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Forest Disturbance Drives Changes in the Functional Traits of Soil Bacteria: A Metagenomic Study of Kauri (*Agathis australis*) Forest Ecosystems

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ABSTRACT

The native old-growth kauri (*Agathis australis*) forests of Aotearoa New Zealand are increasingly threatened by multiple ecological disturbances, including biodiversity loss, historical deforestation and disease outbreaks. Soil microbial communities play a central role in maintaining forest ecosystem functioning and facilitating recovery following disturbance, yet their responses to disturbance in kauri forests remain poorly understood. This study investigated how soil bacterial communities respond to contrasting historical disturbance regimes across nine kauri forests. We hypothesised that greater forest disturbance intensity would be associated with reduced microbial diversity and functional capacity, with potential consequences for microbial contributions to soil ecosystem processes and forest resilience. Using shotgun metagenomics, we assessed differences in bacterial taxonomic diversity, functional gene diversity, average genome size and predicted growth rates in soils collected from forests spanning low-to-high disturbance intensities. The most pronounced shifts in soil bacterial communities were observed in the most intensively disturbed forest, Kaiaraara. Soil bacterial communities from Kaiaraara Forest were consistent outliers, having the lowest predicted growth rates, functional gene diversity, carbon-degrading gene abundance and most distinct taxonomic composition. Soils from Kaiaraara Forest also had unusually low organic matter and near-neutral pH–abiotic conditions atypical of kauri forests – which likely contributed to these differences. Predicted growth rates of soil bacterial communities remained stable across disturbance levels, declining only at the most severely disturbed forest site of Kaiaraara. Our results revealed contrasting effects of forest disturbance on taxonomic diversity versus functional capacity: bacterial taxonomic diversity was highest in the least- and most-disturbed forests, while average bacterial genome size – a proxy for functional capacity – peaked in intermediately disturbed sites. Overall, our findings highlight how forest disturbance alters both the structure and function of kauri soil bacterial communities. These insights are critical for evaluating the resilience of kauri forests to future environmental pressures.

1 | Introduction

Native old-growth forests support a wide range of critical ecosystem roles and functions, storing vast amounts of above-and-belowground carbon (C) (Zhou et al. 2006; Luyssaert et al. 2008; Watson et al. 2018), providing vital habitats to support a high biodiversity of unique and often forest-dependent species (Lindenmayer et al. 2020; Martin et al. 2021; Gilhen-Baker et al. 2022), and being essential reservoirs of genetic resources that offer valuable insights into plant evolutionary fitness and adaptation over long time frames (Cannon et al. 2022; Milesi et al. 2024). Furthermore, native old-growth forests often have high socio-cultural and natural heritage values, particularly for indigenous communities with deep connections to the land

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(Gilhen-Baker et al. 2022; Mikolāš et al. 2023). Globally, native old-growth forest ecosystems are under increasing threat from the combined effects of multiple interacting disturbances, such as deforestation (Song et al. 2018), fragmentation and edge effects (Haddad et al. 2015; Sousa et al. 2017), biodiversity loss (Barlow et al. 2016), severe droughts and wildfires (Booth et al. 2015; Lindenmayer 2017) and increasing outbreaks of native and exotic pests and pathogens (Carnegie et al. 2016; Fortini et al. 2019; Burgess et al. 2022; Hessburg et al. 2022). These stressors threaten the health and resilience of native old-growth forests, eroding their ability to support the delivery of critical ecosystem services (Watson et al. 2018).

The kauri (*Agathis australis*) forests of Aotearoa New Zealand offer an exemplary case study of this global issue. Belonging to a family of ancient conifers (*Araucariaceae*) dating back to the Jurassic and Cretaceous periods, kauri are one of the largest and longest-living tree species worldwide (Steward and Beveridge 2010; Wyse et al. 2014). Kauri trees function as a foundation species, supporting floristically distinct and species-rich forest ecosystems with unique plant communities and soil formation processes (Wyse et al. 2014; Wyse and Burns 2013; Macinnis-Ng and Schwendenmann 2015; Verkaik et al. 2006). The widespread influence of kauri on the surrounding plant and soil environment means its decline would impact kauri forest ecosystem dynamics more than the loss of any other co-occurring plant species (Wyse et al. 2014). Furthermore, kauri are recognised as a taonga (treasured) species, having immense cultural and spiritual significance to indigenous Māori communities in kauri forest regions (Bradshaw et al. 2020). Prior to European settlement, kauri-dominated forests covered over 1 million hectares across the warm temperate zones of the upper North Island (Steward and Beveridge 2010). However, historical land clearance and logging mean less than 1% of primary kauri forest remains, alongside 60,000 ha of secondary regenerating kauri (Steward and Beveridge 2010). Remnant kauri forest fragments are threatened by the spread of dieback disease caused by the invasive soil pathogen *Phytophthora agathidicida* (Beever et al. 2009). Kauri dieback disease is distributed across most of the remnant natural range of kauri and, compounded with the impacts of historical deforestation and fragmentation, anthropogenic disturbances, surrounding alternative land uses and climate change, poses a significant threat to the long-term health and functioning of kauri forests (Jones 2021; Schwendenmann and Michalzik 2019; Beachman 2017; Lewis et al. 2019; Byers, Condron, O'Callaghan, et al. 2020; Byers, Condron, Donavan, et al. 2020).

The soil microbiome is central to the delivery of forest ecosystem processes and functioning, being responsible for the decomposition of dead plant biomass, driving the cycling of major nutrient elements (e.g., C, nitrogen (N), phosphorus (P), sulphur (S)), supporting plant growth and productivity and suppressing the growth and establishment of plant pathogens (Baldrian 2016; Lladó et al. 2017). However, the forest soil microbiome is sensitive to both natural and anthropogenic disturbances (Baldrian 2016; Bowd et al. 2022), particularly when these disturbances are associated with shifts in soil abiotic conditions or large-scale changes in plant biomass and community composition (Hermans et al. 2017; Szoboszlay et al. 2017; Berkelmann et al. 2020; Guerra et al. 2021). Given the functional significance of the forest soil microbiome, exploring the impacts of environmental disturbances on soil microbial activity, diversity and function is essential for capturing the broader impacts of disturbance on forest ecosystem processes, as well as the recovery and resilience of forest ecosystems post-disturbance (Bowd et al. 2022; Nelson et al. 2024).

Previous research has begun to explore the soil microbiome associated with kauri forests, particularly in relation to patterns of disease outbreaks and forest disturbance history (Byers, Condron, O'Callaghan, et al. 2020; Byers, Condron, Donavan, et al. 2020; Michael 2023). Although this research made significant steps towards advancing our knowledge of the kauri forest soil microbiome, it was limited to a select range of kauri forests and primarily focused on studying the impacts of tree dieback on soil microbial diversity and composition. However, across the remnant range of extant kauri forests, there exists a high degree of variation in the nature and intensity of both historical disturbances (e.g., deforestation, forestry management) and present-day disturbances (e.g., dieback distribution, urban development, proximity to alternate land uses) (Steward and Beveridge 2010; Beever et al. 2009; Beachman 2017; Lewis et al. 2019; Bellgard et al. 2013; Froud et al. 2021). To capture this variability and better understand the impacts of disturbance intensity on the soil microbiome, we examined the functional profiles of soil bacterial communities from nine kauri forests spanning a gradient of disturbance intensity. We hypothesised that increasing forest disturbance would be associated with reduced microbial functional capacity, reflected by lower functional gene diversity, smaller average genome sizes and reduced predicted growth rates. Using metagenomic analyses, we tested these hypotheses by quantifying variation in the (1) predicted growth rate, (2) average genome size, (3) taxonomic diversity, (4) functional gene diversity and (5) metabolic profiles of functional genes.

2 | Materials and Methods

2.1 | Field Sites

Soil samples were collected from nine kauri forests across the North Island of Aotearoa New Zealand (Figure 1). The disturbance profiles of the kauri forests spanned a range of low-to-high disturbance intensity in the order as follows: Hirakimatā, Puketī, Glenfern, Windy Hill, Laingholm, Silverdale, Gadgil, Oratia and Kaiaraara (Figure 2). In support of the information presented in Figure 2, more detailed descriptions and references for each forest site have been provided in Table S1. Four mainland forest sites were sampled: Puketī, Laingholm, Silverdale and Oratia (Figure 1), descriptions of which have been detailed in previous research (Byers et al. 2024). Five forest sites were located on the offshore island of Aotea Great Barrier: Hirakimatā, Windy Hill, Kaiaraara, Glenfern and Gadgil (Figure 1). Aotea Great Barrier was selected for this research as the island contains a range of kauri forests associated with different levels of historical and present-day disturbances. Many kauri forests across Aotea Great Barrier were heavily disturbed from productive forestry operations during the mid-19th to mid-20th century. Two forest sites included in this study, Kaiaraara and Gadgil, were both formerly part of the Great Barrier State Forest, which was under management by the New Zealand Forest Service ([NZFS], disestablished

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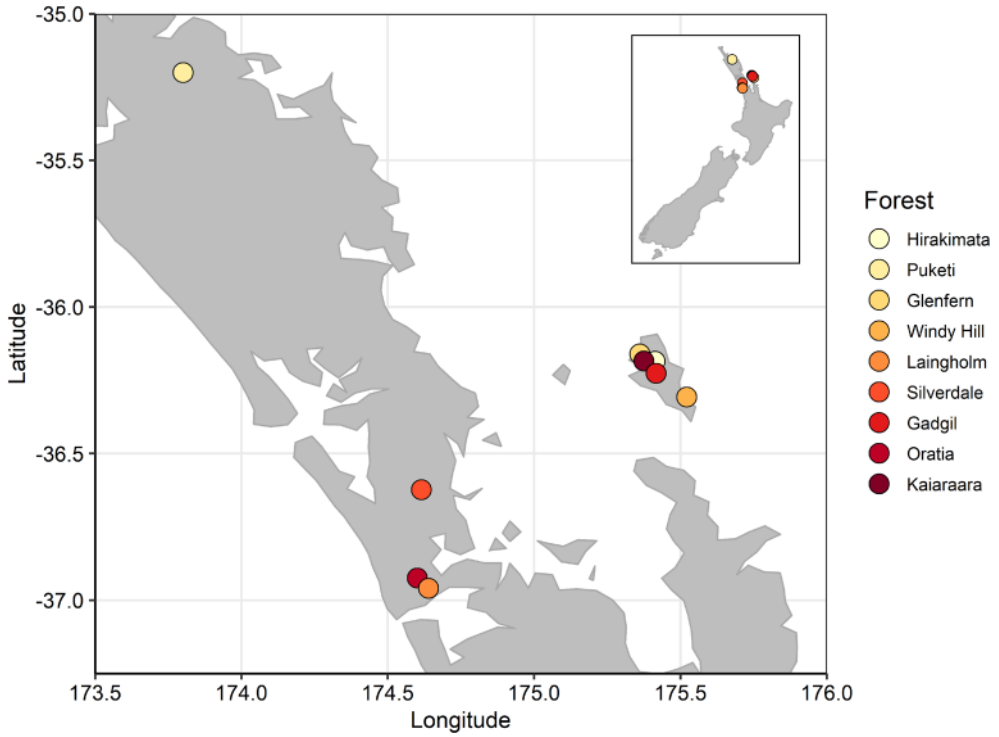


FIGURE 1 | Locations of the nine kauri forest sites targeted for soil sampling across the North Island of Aotearoa New Zealand. Four kauri forests were located on the mainland: Laingholm, Silverdale, Oratia, and Puketi. Five kauri forests were located on the offshore island of Aotea Great Barrier: Hirakimatā, Glenfern, Windy Hill, Gadgil, and Kaiaraara. Forests are coloured according to their disturbance intensity, from low (Hirakimatā) to high disturbance (Kaiaraara).

in 1987) (Beachman 2017; Gadgil 1974). These sites were subject to disturbance from silvicultural practices such as tree stand improvement, artificial thinning and trial plantations of wilding and nursery kauri stock (Beachman 2017). Furthermore, the first recorded case of kauri dieback disease was detected on Aotea Great Barrier in 1972, within kauri forests under productive forestry management (the 'Gadgil' site, included in this study) (Gadgil 1974). Despite having a widespread occurrence of intensively disturbed kauri forests, Aotea also contains examples of relatively undisturbed kauri forests, fostered by active restoration efforts from local community groups and conservation projects, including pest management to facilitate the growth of threatened ground-nesting seabird populations (Table S1). In this study, the sites Hirakimatā, Glenfern and Windy Hill experienced low levels of historical disturbance and are currently under conservation protection and active restoration (Figure 2, Table S1).

2.2 | Soil Collection

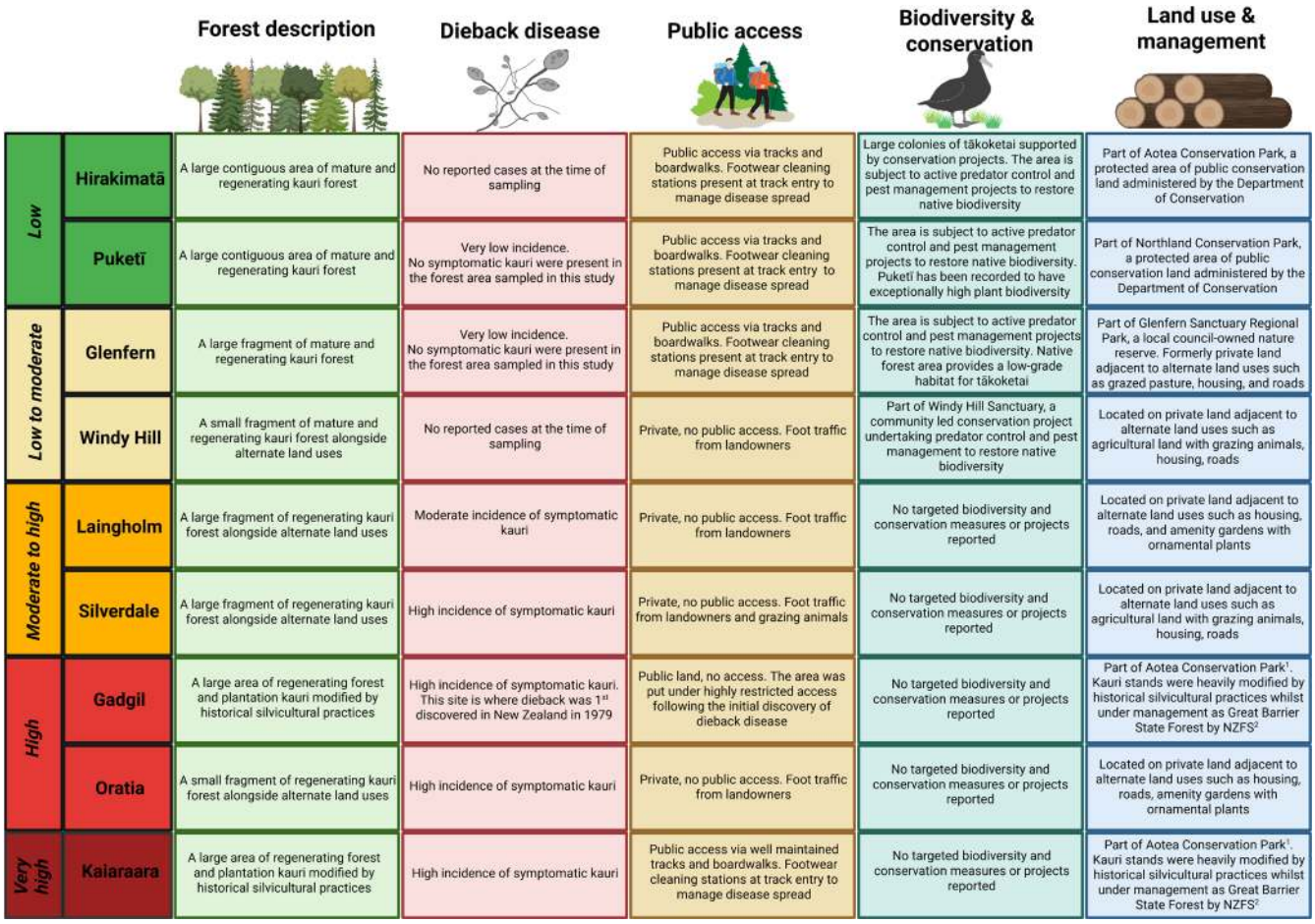
All soils collected from mainland kauri forests of Puketī, Oratia, Silverdale and Laingholm were sampled initially in a previous study (Byers et al. 2024). Soil sampling was conducted exclusively beneath mature kauri trees; seedlings and ricker-stage individuals were excluded from sampling (Steward and Beveridge 2010). Within each forest, a random sampling technique was employed to select mature kauri trees for soil sampling, while accounting for the physically challenging terrain. The number of kauri trees sampled per forest was as follows: 12 each in Silverdale and Laingholm; 10 each in Puketī, Hirakimatā, Windy Hill, Glenfern, Gadgil and Kaiaraara; and 8 in Oratia. Each kauri tree sampled received a canopy health rating (Waipara et al. 2013), and any symptoms of dieback disease were recorded (Table S1). For soil sampling, the top 10 cm of soil was targeted following removal of the litter layer. Four 125 g subsamples were collected from the cardinal points 100 cm from the base of each tree and combined to form a 500 g composite sample (Waipara et al. 2013). To prevent cross-contamination of soil samples between individual trees, all sampling equipment was sterilised with 97% ethanol, and fresh gloves and boot covers were used for each tree sampled.

As previously described by Byers et al. (Byers et al. 2024), soil samples were air-dried at 35°C and sieved to less than 2 mm before the determination of pH, Olsen phosphorus (Olsen P; mg L^{-1}), total C (%) and total N (%). All 90 soil samples were analysed for total %C and %N. Due to insufficient sample volumes remaining for analysis, soil samples from the mainland kauri forests (Silverdale, Laingholm, Oratia and Puketi) were not analysed for Olsen P or pH. Therefore, Olsen P and pH measurements were only performed on soils collected from the five kauri forests on Aotea Great Barrier (Hirakimatā, Glenfern, Windy Hill, Gadgil and Kaiaraara).

2.3 | Shotgun Metagenomics Sequencing and Bioinformatics Analysis

Genomic DNA was extracted using the Qiagen DNeasy PowerSoil Pro Kit according to the manufacturer's instructions. For each sample, three replicate extractions of 0.25 g were

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		Forest description	Dieback disease	Public access	Biodiversity & conservation	Land use & management
Low	Hirakimatā	A large contiguous area of mature and regenerating kauri forest	No reported cases at the time of sampling	Public access via tracks and boardwalks. Footwear cleaning stations present at track entry to manage disease spread	Large colonies of tākoketai supported by conservation projects. The area is subject to active predator control and pest management projects to restore native biodiversity	Part of Aotea Conservation Park, a protected area of public conservation land administered by the Department of Conservation
	Puketī	A large contiguous area of mature and regenerating kauri forest	Very low incidence. No symptomatic kauri were present in the forest area sampled in this study	Public access via tracks and boardwalks. Footwear cleaning stations present at track entry to manage disease spread	The area is subject to active predator control and pest management projects to restore native biodiversity. Puketī has been recorded to have exceptionally high plant biodiversity	Part of Northland Conservation Park, a protected area of public conservation land administered by the Department of Conservation
Low to moderate	Glenfern	A large fragment of mature and regenerating kauri forest	Very low incidence. No symptomatic kauri were present in the forest area sampled in this study	Public access via tracks and boardwalks. Footwear cleaning stations present at track entry to manage disease spread	The area is subject to active predator control and pest management projects to restore native biodiversity. Native forest area provides a low-grade habitat for tākoketai	Part of Glenfern Sanctuary Regional Park, a local council-owned nature reserve. Formerly private land adjacent to alternate land uses such as grazed pasture, housing, and roads
	Windy Hill	A small fragment of mature and regenerating kauri forest alongside alternate land uses	No reported cases at the time of sampling	Private, no public access. Foot traffic from landowners	Part of Windy Hill Sanctuary, a community led conservation project undertaking predator control and pest management to restore native biodiversity	Located on private land adjacent to alternate land uses such as agricultural land with grazing animals, housing, roads
Moderate to high	Laingholm	A large fragment of regenerating kauri forest alongside alternate land uses	Moderate incidence of symptomatic kauri	Private, no public access. Foot traffic from landowners	No targeted biodiversity and conservation measures or projects reported	Located on private land adjacent to alternate land uses such as housing, roads, and amenity gardens with ornamental plants
	Silverdale	A large fragment of regenerating kauri forest alongside alternate land uses	High incidence of symptomatic kauri	Private, no public access. Foot traffic from landowners and grazing animals	No targeted biodiversity and conservation measures or projects reported	Located on private land adjacent to alternate land uses such as agricultural land with grazing animals, housing, roads
High	Gadgil	A large area of regenerating forest and plantation kauri modified by historical silvicultural practices	High incidence of symptomatic kauri. This site is where dieback was 1st discovered in New Zealand in 1979	Public land, no access. The area was put under highly restricted access following the initial discovery of dieback disease	No targeted biodiversity and conservation measures or projects reported	Part of Aotea Conservation Park[1]. Kauri stands were heavily modified by historical silvicultural practices whilst under management as Great Barrier State Forest by NZFS[2]
	Oratia	A small fragment of regenerating kauri forest alongside alternate land uses	High incidence of symptomatic kauri	Private, no public access. Foot traffic from landowners	No targeted biodiversity and conservation measures or projects reported	Located on private land adjacent to alternate land uses such as housing, roads, amenity gardens with ornamental plants
Very high	Kaiaraara	A large area of regenerating forest and plantation kauri modified by historical silvicultural practices	High incidence of symptomatic kauri	Public access via well maintained tracks and boardwalks. Footwear cleaning stations at track entry to manage disease spread	No targeted biodiversity and conservation measures or projects reported	Part of Aotea Conservation Park[1]. Kauri stands were heavily modified by historical silvicultural practices whilst under management as Great Barrier State Forest by NZFS[2]

FIGURE 2 | Descriptions of the nine kauri forests that were targeted for soil sampling. The kauri forests varied based on the intensity of their disturbance profiles, from low (Hirakimatā) to high (Kaiaraara) disturbance intensity. The disturbance intensity of each site was related to features such as the distribution of dieback disease, public access, historical and present-day land use and management, and the support of native biodiversity through conservation projects and/or protection. [1]Aotea Conservation Park is public conservation land administered by the Department of Conservation. [2]The New Zealand Forestry Service was disestablished in 1987, upon which the former NZFS native plantations were placed under management by the Department of Conservation.

performed and pooled to yield a single DNA extract per tree. DNA quality was assessed with a Nanodrop spectrophotometer and quantity was determined on a Qubit 2.0 fluorometer. DNA samples were sent for shotgun metagenomics sequencing through the Illumina NovaSeq PE150 platform (NovogeneAIT Genomics, Singapore). Quality-filtered, paired-end sequencing reads were co-assembled by forest site via megaHIT v1.2.9 with default k-mer parameters (Li et al. 2015). Assembled contigs were binned into metagenome-assembled genomes (MAGs) using metaBAT2 v2.15 (Kang et al. 2019) and MaxBin2 v2.2.7 (Wu et al. 2015) and then consolidated into a final bin set using DAS_Tool v1.1.5 (Sieber et al. 2018). MAGs from multiple co-assemblies were dereplicated using dRep v3.4.2 (Olm et al. 2017). Genome quality and assembly statistics of all MAGs were assessed using CheckM2 v1.0.1 (Chklovski et al. 2023). Only MAGs with a minimum completeness of 50% and maximum contamination of <10% were retained for downstream analysis (Ma et al. 2023). Each MAG was taxonomically classified against the Genome Taxonomy Database using GTDB-Tk v2.1.0 (Chaumeil et al. 2019; Parks et al. 2021). The genome quality and assembly statistics of all qualifying MAGs are presented in Table S2.

2.4 | Calculation of Predicted Microbial Growth Rate and Average Genome Size

The maximum growth rate of bacterial communities in each soil sample was predicted using gRodon2 following the methods developed in a previous study by Osburn et al. (2024). The gRodon2 package infers community-wide average growth rates from metagenomes based on codon usage, where optimisation of codons in ribosomal protein genes reflects selection for rapid translation and faster growth (Osburn et al. 2024; Foley et al. 2024). Metagenomic sequencing reads were taxonomically assigned using Kraken2 v2.1.3 (Wood et al. 2019) and filtered to remove non-bacterial reads using KrakenTools v1.2 (Lu et al. 2022). Contigs were assembled using megaHIT v1.2.9 (Li et al. 2015) and protein-coding regions predicted using prodigal v2.6.3 (Hyatt et al. 2010). Ribosomal protein genes were identified using blastn v2.16.0 (Sayers et al. 2022) using a database compiled by Osburn et al. (Osburn et al. 2024). Relative gene coverage was calculated by aligning sequencing reads to predicted coding regions using BWA-MEM v0.7.18 (Li and Durbin 2010) and SAMtools v1.19 (Li et al. 2009). The gRodon2 models were run using

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default parameters with MMv2 in abundance-corrected mode (Weissman et al. 2022). Community-averaged minimum doubling times were converted to maximum predicted growth rates (h^{-1}) (Osburn et al. 2024). The average bacterial genome size of each metagenome community was calculated using MicrobeCensus, which utilised Kraken-filtered metagenomic sequencing reads as input (Nayfach and Pollard 2015). Kraken2 v2.1.3 and Bracken v2.7 were used to calculate the relative abundances of bacterial taxonomic groups in each sample (Wood et al. 2019; Lu et al. 2017).

2.5 | Functional Annotation of Soil Metagenomes

EggNOG-mapper v2.1.12 was used to functionally annotate protein-coding genes against the eggNOG database of orthologous groups (OGs) using the DIAMOND search mode and a hit cut-off *e*-value of 10^{-5} (Huerta-Cepas et al. 2018; Cantalapiedra et al. 2021). METABOLIC and DRAM were used to assign more targeted functional gene annotations related to microbial metabolism and biogeochemical cycling (Shaffer et al. 2020; Zhou et al. 2022), which were validated with previous literature (Fan et al. 2025; Zhang et al. 2024). The refined gene list and associated metabolic functions are presented in Table S3. In addition, genes were annotated against the Carbohydrate-Active Enzyme database (CAZy) via dbCAN3 to identify genes involved in carbohydrate breakdown, modification, or biosynthesis (Drula et al. 2022; Zheng et al. 2023). To calculate per-sample gene coverage, metagenomic reads were mapped to the gene collections from the input MAGs using Bowtie2 v2.5.4 (Langmead and Salzberg 2012). The SAM file was converted to a sorted BAM format using BAMtools v2.4.0 (Barnett et al. 2011) and gene coverage calculated using metaBAT2 v2.15 (Kang et al. 2019). To account for differences in sequencing depth across samples, gene coverage values were normalised by read depth and scaled by average library size using SAMtools v1.15.1 (Danecek et al. 2021).

2.6 | Statistical Analysis

Kruskal-Wallis tests were used to determine significant differences in soil chemistry, maximum predicted growth rate and average bacterial genome size between forests. Multiple pairwise comparisons were performed using the Wilcox tests with Holm *p*-value adjustment. All taxonomic and functional gene datasets were handled using Phyloseq R (McMurdie and Holmes 2013). The alpha diversity of bacterial taxa at the genus level and microbial functional genes in each sample was calculated using the Observed Richness and Shannon Diversity metrics (Oksanen et al. 2025). Significant differences in alpha diversity were determined between forest sites using Kruskal-Wallis and Wilcoxon tests, as described previously in the text. Differences in the community composition of bacterial genera and functional genes between forests were calculated using Bray–Curtis dissimilarity matrices and tested for significance using PERMANOVA (Oksanen et al. 2025) and pairwiseAdonis (Martinez Arbizu 2020). Non-metric multidimensional scaling (NMDS) ordination plots were used to visualise differences in beta diversity between forest sites. Analysis of Compositions of Microbiomes with Bias Correction 2 (ANCOM-BC2) was used to perform differential abundance analysis of bacterial genera and functional genes between forests (Lin and Peddada 2020). Before ANCOM-BC2 analysis, the taxonomic dataset was filtered to remove low-abundance bacterial genera with a total abundance of $< 0.5\%$ and prevalence of $< 20\%$. A Spearman's correlation matrix was calculated to measure the relationship between soil chemistry, maximum predicted growth rate, average genome size, the alpha diversity of bacterial genera and functional genes and the normalised abundance of functional genes related to microbial metabolism and biogeochemical cycling.

3 | Results

3.1 | Soil Chemical Properties

There were significant differences in total soil %C, total soil %N and the soil C/N ratio across the nine kauri forests (Figure 3). The lowest soil %C and %N values were observed in the most disturbed kauri forest of Kaiaraara, which had total soil %C and %N values at least five times lower than all other kauri forests (Figure 3). In contrast, soils from Silverdale, Puketī and Hirakimatā had the highest total %C values, approximately 20 times higher than the total %C values observed in Kaiaraara Forest (Figure 3). Soil pH and Olsen P data for the mainland kauri forests of Silverdale, Oratia, Laingholm and Puketī could not be reported due to insufficient volumes of soil sample remaining for analysis. However, we could still compare differences in soil pH and Olsen P for the five kauri forests on Aotea. Compared to the other kauri forests on Aotea Great Barrier, Kaiaraara had a high soil pH of 5.95 (Figure 3). This value is also higher than the average soil pH values reported for kauri forest ecosystems in the literature (~pH 4; 21). Furthermore, Kaiaraara Forest soils had a low amount of plant-available P (i.e., Olsen P) compared to the other kauri forests on Aotea, particularly Hirakimatā Forest (Figure 3).

3.2 | Microbial Genome Size and Predicted Growth Rate

We observed significant differences in the average genome size and maximum predicted growth rate of soil bacterial communities between kauri forests (Figure 4). The lowest average genome sizes were observed in soil bacterial communities from the forests of Puketī, Hirakimatā and Kaiaraara; forests that spanned this study's spectrum of low-to-high disturbance intensities. In contrast, the largest average genome sizes were observed in the soil bacterial communities from Gadgil, Glenfern and Windy Hill. These forests sat in the middle of our disturbance intensity gradient, suggesting that moderate levels of disturbance were associated with the largest genome sizes. Spearman's correlation analysis identified that average bacterial genome size shared a strong negative correlation with the alpha diversity of bacterial taxa (rho −0.8, $p < 0.001$) and a weak negative correlation with total soil %C and %N (rho −0.5, $p < 0.001$) (Figure 5). In addition, the average bacterial genome size positively correlated with the alpha diversity of bacterial functional genes, including the number of metabolic genes and CAZy gene families (rho 0.8, $p < 0.001$).

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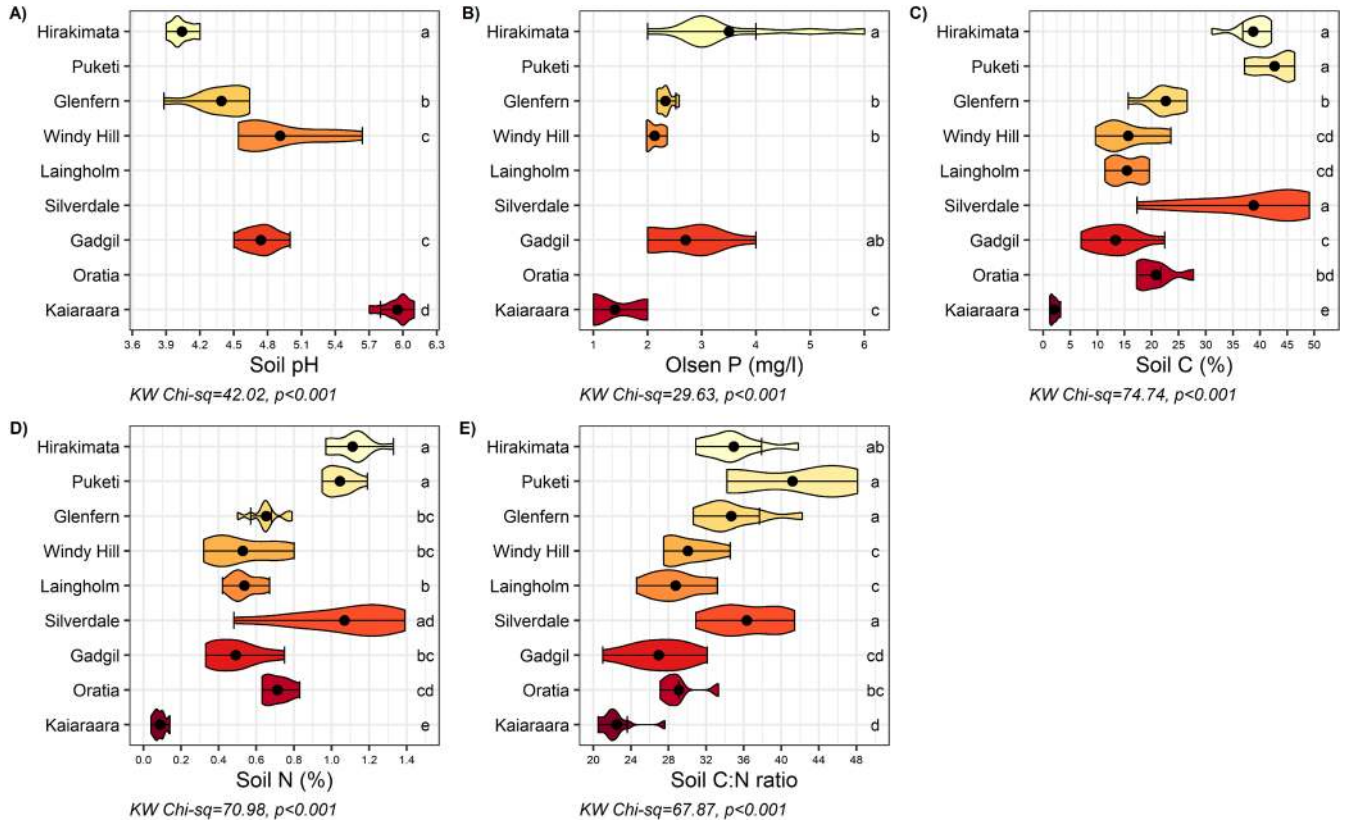


FIGURE 3 | Differences in the (A) pH, (B) Olsen P, (C) total %C, (D) total %N, and (E) C/N ratio of soils associated with the nine different kauri forests. Black circles represent the group mean. Forests not sharing any common letter were determined significantly different by the pairwise Wilcoxon test based on the Holm p-adjusted value ≤0.05. Forests are coloured and ordered according to their disturbance intensity, from low (Hirakimatā) to high disturbance (Kaiaraara).

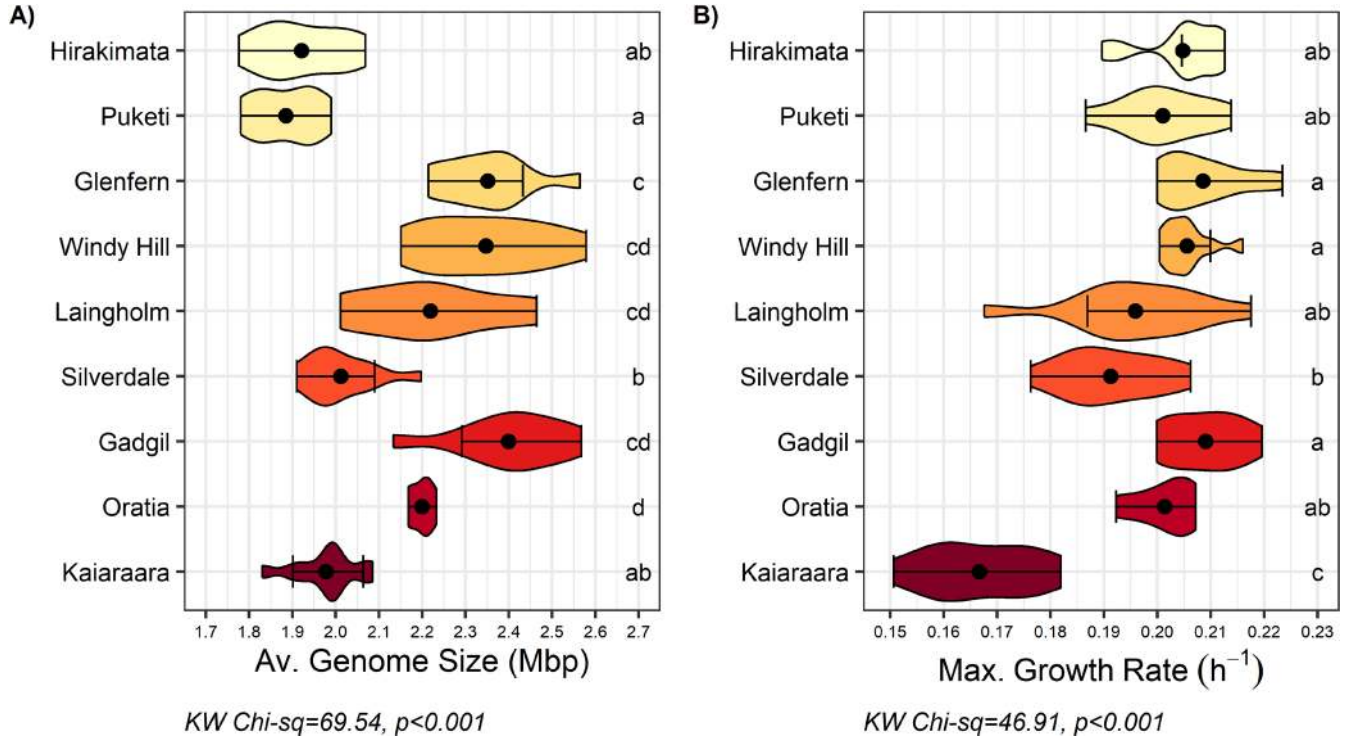


FIGURE 4 | Differences in the (A) maximum predicted growth rate, and (B) average genome size of soil bacterial communities associated with the nine different kauri forests. Black circles represent the group mean. Forests not sharing any common letter were determined significantly different by the pairwise Wilcoxon test based on the Holm p-adjusted value ≤0.05. Forests are coloured and ordered according to their disturbance intensity, from low (Hirakimatā) to high disturbance (Kaiaraara).

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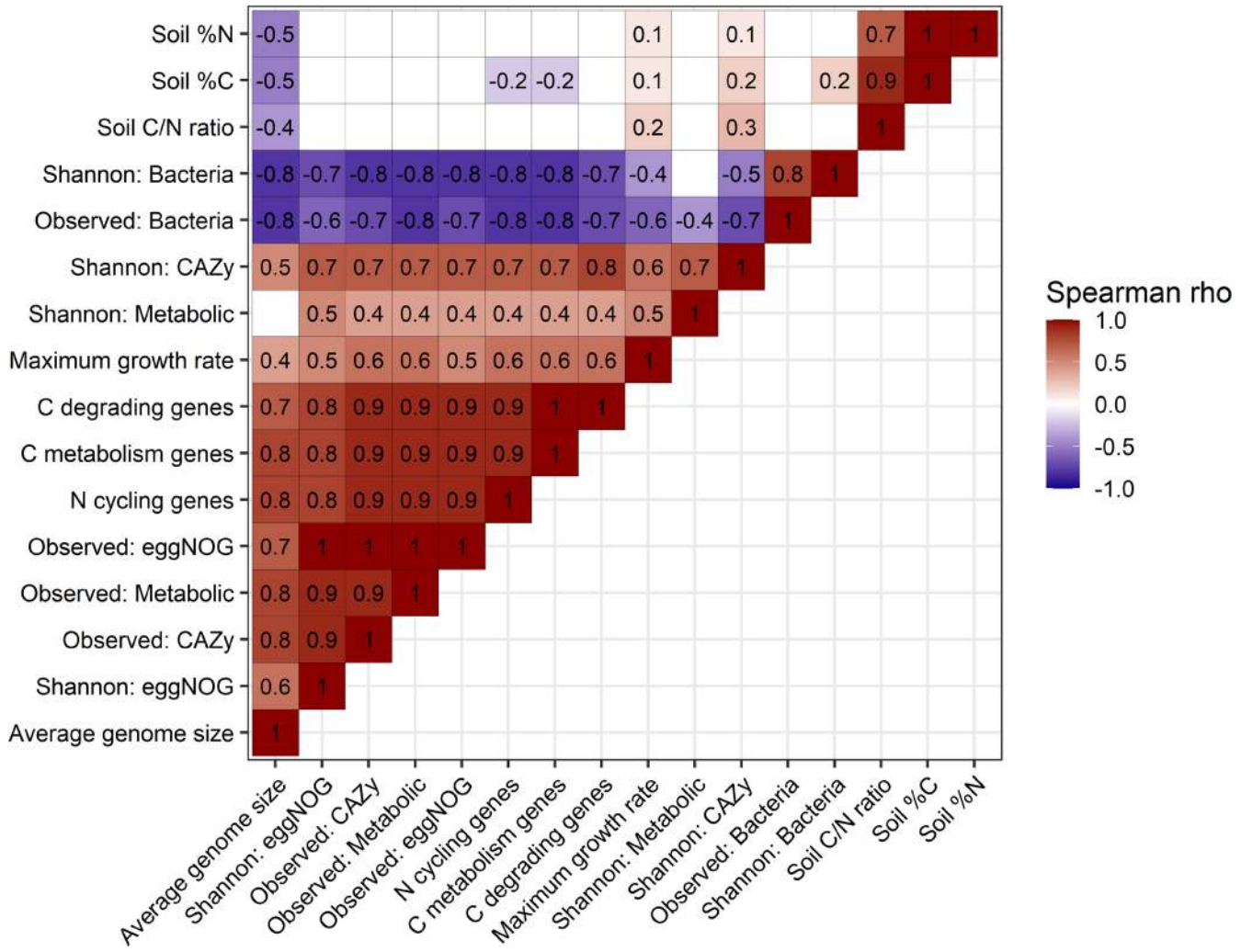


FIGURE 5 | Spearman's correlation matrix displaying the relationship between soil chemical properties, the alpha diversity of bacterial taxa and functional genes, and the normalised abundance of functional genes related to microbial metabolism. Red cells indicate positive correlation values, blue cells represent negative correlation values, and blank cells represent non-significant correlations ($p > 0.05$). Correlation matrix variables were ordered along each axis according to the Ward's hierarchical clustering method.

Soil bacterial communities from the most disturbed forest of Kaiaraara also had the lowest maximum predicted growth rate, significantly lower than all other kauri forests (Figure 4). Overall, the maximum predicted growth rate of soil bacterial communities displayed a J-shaped distribution to forest disturbance intensity (Figure 4). In other words, the predicted growth rate remained relatively stable with increasing states of disturbance until values sharply dropped under the most intense states of disturbance in Kaiaraara. Like average genome size, the maximum predicted growth rate of soil bacterial communities negatively correlated with the alpha diversity of bacterial taxa, while positively correlating with the alpha diversity of bacterial functional genes (Figure 5).

3.3 | Diversity and Composition of Soil Bacterial Taxa

There were significant differences in the alpha diversity of bacterial taxa between kauri forests, with soil bacterial communities from the most disturbed forest of Kaiaraara having the highest number of observed taxa and Shannon diversity (Figure 6). The greater diversity of bacterial taxa observed in Kaiaraara contrasts with the patterns observed for bacterial community growth rate and average genome size, which were relatively low (Figure 4). Soil bacterial communities from the forests Puketī and Hirakimatā also had a higher Shannon diversity compared to many of the other kauri forests (Figure 6). Changes in the diversity of soil bacterial taxa along our forest disturbance intensity gradient shared an inverse relationship with average bacterial genome size, with the most (Kaiaraara) and least-disturbed (Hirakimatā and Puketī) kauri forests having the highest diversity of bacterial taxa but the lowest average genome size (Figures 4, 6). In contrast, the moderately disturbed kauri forests had a relatively low diversity of bacterial taxa and a higher average genome size (Figures 4, 6). The alpha diversity of bacterial taxa shared significant negative correlations with many other properties, including the alpha diversity of bacterial functional genes, maximum predicted growth rate and average bacterial genome size (Figure 5). Overall, these results show that the most disturbed kauri forest supported the highest bacterial taxonomic diversity, despite

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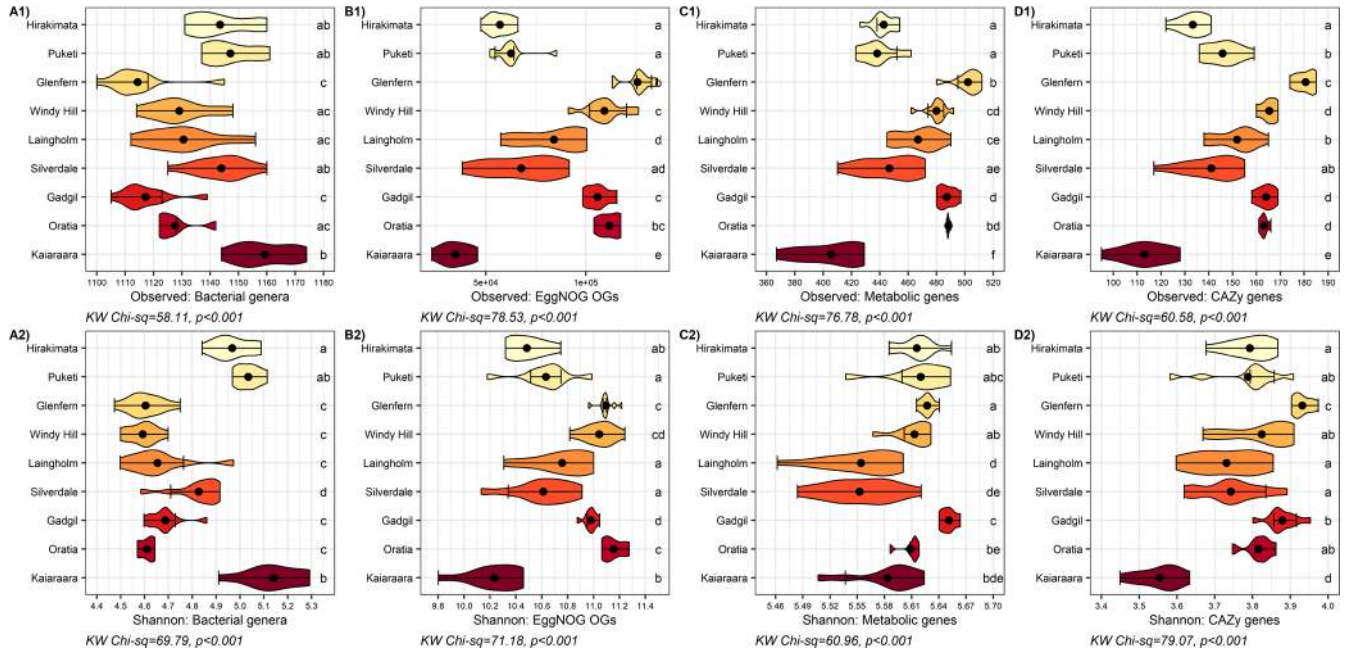


FIGURE 6 | Differences between kauri forests in the alpha diversity of (A) bacterial taxa, (B) eggNOG orthologous groups, (C) metabolic functional genes, and (D) CAZy gene families. Black circles represent the group mean. Forests not sharing any common letter were determined significantly different by the pairwise Wilcoxon test based on the Holm *p*-adjusted value ≤0.05. Alpha diversity was calculated using two different metrics: Observed (A1 to D1) and Shannon Diversity (A2 to D2). Forests are coloured and ordered according to their disturbance intensity, from low (Hirakimatā) to high disturbance (Kaiaraara).

harbouring communities with reduced average genome size and predicted growth rates. This contrast highlights divergent microbial responses to disturbance and may have important implications for how we monitor the effects of disturbance on microbial contributions to soil ecological functioning. The community composition of soil bacterial taxa exhibited significant differences between the kauri forests (Figure 7). Soil bacterial communities from Kaiaraara Forest had the most distinctive bacterial community composition, with the most considerable differences in community dissimilarity observed between Kaiaraara vs. Glenfern ($R^2 = 0.84$, $p < 0.05$), Oratia ($R^2 = 0.82$, $p < 0.05$) and Windy Hill ($R^2 = 0.79$, $p < 0.05$) (Table S4).

Bacterial phyla with the highest relative abundance across all kauri forests were the Pseudomonadota (61.3%) and Actinomycetota (31.7%) (Table S5). Bacterial classes with the highest mean relative abundance included the Alphaproteobacteria (39.5%), Actinobacteria (30.8%), Betaproteobacteria (11.7%) and Gammaproteobacteria (7.7%) (Table S5). The most dominant bacterial genera were *Bradyrhizobium* (15.5%), *Streptomyces* (6.7%), *Mycobacterium* (5.3%), *Pseudomonas* (2.7%) and *Burkholderia* (2.4%) (Table S5). Consistent with the results of beta-diversity analysis, Kaiaraara Forest had the most distinct taxonomic profile and accounted for many of the significant pairwise differences in bacterial genera between forests (Figure 8). On the basis of the results of ANCOM-BC2 analysis, many bacterial genera belonging to the Pseudomonadota phylum had a higher differential abundance in Kaiaraara Forest, such as *Thauera*, *Variovorax, Massilia, Cupriavidus, Acidovorax, Ralstonia, Achromobacter, Bordetella, Burkholderia*, *Sorangium*, *Pseudomonas* and *Stenotrophomonas* (Figure 8; Table S6). In addition, many bacterial genera belonging to the Actinomycetota phylum had a lower differential abundance in Kaiaraara, such as *Thermomonospora, Mycobacterium, Streptosporangium, Nocardiopsis, Kitasatospora* and *Nonomurea* (Figure 8; Table S6).

3.4 | Recovery of Prokaryotic MAGs

In total, 121 prokaryotic MAGs were recovered from the 90 kauri forest soil samples, with an average genome completeness of 80.8% and contamination of 4.6% (Table S2). The highest number of MAGs was recovered from Puketī forest, followed by Glenfern, Gadgil, Windy Hill, Laingholm, Silverdale, Oratia, Hirakimatā and Kaiaraara (Table 1). The average contig N50 was 14,731 bp, with the largest contig N50 observed in MAGs recovered from Silverdale and the lowest observed in Kaiaraara and Hirakimatā (Table 1). There were no notable differences in the taxonomic affiliations of MAGs between forests (Figure 9). The most frequently identified bacterial phyla were the Pseudomonadota (39 MAGs), Actinomycetota (31 MAGs) and Acidobacteriota (14 MAGs). The most frequently identified bacterial orders were the Rhizobiales (14 MAGs), Acidimicrobiales (11 MAGs), Chthoniobacterales (11 MAGs) and Solirubrobacterales (9 MAGs) (Figure 9).

On average, 70.35% ± 1.67% of genes were assigned a known function when annotated against the eggNOG database (Table S7). EggNOG COG categories with the highest relative gene coverage across all kauri forests included lipid metabolism (10.1%), energy production and conversion (7.7%) and amino acid metabolism (7.3%) (Figure S1). When genes were functionally annotated using METABOLIC and DRAM analysis, 5.99% ± 0.31% were predicted to be involved in metabolic

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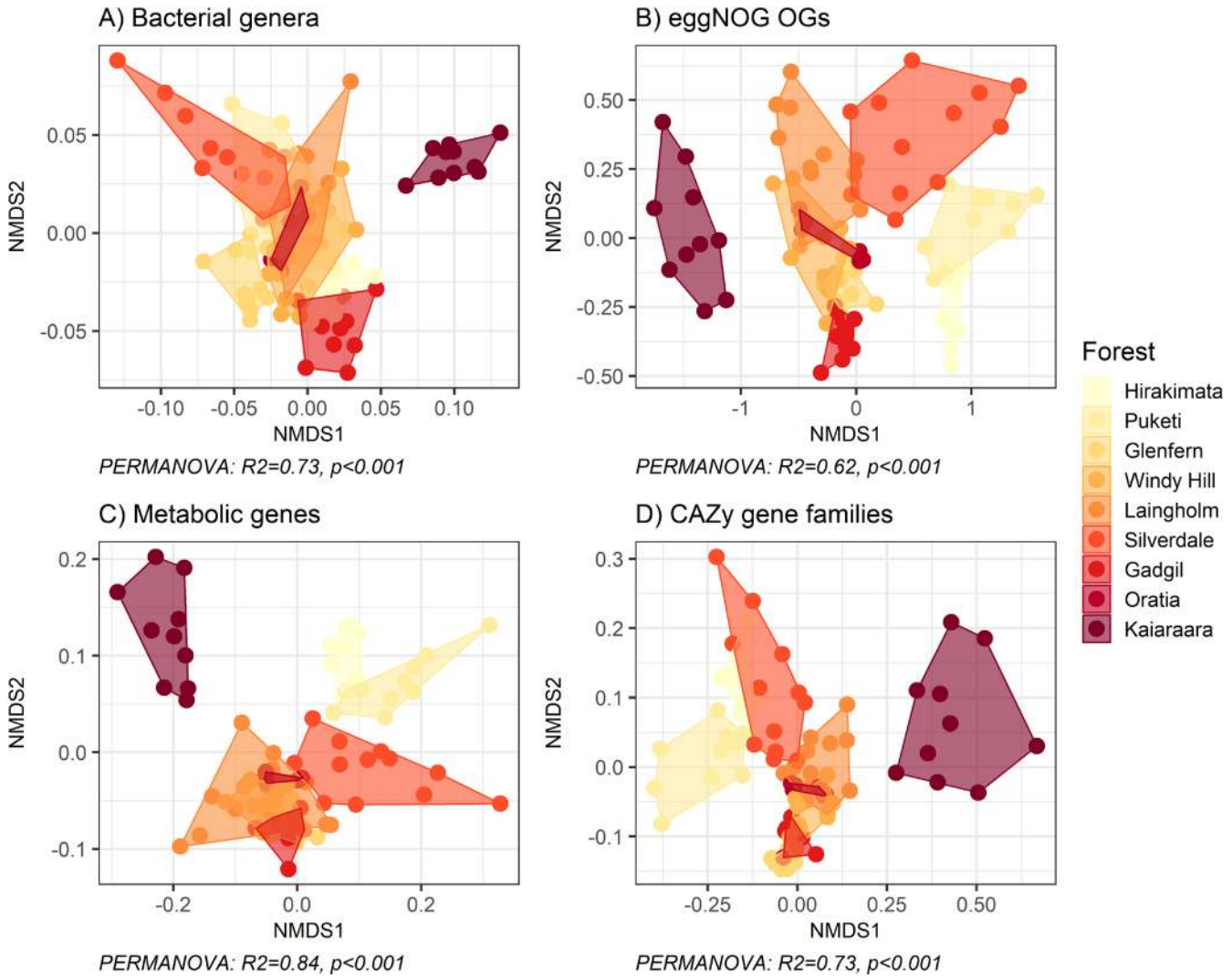


FIGURE 7 | NMDS ordination plots displaying differences between kauri forests in the community composition of (A) bacterial taxa, (B) eggNOG orthologous groups, (C) metabolic functional genes, and (D) CAZy gene families. Forests are coloured and ordered according to their disturbance intensity, from low (Hirakimatā) to high disturbance (Kaiaraara).

processes (Table S8). Of these metabolic genes, processes with the highest average relative gene coverage included central C metabolism (35.4%), amino acid metabolism (27.2%), S metabolism (9.9%) and C1 metabolism (6.1%) (Figure 10; Figure S1). Furthermore, when annotated against the CAZy database, 2.81% ± 0.11% of genes were identified as involved in C breakdown, modification, or biosynthesis (Table S8). Of the CAZy annotated genes, enzyme classes with the highest relative gene abundance were glycosyltransferases (47.2%) and glycoside hydrolases (32%) (Figure S2).

3.5 | Microbial Functional Gene Diversity and Composition

There were significant differences in the alpha diversity of bacterial functional genes between kauri forests, including eggNOG orthologous groups, metabolic genes and CAZy gene families (Figure 6). In contrast to the patterns observed in the alpha diversity of bacterial taxa, soil bacterial communities from the most disturbed forest of Kaiaraara had the lowest observed number of functional genes, as well as the lowest Shannon diversity of eggNOG OGs and CAZy gene families (Figure 6). Glenfern Forest had the highest observed number of bacterial functional genes, whilst also having the highest Shannon diversity of CAZy gene families (Figure 6). The alpha diversity of bacterial functional genes positively correlated with average bacterial genome size and maximum predicted growth rate, but strongly negatively correlated with the alpha diversity of bacterial taxa (Figure 5). Collectively, these results demonstrate that forest disturbance elicits contrasting responses in bacterial taxonomic diversity and functional capacity, with the most disturbed forest exhibiting a reduced functional gene diversity, genome size and growth rate, despite elevated taxonomic diversity. These findings indicate that increasing forest disturbance may reduce the functional capacity of kauri soil microbial communities, even when taxonomic diversity is maintained. There were significant differences in the beta diversity of all bacterial functional gene types between kauri forests (Figure 7). The most considerable differences in community dissimilarity of bacterial functional genes were observed between the forests of Glenfern vs.

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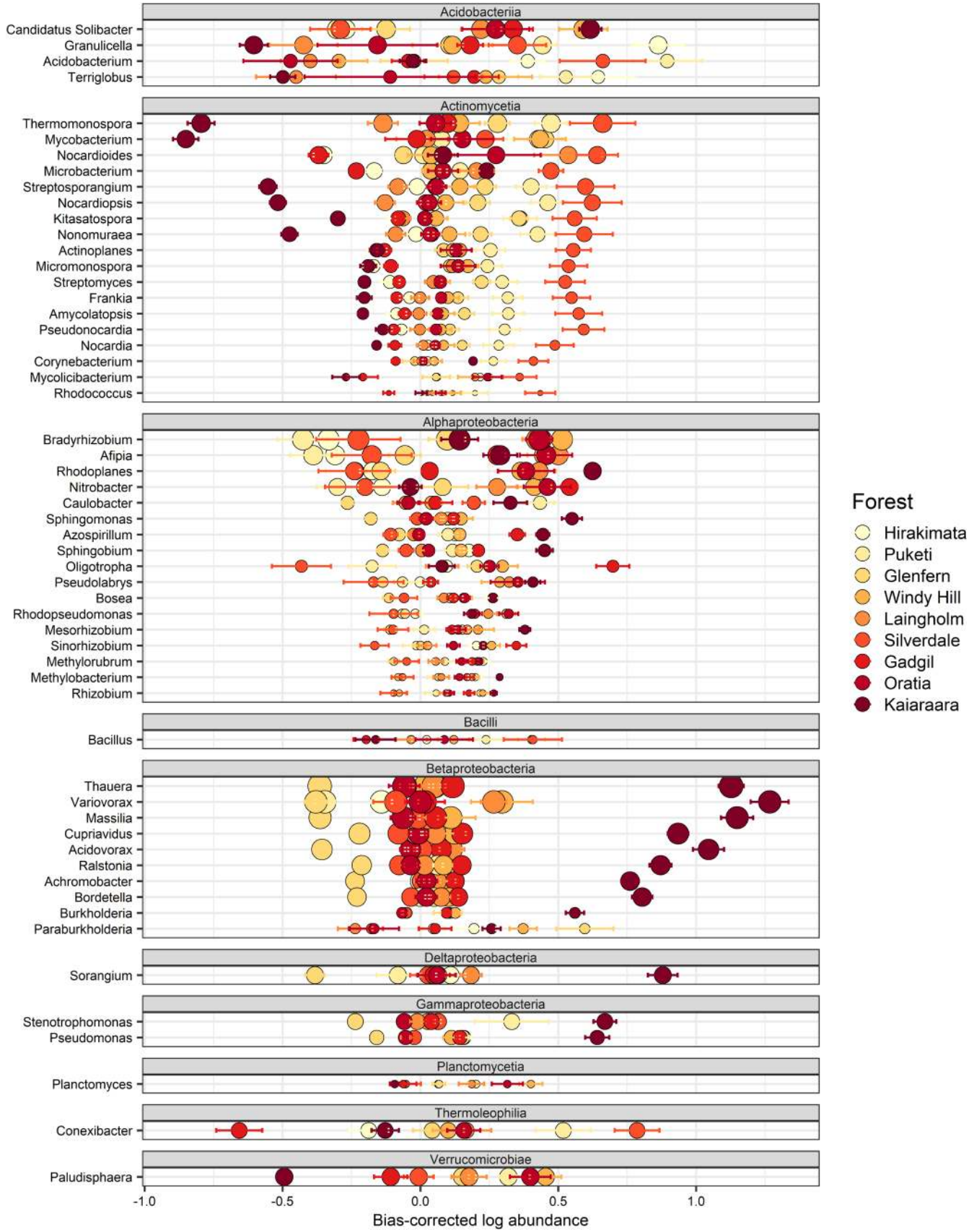


FIGURE 8 | Mean ± SE values for the bias-corrected log abundance of bacterial genera across the nine kauri forest sites. Forests are coloured according to their disturbance intensity, from low (Hirakimatā) to high disturbance (Kaiaraara). The size of each data point is proportional to the ANCOM-BC2 test statistic (W-value), with larger data points indicating larger W-values.

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TABLE 1 | Genome assembly statistics of the prokaryotic MAGs recovered from kauri forest soil samples. Values represent the mean ± SD for each kauri forest. Only MAGs with a minimum genome completion of ≥ 50% and maximum genome contamination of ≤ 10% were included in the final dataset.

Genome statistics	Hirakimatā	Puketī	Glenfern	Windy Hill	Silverdale	Laingholm	Gadgil	Oratia	Kaiaraara
Number of MAGs	8	21	20	15	12	14	15	9	7
Completeness (%)	77.32 ± 10.38	80.43 ± 13.4	79.56 ± 13.61	82.41 ± 10.84	85.7 ± 12.77	79.25 ± 12.49	78.84 ± 11.64	80.19 ± 10.14	85.91 ± 7.89
Contamination (%)	4.79 ± 3.66	4.33 ± 2.93	4.64 ± 2.93	3.86 ± 2.75	3.72 ± 2.49	5.7 ± 2.66	5.25 ± 2.74	5.61 ± 2.89	3.7 ± 2.1
Contig N50	9556 ± 3095	16347 ± 16558	14805 ± 14635	13707 ± 13740	30751 ± 34183	10825 ± 7240	13629 ± 14518	13240 ± 12606	9719 ± 5310
Gene length (bp)	281 ± 20	295 ± 20	285 ± 31	274 ± 19	295 ± 17	288 ± 16	272 ± 21	276 ± 24	283 ± 36
Genome size (Mbp)	3.52 ± 1.4	3.1 ± 1.23	4.14 ± 1.55	3.95 ± 1.53	3.24 ± 1.14	3.53 ± 1.51	4.06 ± 1.8	4.28 ± 1.86	3.67 ± 1.33
GC content (%)	60.88 ± 2.95	60.81 ± 10.21	60.8 ± 9.34	58.27 ± 7.9	62.92 ± 8.56	64.29 ± 6.02	61.87 ± 6.44	65.56 ± 6.06	57.43 ± 11.96
Coding regions	3671 ± 1444	3205 ± 1263	4332 ± 1804	4226 ± 1609	3300 ± 1157	3694 ± 1441	4413 ± 2000	4716 ± 2186	3876 ± 1240

Kaiaraara, Glenfern vs. Hirakimatā and Gadgil vs. Kaiaraara (Table S4).

3.6 | Differential Abundance Analysis of Microbial Metabolic Genes

ANCOMBC2 analysis identified significant differences in the total abundance of bacterial functional genes related to various metabolic processes. These included hydrogen metabolism, C degradation, central C metabolism, fatty acid degradation, N cycling, C1 metabolism and S metabolism (Figure 10). Furthermore, significant differences were identified in the gene abundance of several CAZy enzyme classes, including polysaccharide lyases, carbohydrate-binding modules, glycoside hydrolases, carbohydrate esterases, auxiliary activities and glycosyltransferases (Figure 10).

When examining differences between forests, the most disturbed forest of Kaiaraara had a significantly lower abundance of bacterial functional genes related to hydrogen metabolism and the degradation of C, fatty acids and AOX compounds (Figure 10; Table S9). This included a lower abundance of bacterial C-degrading genes responsible for the breakdown of D-galacturonate (*uxaA*, *uxaC*), cellulose (*BGL*, *EG*), hemicellulose (*abfA*, *fucA*, *lacZ*, *manA*, *xylA*, *xylB*), D-gluconate (*dgoD, dgoK*), galactose (*gal*, *galM*), pectin (*ramA*) and starch (*SGA1*, *scrK*) (Figures 11, 12). Overall, the kauri forests of Puketī and Silverdale had the highest total abundance of bacterial C-degrading genes (Figure 10). Furthermore, the least disturbed kauri forests of Hirakimatā and Puketī had a higher abundance of bacterial genes responsible for the degradation of pectin (*ramA*), chitin (*CHIA*) and hemicellulose (*fucl, abfA, uidA*; Figure 12). The gene abundance of carbohydrate esterases and glycoside hydrolases – two CAZy enzyme classes involved in C degradation – was lowest in Kaiaraara (Figure 10). This included gene families such as GH146, GH42, GH51, GH116, GH27, GH127, GH18 and GH33 (Figure S2).

Spearman's correlation analysis identified no significant correlation between total soil %C, soil %N, or the soil C/N ratio and the abundance of bacterial C-degrading genes (Figure 5). When examining different forms of C, the abundance of pectin-degrading genes strongly correlated with total soil %C, soil %N and the soil C/N ratio (rho > 0.7; Table S10). This relationship was primarily shaped by the high total soil %C and %N values and the high abundance of pectin-degrading genes observed in the forests of Hirakimatā and Puketī. Although the total soil %C and/or soil %N significantly correlated with the abundance of cellulose-degrading genes and several CAZy enzyme classes (e.g., polysaccharide lyases, carbohydrate-binding modules, auxiliary activities), the strength of these correlations was weak (Table S10).

Overall, the total abundance of bacterial N cycling genes was highest in Hirakimatā forest, significantly higher when compared to Gadgil, Glenfern, Oratia, Silverdale, Puketī and Kaiaraara forests (Figure 10). These patterns were contributed by Hirakimatā forest, having a higher abundance of bacterial genes related to urea utilisation (e.g., *ureA*, *ureB*, *ureC*) and assimilatory nitrate reduction (*nirA*) (Figures 11, 12). The lowest

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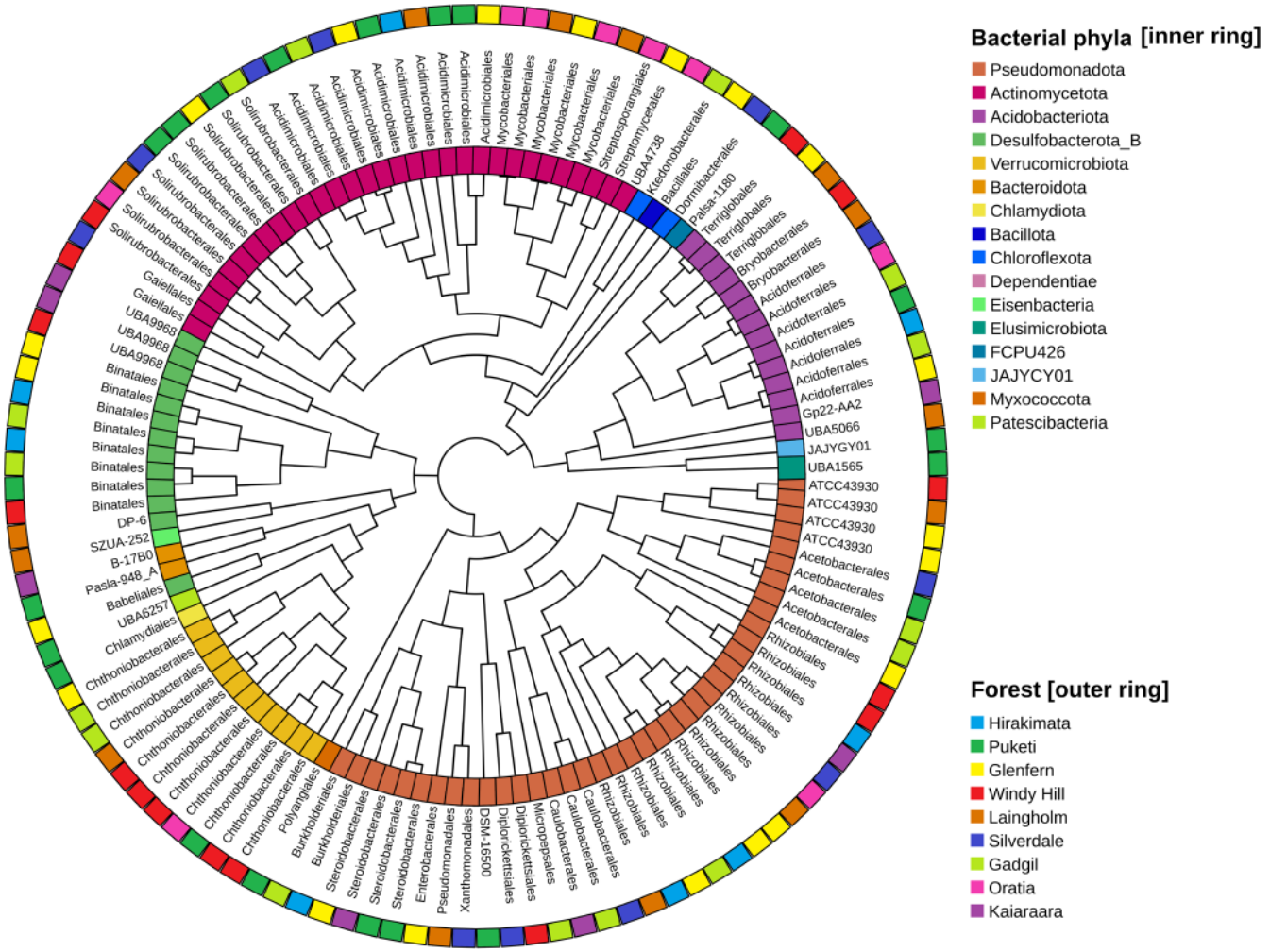


FIGURE 9 | Neighbour-joining phylogenetic tree of prokaryotic MAGs recovered from kauri forest soils. The inner ring is colour-coded according to the bacterial phylum of each MAG, as identified using the Genome Taxonomy Database (GTDB). Tree branches are labelled according to the bacterial order of each MAG. The outer ring is colour-coded according to the kauri forest site.

abundance of bacterial N cycling genes was observed in the forests of Silverdale and Kaiaraara. When examining individual genes, Hirakimatā forest had a significantly lower abundance of *nrfA* (dissimilatory nitrate reduction), *narK* (nitrate assimilation), *nthA* and *nthB* (nitrile hydration) (Figure 12). Other notable observations include Kaiaraara forest having a high differential abundance of denitrification genes, such as *norC*, *narH* and *nirK* (Figures 11, 12). Spearman's correlation analysis revealed that bacterial N cycling gene abundance shared a weak negative correlation with total soil %C (Figure 5). In addition, total soil %C and %N shared a significant negative correlation with the abundance of nitrification (> |0.50|), denitrification (> |0.60|), nitrile hydration and nitrate assimilation genes (> |0.20|; Table S10).

Although the abundance of bacterial genes related to central C metabolism significantly varied across forests, the strength of this observation was weak when based on the ANCOM-BC2 test results (Table S9). Significant differences were detected in the total gene abundance of the 3HP/4HB cycle, photosynthesis, the Wood–Ljungdahl (WL) pathway, pyruvate metabolism and the Calvin cycle (Figure 11). Gene abundances for the WL pathway, photosynthesis and the rTCA cycle were highest in Kaiaraara forest (Figure 11). Although non-significant at the pathway level, the individual abundances of several oxidative phosphorylation genes displayed significant differences between forests (Figure S3). For example, the genes *atpE*, *atpK*, *NDUFS2* and *NDUFS8* had a lower differential abundance in the forests of Hirakimatā and Puketī, while *rnfD*, *rnfG*, *rnfC* and *qcrB* had a higher differential abundance in Kaiaraara forest (Table S11). Other central C metabolism genes displaying notable differences between forests included *Acul* (3HP/4HB cycle), *gap2* (glycolysis/gluconeogenesis), *atpF*, *atpD*, *atpB*, *cydX*, *atpC* (oxidative phosphorylation) and *mal* (glyoxylate cycle) – all of which were highest in Kaiaraara forest and lowest in Glenfern forest (Figure S3). Like patterns observed for bacterial N cycling genes, the total abundance of central C metabolism genes, as well as several central C metabolism pathways, shared a weak negative correlation with total soil %C (Figure 5; Table S10).

The total abundance of C1 metabolism genes significantly varied across forests, with Puketī and Gadgil forests having the lowest differential abundance of C1 metabolism genes and Laingholm and Silverdale forests having the highest (Figure 10, Table S9). Significant differential abundances

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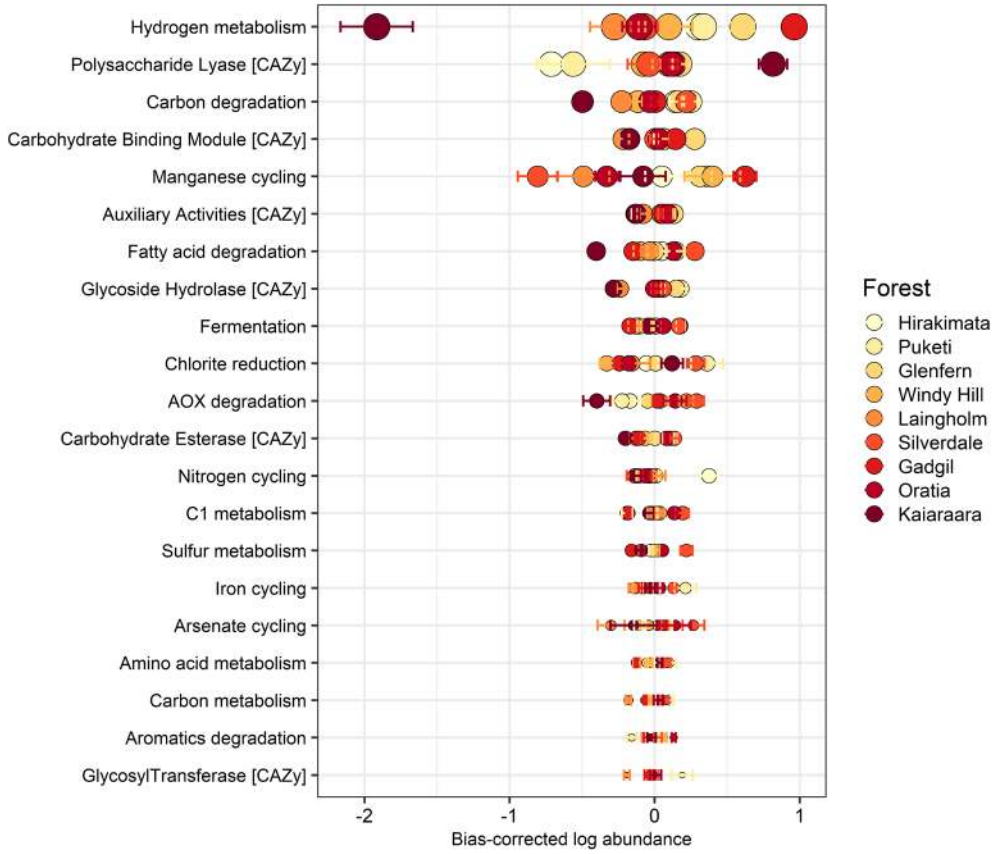


FIGURE 10 | Mean ± SE values for the bias-corrected log abundance of microbial metabolic categories across the nine kauri forests. Forests are coloured according to their disturbance intensity, from low (Hirakimatā) to high disturbance (Kaiaraara). The size of each data point is proportional to the ANCOM-BC2 test statistic (W-value), with larger data points indicating larger W-values. Only gene categories with at least one significant pairwise difference (Holm *p*-adjusted <0.05) between forests are displayed on the plot.

were observed for genes responsible for anaerobic CO oxidation, formaldehyde oxidation, formate oxidation, aerobic CO oxidation, general methane metabolism and methanogenesis (Figure 11). Bacterial genes related to methane metabolism were lowest in the forests of Gadgil and Windy Hill, whilst highest in Silverdale (e.g., *mer*, *cofD*, *comA*) and Kaiaraara (e.g., *comC*). In addition, Kaiaraara Forest had a higher abundance of genes related to methanogenesis (e.g., *hdrB2, mtrA, mch, fmdA* and *ftr*) and formaldehyde oxidation, particularly when compared to Puketī Forest (Figure 11, Figure S4). The more intensively disturbed forests of Gadgil and Kaiaraara had a high abundance of anaerobic CO oxidation genes, particularly when compared to Glenfern and Windy Hill forests (Figure 11, Figure S4).

Overall, the abundance of bacterial genes related to S metabolism was highest in soils from Silverdale Forest (Figure 10). When analysed at a pathway level, this was due to a high differential abundance of genes related to DMSO metabolism (e.g., *sfnG*, *dmoB*) and cysteine/methionine metabolism (e.g., *metH*, *malY*, *metY*, *metE*, *megL*, *cysN*) (Figure 11). Other notable findings include Hirakimatā forest having a higher differential abundance of genes related to sulphite production (Figure 11), particularly compared to Kaiaraara and Laingholm forests (e.g., *ssuD*, *msmA*, *tauD*; Figure S5). Furthermore, genes related to dissimilatory S reduction and thiosulfate oxidation had a high differential abundance in Windy Hill forest and a low abundance in Hirakimatā and Puketī forests (e.g., *soxA*, *soxZ*, *soxX*, *soxY* and *soxB*; Figure S5).

4 | Discussion

4.1 | Disturbance-Driven Changes in the Soil Environment Induce Changes in the Taxonomic and Functional Attributes of the Soil Microbiome

The most distinctive and pronounced shifts in soil bacterial communities were observed in the most intensively disturbed forest site: Kaiaraara Forest. In line with our original hypothesis that greater forest disturbance intensity would be associated with reduced microbial functional capacity, soil bacterial communities associated with Kaiaraara Forest had a low predicted growth rate, average genome size, functional gene diversity and abundance of C-degrading genes. The considerable differences in soil organic matter and pH in Kaiaraara Forest may be a key factor influencing the reduced functional capacity of soil bacterial communities. Kaiaraara Forest had incredibly low soil %C and %N values, at least five times lower than the other eight kauri forests. Moreover, soil %C values in Kaiaraara Forest were roughly 20 times lower than in the less disturbed forests of Hirakimatā, Puketi and Silverdale. Kauri forest stands in Kaiaraara were heavily modified by productive forestry operations during the mid-19th to

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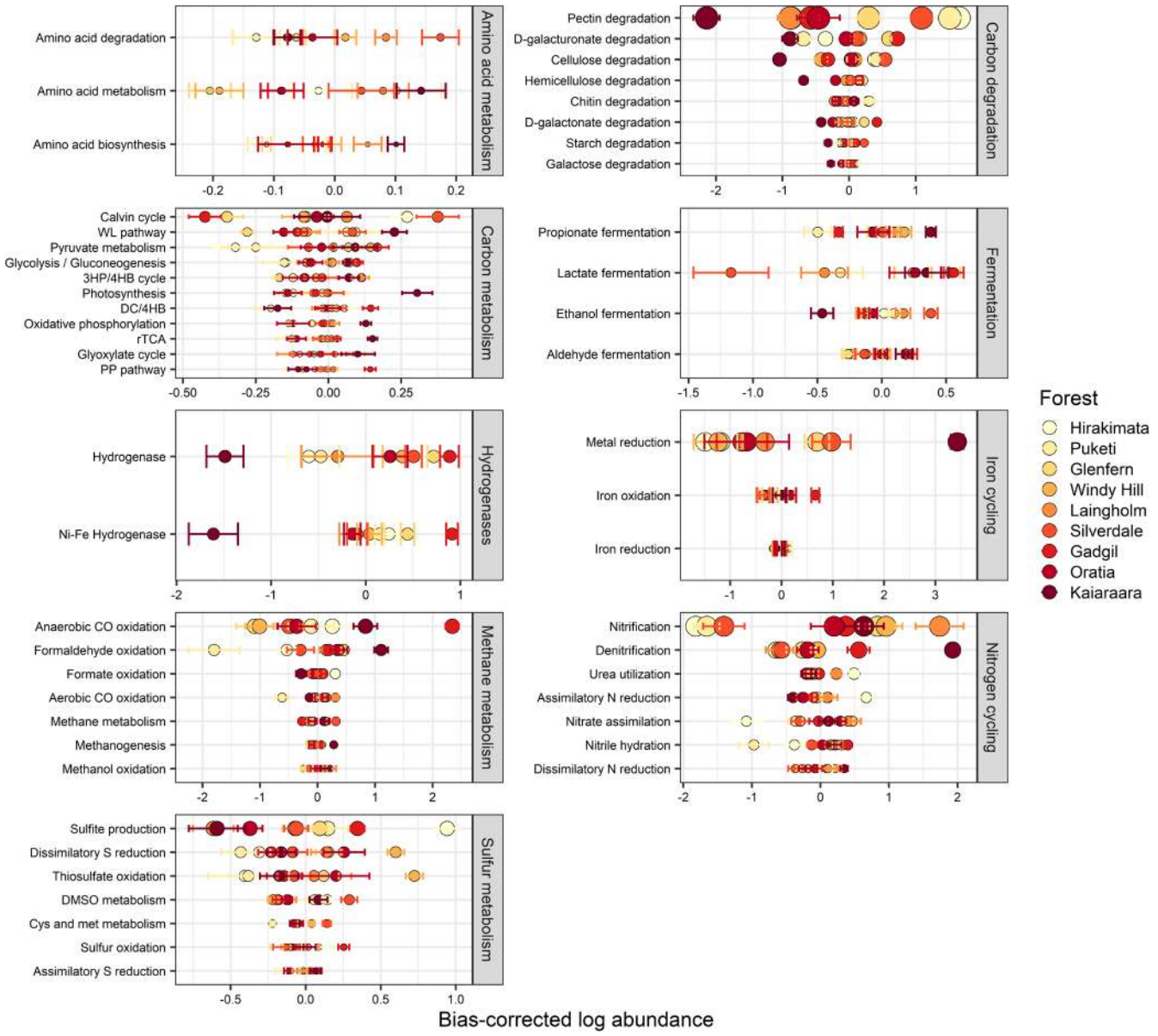


FIGURE 11 | Mean ± SE values for the bias-corrected log abundance of microbial metabolic functions across the nine kauri forests. Forests are coloured according to their disturbance intensity, from low (Hirakimatā) to high disturbance (Kaiaraara). The size of each data point is proportional to the ANCOM-BC2 test statistic (W-value), with larger data points indicating larger W-values.

mid-20th century, which included silvicultural practices such as tree stand improvement (TSI) and experimental plantings of wilding and nursery kauri stock (Beachman 2017). Although there is little evidence of its efficacy, TSI aimed to selectively improve the growth rate and form of kauri trees by removing or reducing the surrounding competitive native vegetation, such as kānuka (*Kunzea ericoides*) and other tree ferns (Beachman 2017). The prolonged history of mass forestry clearances across Kaiaraara Forest would have resulted in sustained losses of soil organic matter, which may partly explain the very low soil %C and %N values we observed in our dataset. Furthermore, the wider area of Kaiaraara Forest was subject to an intense storm in 2014, which washed away large volumes of plant biomass and resulted in substantial physical disturbances to the soil environment (Beachman 2017). Compounded with the impacts of historical anthropogenic disturbances, this major flooding event would have also led to significant losses of soil organic matter. Soil bacterial communities are sensitive to changes in soil C following disturbances, with the amount and availability of soil C significantly influencing soil microbial diversity, biomass, activity and function (Bastida et al. 2021; de Graaff et al. 2010; Tang et al. 2023). This was reflected in our study, with the most disturbed forest site of Kaiaraara being characterised by a significantly reduced soil C content and a corresponding decline in the abundance of bacterial C-degrading genes. This may indicate an adaptive response by the soil bacterial communities under periods of abiotic stress and low soil C bioavailability, shifting metabolic energy requirements away from growth and resource acquisition by limiting the production of soil C-degrading enzymes. Furthermore, the distinctive composition of bacterial functional genes in Kaiaraara Forest compared to the less intensively disturbed kauri forests suggests community-level shifts in functional activity in response to

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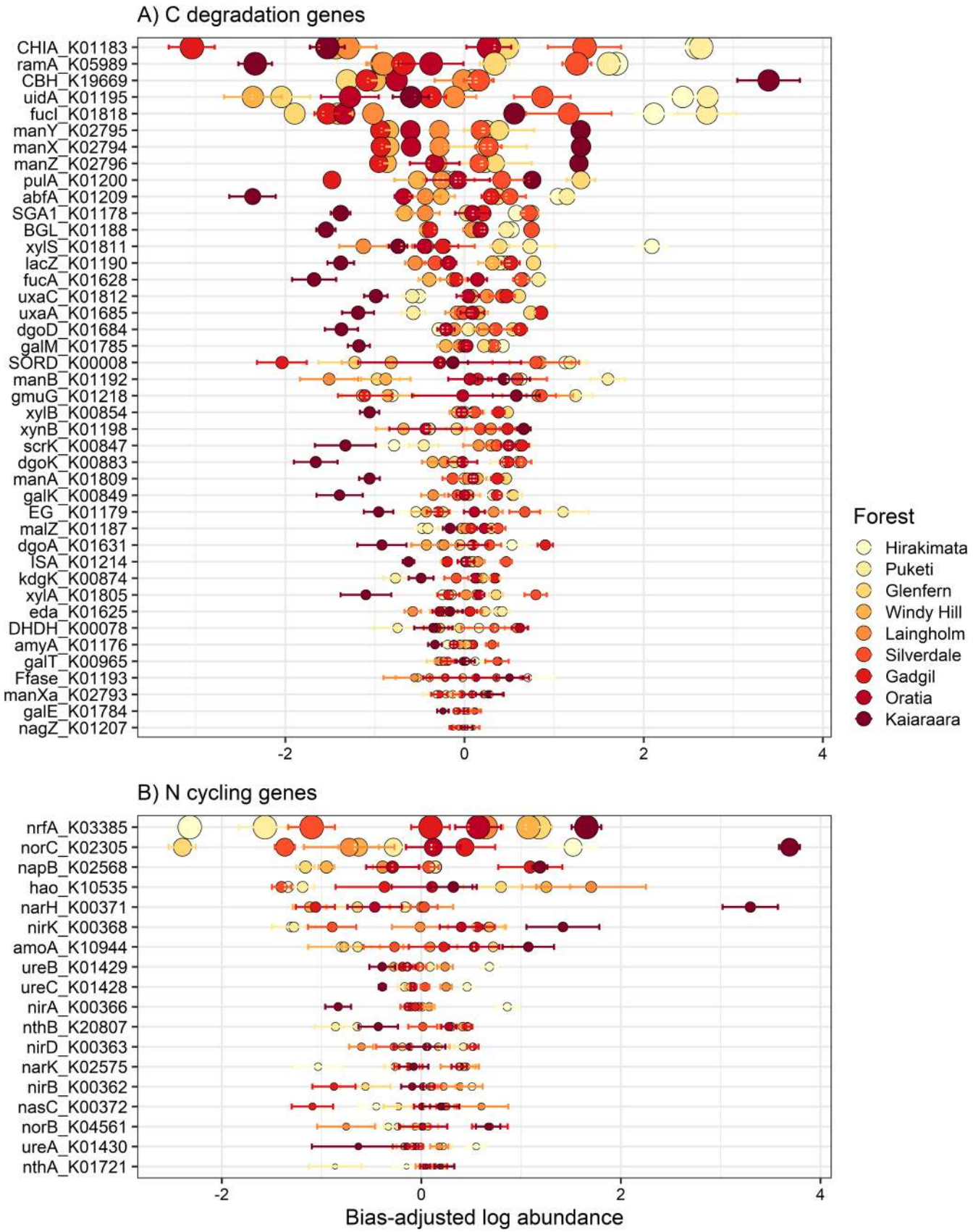


FIGURE 12 | Mean ± SE values for the bias-corrected log abundance of microbial C-degradation and N cycling genes across the nine kauri forests. Forests are coloured according to their disturbance intensity, from low (Hirakimatā) to high disturbance (Kaiaraara). The size of each data point is proportional to the ANCOM-BC2 test statistic (W-value), with larger data points indicating larger W-values.

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environmental stress. The low soil C environment associated with Kaiaraara Forest may have encouraged the growth and establishment of soil bacteria that yield energy via alternative metabolic pathways (Wu et al. 2022; Tao et al. 2023). Our results identified that Kaiaraara Forest had a higher abundance of bacterial functional genes related to several central C metabolism pathways, such as oxidative phosphorylation, the reverse TCA cycle and photosynthesis. This may provide evidence that soil bacterial communities in Kaiaraara Forest shifted away from direct resource acquisition for growth via the degradation of soil C towards alternative forms of energy generation that facilitate cell maintenance and survival under a low-energy, low-nutrient soil environment. Overall, these findings indicate that disturbance-related losses of forest soil C may be an important mechanism underlying significant shifts in the functional and metabolic traits of soil microbial communities.

The soils from Kaiaraara Forest were less acidic (~pH 6) than what is typically reported of kauri forest soils in the literature (~pH 4; (Wyse et al. 2014)) and were observed for the other kauri forests in this study (~pH 3.6). Soil pH is a major factor shaping global soil bacterial diversity (Lauber et al. 2009; Bahram et al. 2018), with near-neutral soils supporting the greatest soil bacterial diversity (Yavitt et al. 2021). This may explain the higher bacterial diversity observed in Kaiaraara Forest compared to the more acidic soils observed in the other kauri forests. Furthermore, the distinctive bacterial community profiles at Kaiaraara Forest may also reflect its atypical soil pH values (Yavitt et al. 2021). While taxonomic data have several limitations in predicting bacterial pH preferences, bacterial taxa have been reported to exhibit pH-related distributional patterns (Ramoneda et al. 2023; Zhou et al. 2024). Our study observed a clear difference in the abundance of Pseudomonadota and Actinomycota-affiliated taxa between forests, which may be linked to differences in soil pH. For example, the near-neutral forest soils in Kaiaraara had a higher abundance of Pseudomonadota, whereas the more acidic soils of the other forests had a higher abundance of Actinomycetota. In addition, other environmental factors may have influenced the distinct taxonomic profile of soil bacterial communities in Kaiaraara Forest, such as shifts in nutrient acquisition strategies in response to low resource availability and high abiotic stress. Oligotrophic bacteria are adapted to nutrient-poor environments by exhibiting a greater resource use efficiency, a preference for recalcitrant C sources, more streamlined genomes and slower growth rates (Lladó et al. 2017; Dragone et al. 2024; Fierer et al. 2007). Consequently, oligotrophic bacteria often dominate copiotrophic bacteria in low soil C environments (Fierer et al. 2007), such as the forest soils in Kaiaraara. Indeed, soil bacterial communities in Kaiaraara Forest shared many functional traits commonly observed in oligotrophic bacteria, such as low growth rate and genome size (Dragone et al. 2024). It is important to consider that, like pH preference, there are flaws in using taxonomic information to determine oligotrophic-copiotrophic behaviours in soil bacteria, with a diverse range of nutritional strategies identified among bacterial taxa within the same phylum (Stone et al. 2023). This was evidenced in our study, as despite identifying a greater abundance of Pseudomonadota-affiliated genera in the low C soils of Kaiaraara Forest, Pseudomonadota (formerly Proteobacteria (Oren and Garrity 2021)) are generally considered copiotrophs, exhibiting nutritional preferences for readily available, labile pools of soil C (Lladó et al. 2017; Fierer et al. 2007; Barberán et al. 2011).

4.2 | Bacterial Community Growth Rate Remained Stable Until the Most Intense States of Disturbance

Bacterial community growth rate is an important indicator of soil ecological functioning and resilience, influencing nutrient cycling efficiency, organic matter turnover, competition against pathogens, disease suppression and the capacity of soil microbiomes to respond and adapt to environmental change (Osburn et al. 2024; Foley et al. 2024; Mazzola 2004; Fierer 2017). In our study, bacterial community growth rates showed little variation with increasing forest disturbance, except at the most intensively disturbed site of Kaiaraara Forest, where growth rates were markedly lower. These findings indicate a degree of resistance in bacterial community growth rates to increasing forest disturbance, up to a potential tipping point reached under the most intense states of disturbance in Kaiaraara Forest. The low growth rates at this forest site, together with reduced diversity of functional genes and a low abundance of C-degrading genes, indicate a diminished capacity to support critical soil ecological processes, including nutrient cycling, C turnover and pathogen suppression. Collectively, these findings suggest that the soil bacterial communities in Kaiaraara Forest may have limited functional resilience, potentially compromising the forest's long-term ability to respond and adapt to future environmental stress. Previous research identified that, globally, bacterial growth rates positively correlate with ecosystem productivity, soil C and C/N ratio and negatively with soil pH (Osburn et al. 2024). These findings may explain the low bacterial community growth rates in soils from Kaiaraara Forest, which had the lowest soil %C and C/N ratios, and the highest soil pH values compared to the other forests. It is important to note that our analysis did not identify a strong correlation between bacterial community growth rate and total soil %C or the soil C/N ratio. However, this may be due to the J-shaped distribution observed in bacterial community growth rate along our forest disturbance gradient, as discussed earlier in this section.

4.3 | Patterns in the Diversity of Bacterial Taxa Followed a Non-Unimodal Diversity–Disturbance Relationship

The most disturbed forest in our study, Kaiaraara Forest, had the highest diversity of bacterial taxa compared to the other kauri forests. Despite this, many other key metrics of the soil bacterial communities were lower in Kaiaraara Forest, such as the predicted growth rate, genome size, functional gene diversity and abundance of C-degrading genes. Thus, the impact of forest disturbance on the diversity of soil bacterial taxa did not mirror the effects of those same disturbances on soil bacterial community growth rate and function. The high taxonomic diversity but low genome size and functional gene diversity of soil bacterial communities in Kaiaraara Forest may suggest functional redundancy among the resident bacterial taxa. Although soil microbial diversity is commonly applied as an indicator of soil health (Van Der Heijden et al. 2008; Fierer et al. 2021), this metric is flawed due to the high functional redundancy observed in soil microbiomes,

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with microbial species richness and diversity having been identified as weak and inconsistent indicators of microbial functionality and contribution to ecosystem services (Nielsen et al. 2011; Miki et al. 2014; Chen et al. 2022). We observed this in our study, particularly for bacterial soil C cycling. Despite having a high diversity of bacterial taxa, the lower abundance of bacterial C-degrading genes in Kaiaraara Forest suggests that these soil microbes have a lower genomic capacity to mineralise soil C. This may reflect a shift in microbial resource-acquisition strategies, as soil microbes reduce metabolic energy costs under the low-C soil environment associated with Kaiaraara Forest. Moreover, microbial diversity may be a flawed indicator of soil health as patterns in soil bacterial diversity are often strongly correlated with soil pH (Fierer et al. 2021). As discussed earlier, the higher soil pH values observed in Kaiaraara (~pH 6) may be a factor influencing the higher diversity of bacterial taxa. However, for the case study of kauri forests, an increased soil pH signals that the ecosystem is moving away from the 'normal' baseline state, as an acidic soil environment (~pH 4) is a characteristic trait that typifies kauri forest ecosystems across Aotearoa New Zealand (Wyse et al. 2014).

Interestingly, on the opposite end of the disturbance intensity gradient examined in our study, kauri forests associated with the lowest disturbance (Hirakimatā and Puketī) also had a relatively high diversity of bacterial taxa compared to the intermediately disturbed forests. Thus, patterns in the diversity of bacterial taxa displayed a bimodal response to increased disturbance intensity (i.e., non-unimodal diversity-disturbance relationship; (Gibbons et al. 2016)), with both the highest and lowest intensively disturbed forests having relatively high diversity of soil bacterial taxa compared to the intermediately disturbed forests. This finding goes against previous research that identified moderate disturbance incidences to stimulate an increase in microbial diversity (i.e., intermediate disturbance hypothesis; (Gibbons et al. 2016; Santillan et al. 2019; Santillan and Wuertz 2022)), as we identified the lowest diversity of bacterial taxa in the intermediately disturbed kauri forests.

4.4 | Patterns in Average Bacterial Genome Size Followed a Unimodal Diversity–Disturbance Relationship

In contrast to patterns observed in the diversity of bacterial taxa, the average bacterial genome size displayed a unimodal response to increased forest disturbance intensity (unimodal diversity-disturbance relationship; (Gibbons et al. 2016)). Put simply, we observed a low average bacterial genome size in soils from the most (Kaiaraara) and the least (Hirakimatā and Puketī) disturbed kauri forests and a higher average genome size in moderately disturbed forests. This finding partially goes against our original hypothesis that disturbance intensity would reduce the functional capacity of the soil microbiome, as we observed increases in average bacterial genome size under moderate levels of disturbance intensity. However, this finding does support the intermediate disturbance hypothesis, as moderate disturbance intensities were associated with a larger bacterial genome size (Gibbons et al. 2016; Santillan et al. 2019; Santillan and Wuertz 2022). Previous research has identified genome size as a potential indicator of soil health, with one study identifying higher soil health ratings associated with lower microbial genome sizes (Wilhelm et al. 2023). Soil microorganisms with a greater genome flexibility demonstrate a better ability to respond and adapt to fluctuating environmental conditions following successive disturbance events (Rodríguez-Gijón et al. 2021; Simonsen 2022). Thus, the increase in average bacterial genome size in moderately disturbed kauri forests may stem from the selection of soil bacteria with a broader range of functional traits, which enables them to respond physiologically and metabolically to environmental instability. In contrast, the stable environmental conditions associated with the low-disturbance kauri forests of Hirakimatā and Puketī may have favoured soil microorganisms with smaller – and thus less energetically costly – genome sizes due to reduced pressure for metabolic flexibility to adapt to changing environmental conditions (Rodríguez-Gijón et al. 2021). In contrast, the low average bacterial genome size observed in Kaiaraara Forest may be driven by genome streamlining, which describes the loss of non-essential microbial genes to minimise energy costs under extremely low nutrient and resource availability (Simonsen 2022; Giovannoni et al. 2014). Overall, the unimodal response of bacterial genome size to disturbance intensity indicates that moderate disturbance may favour soil microbial communities with greater functional and metabolic flexibility, which could support kauri forest resilience under variable environmental conditions by enabling them to be more adaptive to change.

4.5 | Study Limitations

This study did not examine the effects of forest disturbance on the soil fungal communities associated with kauri forests. Given their key role in forest ecosystems (Baldrian 2016; Voříšková et al. 2014), assessing how disturbance intensity affects soil fungal functional attributes is essential for evaluating long-term forest health and resilience. Thus, further studies are needed to examine the impacts of forest disturbance on the growth and function of soil fungal communities associated with kauri forests. Previous research had identified significant differences in the diversity and composition of soil fungal communities between kauri trees symptomatic and non-symptomatic of dieback disease (Byers, Condron, O'Callaghan, et al. 2020). However, this research was limited to studying one kauri forest region; thus, it did not capture the variability in ecological disturbances afflicting modern-day kauri forest landscapes, such as those captured across the nine kauri forests investigated in this study.

5 | Conclusions

Our findings demonstrate that forest disturbance significantly alters the growth, diversity and functional traits of soil bacterial communities in kauri forests. Predicted bacterial growth rates remained relatively stable with increasing disturbance until the most severely impacted site, Kaiaraara Forest, where they declined sharply. Soils from Kaiaraara Forest exhibited reduced functional gene diversity and smaller average genome sizes, which may constrain the adaptive capacity of soil bacterial communities and limit the long-term resilience of this forest to future environmental change. Compared to the less disturbed kauri forests, Kaiaraara Forest soils had a lower abundance of bacterial C-degrading genes and a higher abundance of many

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central C metabolism genes, indicating potential shifts in microbial resource acquisition strategies in response to the low soil C environment. Consistent with the intermediate disturbance hypothesis, bacterial genome size was highest in the moderately disturbed kauri forests, suggesting that soil bacterial communities may adapt to moderate disturbance by favouring soil bacteria with a greater genome flexibility that enhance responsiveness to environmental instability. Despite having a lower functional capacity, soil bacterial communities associated with the most intensively disturbed kauri forest (Kaiaraara) had the highest diversity of bacterial taxa, potentially driven by the near-neutral soil pH observed in this site (~pH 6), which contrasts strongly with the typically acidic conditions observed in kauri forest soils (~pH 4). Overall, our results highlight the contrasting responses of soil bacterial communities to disturbance, with the most disturbed forest supporting high taxonomic diversity despite reduced genome size and growth potential. These findings have important implications for monitoring the soil microbiome and understanding its role in maintaining soil ecosystem health. Traits such as functional gene diversity, genome size and growth-related attributes may serve as sensitive indicators of disturbance intensity and ecosystem resilience, providing a framework to assess soil recovery and guide restoration priorities in kauri forest management. While these results advance our understanding of how disturbances impact kauri soil bacterial communities, further research is needed to evaluate the effects on soil fungal communities. Given the critical role of fungi in supporting forest ecosystem health, examining their response to disturbance is essential for assessing the long-term health and resilience of kauri forest ecosystems across Aotearoa New Zealand.

Author Contributions

Alexa K. Byers: conceptualization (equal), formal analysis (equal), investigation (equal), methodology (equal), validation (equal), visualization (equal), writing – original draft (equal), writing – review and editing (equal). **Leo Condron:** supervision (equal), writing – review and editing (equal). **Nick Wairapa:** supervision (equal), writing – review and editing (equal). **Amanda Black:** conceptualization (equal), funding acquisition (equal), project administration (equal), supervision (equal), writing – review and editing (equal).

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

Metagenomic datasets generated in this study are available in the Aotearoa Genomic Data Repository (https://data.agdr.org.nz) under the project codes AGDR00081: https://doi.org/10.57748/q89d-d037, AGDR00086: https://doi.org/10.57748/q89d-d037, and AGDR00087: https://doi.org/10.57748/q89d-d037.

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