and nutrient dynamics is affecting the quality and quantity of soil organic matter in tundra and boreal forest soil, leading to subsequent impacts on the diversity and abundance of microbial communities, carbon cycling processes, and the availability of nutrients. This study describes two new species of *Janthinobacterium* from subarctic tundra heath and boreal forest soils. The genome-based functional analysis of these new species suggests that they play a role in degrading complex carbon and

TABLE 2 | Unique gene clusters and their functions predicted by COG20 and KEGG modules in the subarctic *Janthinobacterium* isolates. The gene clusters include functions, such as stress response, carbohydrate transport and metabolism, predation, and energy generation and conservation.

	Enrichment score	Adjusted *q* value	Accession	Gene clusters IDs
COG20 function				
Carbohydrate-selective porin OprB	36.0	0.02	COG3659	GC_00006630, GC_00026065
Thiol-disulfide isomerase or thioredoxin (TrxA), Cytochrome c biogenesis protein CcdA	36.0	0.02	COG0526!!!COG0785	GC_00006223
AraC-type DNA-binding domain and AraC-containing proteins, Predicted enzyme of the cupin superfamily	25.1	0.27	COG2207!!!COG3450	GC_00007862
Adenylate cyclase, DNA-binding transcriptional regulator DnrI/AfsR/EmbR	16.3	0.73	COG2114!!!COG3629!!! COG3899!!!COG3903	GC_00009837
COG20 category				
Posttranslational modification, protein turnover, chaperones, energy production, and conversion	36.0	0.01	O!!!C!!!O	GC_00006223
Signal transduction mechanisms, Transcription	16.3	0.65	T!!!K!!!R!!!R	GC_00009837
Signal transduction mechanisms, intracellular trafficking, secretion, vesicular transport, and extracellular structures	10.3	1	T!!!U!!!W	GC_00008188
KOfam				
Suppressor for copper-sensitivity B	44.0	0.01	K08344	GC_00006774
Polyamine oxidase [EC:1.5.3.17 1.5.3.-]	44.0	0.01	K17839	GC_00006657
High-affinity Mn2+ porin	36.0	0.01	K16080	GC_00006630, GC_00026065
KEGG module				
Ceramide biosynthesis, Sphingosine biosynthesis	10.3	1	M00094!!!M00099	GC_00008169

polyphenols. Additionally, the presence of stress response proteins in the genome indicates their potential for adaptation to the cold and harsh subarctic climate. The tundra heath and boreal forest soils are nitrogen-limited, and to survive in these conditions, the *Janthinobacterium* strains show the potential to assimilate nitrogen from both organic and inorganic sources. These strains also show potential for resistance mechanisms to a variety of antibiotics and other toxic compounds present in the soil or released by other organisms. Furthermore, they harbor secondary metabolite gene clusters with potential antimicrobial activity, which may enhance their survival in these habitats. The comparative genome analysis indicated that they have unique gene clusters for stress responses, carbohydrate transport and metabolism, and energy generation and conservation. The genome-based analysis of the *Janthinobacterium* species elucidated their potential roles in carbon degradation and the release of stored carbon from subarctic tundra and forest soils.

4.1 | Description of *J. saanense* sp. nov

J. saanense (sa.a.nen'se. N.L. neut. adj. *saanense* pertaining to Mount Saana, Finland, from where the species was isolated).

Cells are Gram-negative, nonmotile, aerobic rods. Colonies are white when grown on R2A agar. Growth occurs at 4°C–35°C and pH 6–9. The major cellular fatty acids are C16:0, C17:1 ω10c, C16:1 ω7c, C12:0, and C10:0 3-OH. The DNA G + C content determined from the genome sequence of the type strain is 60.2%. The type strain is S3T4^T (= DSMZ 120996 = HAMBI 3823) isolated from tundra soil on Mount Saana, Kilpisjärvi, Finland (69°01′ N, 20°50′ E). NCBI accession numbers for the 16S rRNA gene sequence of the type strain are PX226026, and the IMG Project ID for the genome assembly is Gp0453383.

4.2 | Description of *J. silvisoli* sp. nov

J. silvisoli (sil.vi.so'li. L. fem. n. *silva*, forest; L. neut. n. *solum*, soil; N.L. gen. neut. n. *silvisoli*, of forest soil).

Cells are Gram-negative, nonmotile, aerobic rods. Colonies are white when grown on R2A agar. Growth occurs at 4°C–35°C and pH 6–9. The major cellular fatty acids are C16:0, C17:1 ω10c, C16:1 ω7c, C12:0, and C10:0 3-OH. The DNA G + C content determined from the genome sequence of the type strain is 59.72%. The type strain is K2Li3^T (= DSMZ 121001 = HAMBI 3838) isolated from soil from an oligotrophic lichen-dominated Scots pine forest located in Kätkäsuvanto (68°08′ N, 23°21′ E) in Finnish Lapland. NCBI accession numbers for the 16S rRNA gene sequence of the type strain PX226025 and the IMG Project ID for the genome assembly are Gp0453385.

Author Contributions

Anil Kumar: conceptualization, methodology, investigation, formal analysis, data curation, visualization, writing – review and editing. **Minna Männistö:** conceptualization, methodology, investigation, review and editing, project administration, resources. **Lee J. Kerkhof:** investigation, supervision, review and editing, resources. **Max M. Häggblom:** conceptualization, review and editing, supervision, project administration, resources.

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Ethics Statement

The authors have nothing to report.

Conflicts of Interest

None declared.

Data Availability Statement

Type strains are deposited in the German Collection of Microorganisms and Cell Cultures (DSMZ) and the University of Helsinki HAMBI Culture Collection. IMG Taxon IDs and NCBI accession numbers for the newly assembled *Janthinobacterium* genomes are *J. silvisoli* K2Li3, 2849242232, GCA_014200695.1 (Project ID Gp0453385); *J. silvisoli* K2C7, 2849236846, GCA_014200685.1; *J. silvisoli* K2E3, 2849247614, GCA_014200725.1; *J. saanense* S3T4, 2849231242, GCA_014200675.1 (Project ID Gp0453383); and *J. saanense* S3M3, 284922563 GCA_014200645.15. Accession numbers for 16S rRNA genes are *J. silvisoli* K2Li3, PX226025; *J. silvisoli* K2C7, NZ_JACHCJ010000019; *J. silvisoli* K2E3, NZ_JACHCL010000016; *J. saanense* S3T4, PX226026; and *J. saanense* S3M3, NZ_JACHCH010000008.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.
Kumar et al_Janthinobacterium_Supplementary Data.