Soil microbial genomic responses to aridity-driven elemental imbalance across global biomes

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Abstract

Aridification is known to disrupt soil biogeochemical cycles by altering the stoichiometry of key elements, such as carbon (C), nitrogen (N) and phosphorus (P). However, how soil microbiome metabolically responds to these imbalances, and the resulting implications for terrestrial ecosystem services, remain virtually unknown. By analyzing soil samples from 200 ecosystems across globally distributed biomes, our results revealed an overall microbial genomic adjustment to elemental imbalances driven by aridity. Genes involved in microbial anabolism were promoted with aridification, whereas those associated with catabolism were suppressed. Thus, while genes encoding extracellular enzymes responsible for the degradation of litter and organic matter decreased, genes related to RNA transcription and the synthesis and transport of intracellular proteins essential for microbial resistance and growth increased. Collectively, our findings highlighted that aridity-driven soil elemental imbalances are strongly associated with shifts in soil microbial metabolism from catabolism to anabolism, reflecting a microbial survival strategy that prioritizes growth over energy and nutrient acquisition under global-scale aridification.

Introduction

Global-scale changes in aridification have been widely recognized as disrupting the fundamental stoichiometric relationships that sustain terrestrial ecosystems [1–3], leading to worldwide elemental imbalances in the cycling of soil organic carbon (SOC), nitrogen (N), and phosphorus (P) (e.g., altered soil C:N, N:P, and C:P ratios) [1,2,4]. For example, low precipitation in arid ecosystems often results in both limited plant productivity (reducing litter-derived organic C and N inputs) and a greater relative availability of P, resulting in low soil C:P and N:P ratios [5]. In contrast, the predominantly abiotic origin of P from bedrock [6], unlike the biological fixation of C and N from the atmosphere, contributes to the higher soil C:P and N:P ratios in wetter ecosystems. These ecological imbalances should be particularly impactful for soil microbes because of their dependence on cellular elemental homeostasis and their intimate link to soil biogeochemistry [7]. Although soil microbes are among the most diverse and abundant organisms on the planet and provide essential ecosystem services that are crucial for human well-being (e.g., food security and climate action) [8,9], little is known about the genomic responses of the soil microbiome under aridity driven elemental imbalances [10]. A deeper understanding of how the soil microbiome respond to aridity-driven changes in soil biogeochemistry is essential for better predicting the fate of soil microbes in a changing world.

Two primary scientific barriers contribute to the current uncertainties regarding the responses of the soil microbiome to climate-driven elemental imbalances. First, there is a significant lack of a global-scale standardized database that simultaneously integrates information on stocks and pools of soil organic C, N, and P with high-resolution functional genomic data such as metagenomes. Most studies have been limited to local scales; however, a global-scale approach is essential because soil elemental imbalances occur at the macroecological level across global biomes, from deserts to tropical forests [11]. Second,

changes in soil C:N:P ratios and/or elemental imbalances may result in important alterations in microbiome metabolism [12]. Recent advances in trait-based microbial ecology have suggested potential trade-offs between anabolism and catabolism [13,14]. For example, a recent study from a successional chronosequence in a subtropical region of China demonstrated that P limitation over time increases the abundance of genes involved in the degradation of recalcitrant compounds, such as lignin and its aromatic derivatives, to acquire P resources [15]. Yet, empirical evidence for such potential responses and itheir consequences on various soil processes, including soil organic C sequestration and nutrient cycling, remains limited on a global scale [16]. Previous studies have highlighted the need for generalizable frameworks for microbial responses to disturbances to enhance our understanding and predictability of ecosystem stability [17]. Understanding these microbial shifts is vital as they may reshape the delivery of terrestrial ecosystem services in the context of climate change [18].

Here we put together a global topsoil survey encompassing 200 terrestrial ecosystems was conducted across all major biomes, from deserts to tropical regions, and across a diverse array of vegetation types, including forests, grasslands, and shrublands (Figs. 1a and 1b). Our objective was to investigate how the soil microbiome responds to aridity-driven elemental imbalances across global environmental gradients [2]. To achieve this, we integrated data on soil C, N, and P stocks as well as stoichiometric ratios with shotgun metagenomic sequencing. This metagenomic approach enabled us to characterize microbial metabolism—both anabolic and catabolic—by analyzing key functional genes and metabolic pathways (a detailed list of genes involved in each metabolism is available in Table S1). The aridity index (mean annual precipitation (MAP) / potential evapotranspiration) was utilized as a proxy for water availability [19], given its capacity to account for both the natural input of water into the ecosystem and potential losses resulting from evapotranspiration. We opted for water availability for simplicity because the aridity index can be counterintuitive (i.e., a higher aridity index indicates greater water availability). Initially, we identified the primary environmental factors associated with soil C:N:P ratios and pinpointed the tipping points in stoichiometric ratios using machine-learning approach. Subsequently, we identified the key anabolic and catabolic genes involved in soil elemental imbalances and examined how these genes are associated with organic C, N, and P contents on a global scale. Based on the Metabolic Theory of Ecology [12], we hypothesized that soil microbes respond to aridity-driven elemental imbalances by shifting their metabolism to enhance anabolism (e.g., resistance to drought stress and sustained growth) while suppressing catabolism (e.g., synthesizing extracellular enzymes for energy and nutrient acquisition).

Results and discussion

Our study offers new insights into the capacity of microbiomes to respond to global-scale soil elemental imbalances driven by changes in aridity. Consistent with existing literature, ecosystems with lower water availability (i.e., a lower aridity index or higher aridity) demonstrated reduced net primary productivity (NPP) and lower soil C:P and N:P ratios (Fig. 1). Moreover, the random forest analysis indicated that both anabolic and catabolic genes were significant predictors of soil elemental ratios (Fig. 2). This suggests

that soil microbiomes may prioritize specific metabolic strategies for survival under soil elemental imbalances resulting from aridification. For example, in arid environments characterized by lower soil C:N and N:P ratios, likely due to diminished organic matter inputs under less productive conditions, the abundance of genes associated with anabolism, such as those involved in RNA transcription and the synthesis and transport of intracellular proteins were increased. This response aims to sustain microbial growth under stressed conditions. Lower soils C:N and N:P ratios were associated with suppressed catabolism, as indicated by the reduced abundance of genes responsible for the degradation of litter and organic matter, processes that facilitate the extraction of N and P (Figs. 2 and 3). Collectively, our findings suggest that the microbiome employs metabolic strategies that involve shifts between catabolism and anabolism in response to worldwide soil elemental imbalances. These microbial metabolic shifts, necessary for survival under stoichiometric imbalances, can diminish the capacity of terrestrial ecosystems to provide multiple ecosystem services such as declining C reservoirs [20], and may further compromise ecosystem stability. For instance, the suppression of genes involved in catabolism result in decreased degradation and transformation of external organic matter into the soil [21], which could impair soil aggregate stability and moisture retention, making the soil more susceptible to erosion and subsequent nutrient depletion. This understanding is critical to better anticipate changes in the soil microbiome, the most abundant and diverse organism on the planet, and their ecological functions in the context of climate change.

Aridity-driven soil elemental imbalances

As anticipated, global-scale aridification— and its impact on ecosystem productivity— played a central role in driving soil elemental imbalances [2]. This finding is crucial for addressing our novel research question: how does the microbiome responds to soil elemental imbalances driven by changes in water availability across global environmental gradients? Decreases in water availability were associated with a relative deficiency of organic C compared with N and P in soils, resulting in declines in soil C:N and C:P ratios, particularly in low-productivity ecosystems. Random forest analysis identified climate variables as strong predictors of variation in soil C, N and P contents (Fig. S1). When combined with other environmental factors,— such as soil physicochemical properties, geography, and vegetation type—, these variables accounted for up to 73% of the observed variation (Figs. S1 and S2). Further analysis revealed that water availability and NPP were the most influential drivers of global variation in the soil C:N, N:P, and C:P ratios (Fig. 1c). Reduced plant productivity can lead to lower soil N:P ratios as N becomes relatively deficient in more arid regions owing to the constrained microbial decomposition of plant litter (Figs. 1d and S3) [22] and decreased biotic N fixation activities [23]. Although most P fractions remained relatively stable with changing water availability, the content of mineral P (represented by primary P) increased significantly with decreasing NPP ($P < 0.05$), likely due to reduced plant uptake (Fig. S4) [24]. Notably, in these biologically inactive ecosystems, diminished plant productivity contributes to lower soil organic C accumulation through decreased inputs of litter and root exudates, further exacerbating elemental imbalances (i.e., lower soil C:N and C:P ratios) (Figs. 1d and S4) [25]. Beyond the conclusion that both C and N stocks and pools are the primary limiting factors for soil microbial growth

in drylands [2], these results provide evidence that their stoichiometric balance will become increasingly significant in light of climate change consequences, such as heightened aridity.

Soil microbiome responses to aridity-driven element imbalances

We further demonstrated that soil microbiomes support a diverse array of taxonomic and genetic responses to elemental imbalances driven by global-scale changes in aridity. First, we explored the correlation between variations in C:N:P and water availability with soil microbial taxa. As expected, soil microbial taxa largely respond to water availability and element imbalances across environmental gradients. For example, the relative abundance of Chloroflexi is known to be greater under low water availability and C:P and N:P ratios (Fig. S5) [26,27]. Similarly, the relative abundance of Acidobacteria, Verrucomicrobia, and Rhizaria were positively correlated with water availability and C:P and N:P ratios ($P < 0.05$) (Fig. S5). Although microbial taxonomic responses to nutrient imbalances have been previously investigated at a local and regional scales, our study provides novel insights on their responses across global biomes. Moreover, much less was known about the responses of microbial functional genes to aridity-driven elemental imbalances. Here, we showed that functional microbial genes and metabolic pathways were associated with the soil elemental stoichiometry (Fig. 2). For example, functional genes and metabolic pathways annotated in the Kyoto Encyclopedia of Genes and Genomes (KEGG) database, along with carbohydrate hydrolases from the Carbohydrate-Active Enzymes (CAZy) database, accounted for up to 51% of the observed variation in soil C, N, and P content (Figs. S6 and S7). In addition, functional genes and metabolic pathways categorized as cellular processes, as well as genetic and environmental information processes (among others), collectively explained up to 24% of the observed variation in the soil C:N, N:P, and C:P ratios (Fig. 2). Specifically, the abundance of genes associated with transcription, protein synthesis and microbial growth increased in soils with lower C:N and C:P ratios, primarily because of the reduced SOC (Figs. S8 and S9). Regarding the soil C:P ratio, microbial metabolism exhibited a lower [28], yet still significant explanatory power (2–5% of the variation), with environmental variables accounting for up to 50% (Figs. 1c and 2). Collectively, our findings indicate that the community composition, diversity and metabolism of the soil microbiome are strongly correlated with aridity-driven soil elemental imbalances, particularly the deficiency of organic C.

Soil elemental imbalances, particularly the relative scarcity of organic C compared with N and P, associated with shifting climatic conditions in areas with low water availability, were associated with changes in microbial metabolism from catabolic to anabolic processes. As the soil C:N, N:P, and C:P ratios decreased, we observed significant increases in genes and pathways related to anabolism, such as nucleotide replication, RNA transcription, and protein folding, sorting, and transport, under conditions of relative soil organic matter deficiency (characterized by reduced organic C and N content; $P < 0.05$) (Figs. S8 and S9). These findings suggest that arid environments, which lead to relative organic C deficiency, limit microbial investment in organic P mineralization and chitin degradation (as indicated by the gene clusters of *phn* and *chi*). Conversely, this conditions accelerated inorganic P transports (as indicated by the *pstA* gene) [29] and N assimilation, including the synthesis of glutamic acid (as indicated

by the *glt* gene cluster) (Fig. 3) [30]. This outcome is theoretically expected because microbial cellular processes, such as biomass production, require substantial amounts of N- and P-rich molecules including proteins and ATP [31]. Further analyses consistently revealed increased relative abundance of genes associated with the synthesis and transport of proteins (as indicated by *secG*, *pcnB*, and *cysM*) under arid conditions with lower soil C:N ratios ($P < 0.05$; Figs. S8 and S10a). Consequently, phospholipid synthesis appears to be compromised compared with the synthesis of proteins and/or carbohydrates under these organic C-limited conditions (Figs. S8 and S9), as microorganisms require more ribosomal RNA to synthesize osmolytes, biofilms, and cell walls to withstand drought [32]. As such, genes encoding intracellular protein and polysaccharide synthesis (e.g., protein processing in the endoplasmic reticulum, phosphoglycerate synthase, and murein polymerase) also exhibited negative correlations with the soil C:P and/or N:P ratios ($P < 0.05$; Figs. S8 and S10b). Murein and phosphoglycerate are critical intermediates in bacterial cell wall synthesis [33,34], whereas protein synthesis in the endoplasmic reticulum is essential for microbial survival in stressed environments [35]. Collectively, these results support our hypothesis and indicate that aridity-driven soil elemental imbalances shift microbial metabolism by activating anabolic processes, that are crucial for microbial resistance and survival in arid environments.

Conversely, in wetter regions with higher organic C content (i.e., elevated soil C:P and C:N ratios), an increased abundance of genes associated with catabolism was observed. Higher organic C resources can stimulate soil microbiome activity, which in turn requires more N and P [36]. As N and P become less available, soil microbes must mine organic matter using extracellular enzymes to access the limiting nutrients [37,38]. We found that genes encoding extracellular enzymes that degrade recalcitrant soil organic matter, such as terpenoids, polyketides [39,40], and arylesters [41], were relatively increased ($P < 0.05$) in soils with relative N and P deficiencies (Figs. S8). For example, the abundance of genes associated with the degradation of aromatic compounds (e.g., *aliA* and *tfdB*), and root exudates such as terpenoids (e.g., *mlhB* and *chnC*) increased in soils with higher organic C (Figs. S11a, S11b and S12). Consistently, we observed an increased abundance of genes associated with signal transduction and membrane transport in soils with higher C:P ratios, which are essential for the production and secretion of extracellular enzymes (Figs. 2a and 2b) [7].

Microorganisms with well-developed synthesis and secretion systems for extracellular enzymes can survive better in nutrient deficient soils [42] because catabolically degrading enzymes release nutrients and energy for microbial uptake (Figs. 2c) [43]. For example, in nutrient-stressed environments, such as those found in areas with high water availability [44], the soil microbiome exhibits overflow metabolism of energy to mineralize organic matter [45]. As evidence, the relative abundance of *phn* gene clusters, which mediate the catabolism of organic P (i.e., phosphonates [46]) increased in soils with high SOC content and elevated C:P and C:N ratios (Fig. 3c). These results align with those of a study demonstrating microbiome-driven coupling of soil C and P in agroecosystems [47]. Furthermore, we observed positive correlations between the C:P ratio and the relative abundance of genes encoding *gcd*, which are involved

in the production of organic acids and subsequent mineral P solubilization [48]. However, we did not find any correlation with the phosphatase gene (*phoD*) (Fig. 3). These results underscore the significance of P solubilization processes in addressing nutrient imbalances caused by climatic conditions, suggesting that P solubilization can be a potential response to P deficiency in comparison to mining organic matter at the global scale. Similarly, we found that nutrient deficiency associated with the increased abundance of genes regulating bacterial flagellar assembly (i.e., the *flg* gene cluster) that are related to motility (Fig. S11c and S12). Enhanced motility increases opportunities for microorganisms to access nutrient-rich environmental patches [49]. The promotion of extracellular enzyme production and motility requires significant energy derived from the consumption of organic C [50]. In this context, increases catabolism of organic matter degradation was observed (Figs. S11a, S11b and S12). Collectively, our findings support our hypothesis that enhanced catabolism at the expense of organic matter represents a potential strategy for the microbiome to cope with elevated C:N and C:P ratios in the environment. Previous studies have reported increased microbial catabolism in stressful environments [51], whereas microbial catabolism tends to decrease in fertile soils, which are typically characterized by higher organic C content [52]. Intriguingly, in this study, we found that microbial catabolism is still elevated in fertile soils, albeit with elemental imbalances.

Potential consequences of shifting from catabolism to anabolism

Our study suggests that aridity-driven soil elemental imbalances may reshape microbial metabolic strategies, with possible cascading consequences on terrestrial ecosystem services. Specifically, elevated abundance of genes involved in anabolism (e.g., microbial growth) may enhance soil microbial resistance and survival under drought stress. Conversely, catabolic processes (e.g., extracellular enzyme production) are suppressed, resulting in diminished degradation of external organic matter and its transformation to soil organic C pools and stocks [20]. For instance, decreases in SOC content were accompanied by a reduction in the abundance of genes encoding the transport and synthesis of xylanase, alpha- glucosidase, and beta-glucosidase ($P < 0.05$; Fig. S9). These opposing effects can destabilize the C-climate feedback loop, particularly in C-limited ecosystems. However, the negative correlations between SOC contents and the abundance of genes encoding chitosanase ($P < 0.05$; Fig. S9) suggest that microbial anabolism can, to some extent, fuel long-term C stabilization through mineral-reactive compounds (e.g., cell wall residues and extracellular polymers [53]).

The adoption of anabolic processes as a survival strategy in response to aridity-driven elemental imbalances may compromise ecosystem stability. The resulting decline in the abundance of genes associated with anabolic processes is intrinsically linked to a reduced capacity to degrade and transform external organic matter into soil organic C pools and stocks [53]. This can lead to diminished soil aggregate formation and water retention, resulting in more erodible soils and nutrient loss. Furthermore, alterations in microbial metabolic processes can reshape the nutrient cycling in terrestrial ecosystems. For instance, studies have demonstrated that increased N availability through fertilization can enrich

genes involved in catabolism [53]. To address resource imbalances, soil microbes may release a greater proportion of organic N as ammonium, thereby modifying N mineralization and terrestrial nutrient cycling [54]. An interesting question remains as to whether changes in soil structure and nutrient availability, driven by metabolic shifts, could affect soil microbial composition and diversity. It is postulated that microorganisms specializing in rapid resource degradation through catabolic genes (e.g., saprophytic fungi) may be favored over other microbial groups with higher energy demands, such as N-fixing bacteria, whose activity relies on energy-demanding anabolic processes. This finding supports those of previous studies, indicating shifts in the fungal:bacterial ratio relative to the stoichiometric ratios of soil elements [26]. If confirmed, it is essential to understand how soil food webs and their functional diversity change, as well as the implications for key ecosystem services when catabolism transitions to anabolism. Our study lays the groundwork for future research to validate these hypotheses and underscores the necessity of expanding sampling efforts across larger and more diverse regions to derive more robust and global patterns.

Conclusion

Taken together, our findings provide novel insights into global-scale responses of the soil microbiome to soil elemental imbalances caused by global-scale changes in aridity. As water availability decreases, ecosystems become less productive and support reduced input of soil organic C, whereas soil N and P become comparatively more available. These soil elemental imbalances were significantly associated with increases in the relative abundance of functional genes and metabolic pathways associated with microbial anabolism, as well as decreases in genes associated with catabolism, particularly those involved in the degradation of external organic matter, especially in recalcitrant forms (Fig. 4). The shift in microbial metabolism from catabolism to anabolism may further influence the capacity of soils to sequester C and provide nutrients, thereby compromising ecosystem services. These findings are crucial for anticipating the future of the soil microbiome under climate change and suggest that soil microbiomes possess a wide array of genetic tools to acclimate to aridification; thus, they prioritize drought resistance and survival over energy and nutrient acquisition.

Methods

Global field survey

We collected topsoil samples (~ 0–10 cm) from 200 ecosystems across all continents to investigate the adaptation strategies of the soil microbiomes in response to climate-driven elemental imbalances. These sampling sites encompassed a variety of ecosystem types, including temperate seasonal forests, tropical seasonal forests, temperate grasslands, tundra grasslands, subtropical woodlands, and shrublands, providing a comprehensive representation of the terrestrial environmental conditions found on Earth (Fig. 1a). The latitude, elevation, and slope of each sampling site were recorded *in situ* using a portable GPS unit. Vegetation types were classified for each location based on the dominant species. A

portion of the soil samples was frozen for molecular analyses at -20°C, whereas the remaining samples were air-dried for biogeochemical analyses.

Climate and ecosystem productivity

The MAP, which ranges from 81 to 2,161 mm; mean annual temperature (MAT), ranging from − 3.5 to 24.8°C; seasonality of precipitation (PSEA); seasonality of temperature (TSEA); and the mean diurnal range of temperature (MDR) for the sample sites were obtained from interpolations provided by WorldClim (http://www.worldclim.org/). We also measured NPP and plant cover as proxies for the functional traits of the vegetated ecosystems across all sampling sites. Perennial vegetation cover was measured *in situ* at each site using the line-intercept method. We used the normalized difference vegetation index (NDVI) as a proxy for NPP, which was obtained from the Moderate Resolution Imaging Spectroradiometer (MODIS) aboard NASA's Terra satellites (http://daac.ornl.gov/index.shtml) at a resolution of 250 m. We believe that the choice of productivity period will not affect our results, as we used average values derived from normalized difference vegetation index measurements taken during the month before, during, and after the sampling dates at each surveyed plot.

Determination of soil C, N and P content

The contents of each component of C, including total organic C, mineral-associated organic C, particulate organic C and total inorganic C; N, comprising total N and dissolved inorganic N; and P, which includes total P, primary P, occluded and non-occluded P, organic P, residual P, and available P, were measured. The total P content of the soil was determined using sodium hydroxide fusion method [55]. Particulate organic C and mineral-associated organic C were separated using a combined density and particle size fractionation method [56]. Inorganic (plant-available) N was measured using a continuous-flow stream autoanalyzer (SEAL-AA3, Norderstedt, Germany). Soil non-occluded P, occluded P, and organic P were quantified using the sequential extraction procedure developed by Hedley et al. in 1982 [57] and modified by Guppy et al. in 2000 [58]. Soil organic C and total N were analyzed using a combination of dichromate oxidation, the Kjeldahl method, and a Flash EA 1112 Series Elemental Analyzer connected via a Conflo III to a DeltaPlus XP isotope ratio mass spectrometer (all Thermo Finnigan, Bremen, Germany). In this study, the soil C:N, N:P and C:P ratios were calculated based on the ratios of soil organic C to total N, total N to total P, and organic C to total P, respectively.

Soil microbial composition and diversity measures

In this study, the diversities of soil bacteria, fungi, protists and invertebrates were measured using an Illumina MiSeq platform for amplicon sequencing. Soil DNA was extracted with the PowerSoil DNA Isolation Kit (MoBio Laboratories) following the manufacturer's instructions. The 16S rRNA gene for bacteria and the 18S rRNA gene for eukaryotes were sequenced using the 341F/805R [59] and

Euk1391f/EukBr [60] primer sets, respectively. The bioinformatic analyses were performed using a combination of QIIME [61], USEARCH [62] and UNOISE3 [63]. The sequences were clustered into soil phylotypes—zOTUs—at a 100% identity level. The representative sequences of zOTUs were annotated against the SILVA (16S rRNA gene) [64] as well as PR2 and SILVA (18S rRNA gene) [65] databases. Before analyses, the zOTU abundance tables were rarefied at 10,000 (for bacteria) and 4,000 (for eukaryotes) sequences per sample to ensure an even sampling depth within each microbial group. Protists were defined as eukaryotic taxa, except fungi, Metazoa (invertebrates and vertebrates) and vascular and non-vascular plants (Streptophyta). Fungal guilds were characterized using the FUNGuild [66]. In this study, we used species richness, which represents the number of phylotypes, as a measure of soil microbial diversity since it is widely used and straightforward.

Metagenomic sequencing and bioinformatic analyses

Metagenomic sequencing was performed at the Next Generation Sequencing (NGS) Facility (Western Sydney University, Australia) using the Illumina NovaSeq platform, which generated approximately 10 Gb of high-quality 150 bp paired-end reads per sample. Clean reads were obtained after quality trimming, using fastp (version 0.20.1) to remove low-quality reads. Metagenome assembly was conducted using Megahit (v1.2.9) [67], retaining only contigs ≥ 1000 bp in length. Open reading frames of the assembled contigs were predicted using the Prodigal software (version 2.6.3). All open reading frames were compiled into a set of unique genes after clustering with CD-HIT at 95% sequence identity to create a non-redundant gene catalog [68]. Read counts and reads per million for each predicted non-redundant gene were calculated using Salmon (v1.10.3) [69]. To investigate how soil microbial metabolism respond to climate-driven elemental imbalances, the predicted genes were annotated against the eggNOG databases (v5.0) using eggnog-mapper (v2.1.12) [70], which provided KEGG Orthology (KO), KEGG pathway, and CAZy family profiles [71]. Before the analysis, genes associated with human diseases and those related to plant and macro-organism systems were excluded. The details of the three levels of KEGG annotation classification are presented in Table S1. The categories of KO-annotated genes involved in soil C degradation, as well as the N and P cycles, are detailed in Table S2.

Statistical modeling

Nonlinear regressions and threshold identification. In this study, we used the Akaike Information Criterion (AIC) in two steps to identify the most appropriate model for the relationship between soil C, N, and P content and environmental gradients in water availability and NPP [72]. The first step involved fitting both linear and nonlinear models, including quadratic models (the simplest form of nonlinear trends) and generalized additive models (GAMs) (which capture more complex trends through smoothing parameters). The lower AIC value for the nonlinear model suggests the existence of a threshold for water availability and NPP. In the second step, to investigate the threshold in each nonlinear regression, we defined thresholds as the points along the water availability and NPP gradients, where the soil C, N, and P contents changed abruptly (i.e., discontinuous thresholds or breakpoints) in relation to water availability and NPP (i.e., continuous thresholds). In the latter case, although an abrupt change in slope

was observed, more subtle and continuous changes that may involve high-degree polynomials were also considered. These changes are typically better represented by the GAM, where the changes in slope do not correspond to a sudden breakpoint, but rather indicate a point of maximum curvature. In both scenarios, despite being continuous, it remains possible to identify thresholds, and these values are reported, as they may provide critical information for their management.

Continuous thresholds can be effectively detected using segmented regression, which isa linear regression that modifies the slope at a threshold or through a more complex GAM regression. In contrast, discontinuous thresholds require an overall change in both intercept and slope. These can be accurately modeled using either step regression, which alters only the intercept at the threshold, or a combination of step and segmented regressions, termed segmented because they involve changes in both the intercept and slope at the threshold. The optimal model was selected based on AIC values. We performed 1,000 bootstrap samplings for each case to identify a set of 1,000 plausible thresholds from which we calculated the mean value as the final threshold value. These analyses were conducted using R packages *chngpt* and *gam*.

Correlation analyses. Spearman's correlation analysis was used to assess the relationships among individual variables along environmental gradients, including soil C, N, and P content, and the abundance of genes (modules) and their associated metabolic pathways. The strength and direction of these relationships are indicated by the correlation coefficients and *P* values. All *P* values were adjusted using the false discovery rate (FDR) [73]. Correlation analyses were conducted using the R package *psych*.

Random forest analyses. To identify potential functional gene modules that respond to variations in soil C, N, and P content, a predictive model utilizing a random forest machine learning method was established with 500 trees and 1,000 permutations implemented using the R package, *RandomForest* [74]. Cross-validation was conducted using the *rfcv* function to select the most appropriate features. The *rfPermute* function was used to estimate the *P* value for the significance of each predictor included in the random forest prediction results, whereas the importance of each predictor was represented by the percentage of the IncMSE value. In this study, only well-classified genes that changed significantly ($P < 0.05$) with soil elemental contents as well as their ratios were represented (Table S1). In addition, the tested parameters were log10 transformed before the analyses to normalize the variance when necessary. All statistical analyses were performed using R, version 4.3.0.

Declarations

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Author contributions

Conceptualization: M.D.-B., B.K.S., F.T.M, and Y.F.; Investigation: C.L., Y.F., T.S.S., C.X., D.E., N.G., Y.L.B.P., V.O., B.G., E.G., M.G.G., E.V., M.B., S.A., J.M.-V., B.J.M., A.A.B., N.A.C., S.A., J.A., F.A., A.I.A., M.B., F.B., N.B., B.B., M.B., C.B., S.C.H, B.D., J.D., C.I.E., A.F., L.F., A.G., L.G.V., K.G., T.G., E.G.M., L.K., M.K., L.L., P.C.I.R., P.L., J.L., A.L., M.A.L., P.M., G.M.-K., T.M., A.M., E.M., D.M., J.P.M., G.M., M.M.-R., A.M., T.U.N., G.N., S.N., C.P., Y.P., P.J.R., A.R., M.A.R.M., A.R., B.R.L., R.R., J.R., A.S., J.S., J.A.S., J.S., S.T., S.U., O.V., M.V., L.W., M.W., E.Z., G.Z., F.T.M., B.K.S., M.D.-B.; Methodology and visualization: C.L., C.X., Y.F. and M.D.-B.; Writing-review & editing: Y.F., C.L., M.D.-B., B.K.S., T.S.S, F.T.M. and C.X. with contributions of all authors.

Conflict of interest

The authors declare no competing interests.

Data availability

All raw sequencing data used in this study have been submitted to the NCBI Sequence Read Archive (SRA) database under the accession numbers PRJNA1162941 (shotgun metagenomics), PRJNA1249113 (16S rRNA gene amplicon), and PRJNA1249114 (18S rRNA gene amplicon). All the materials and protocols used in the article are available upon request and without restriction.

Code availability

All R codes supporting the conclusions of this article are included in figshare at https://doi.org/10.6084/m9.figshare.28829420.

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Figures

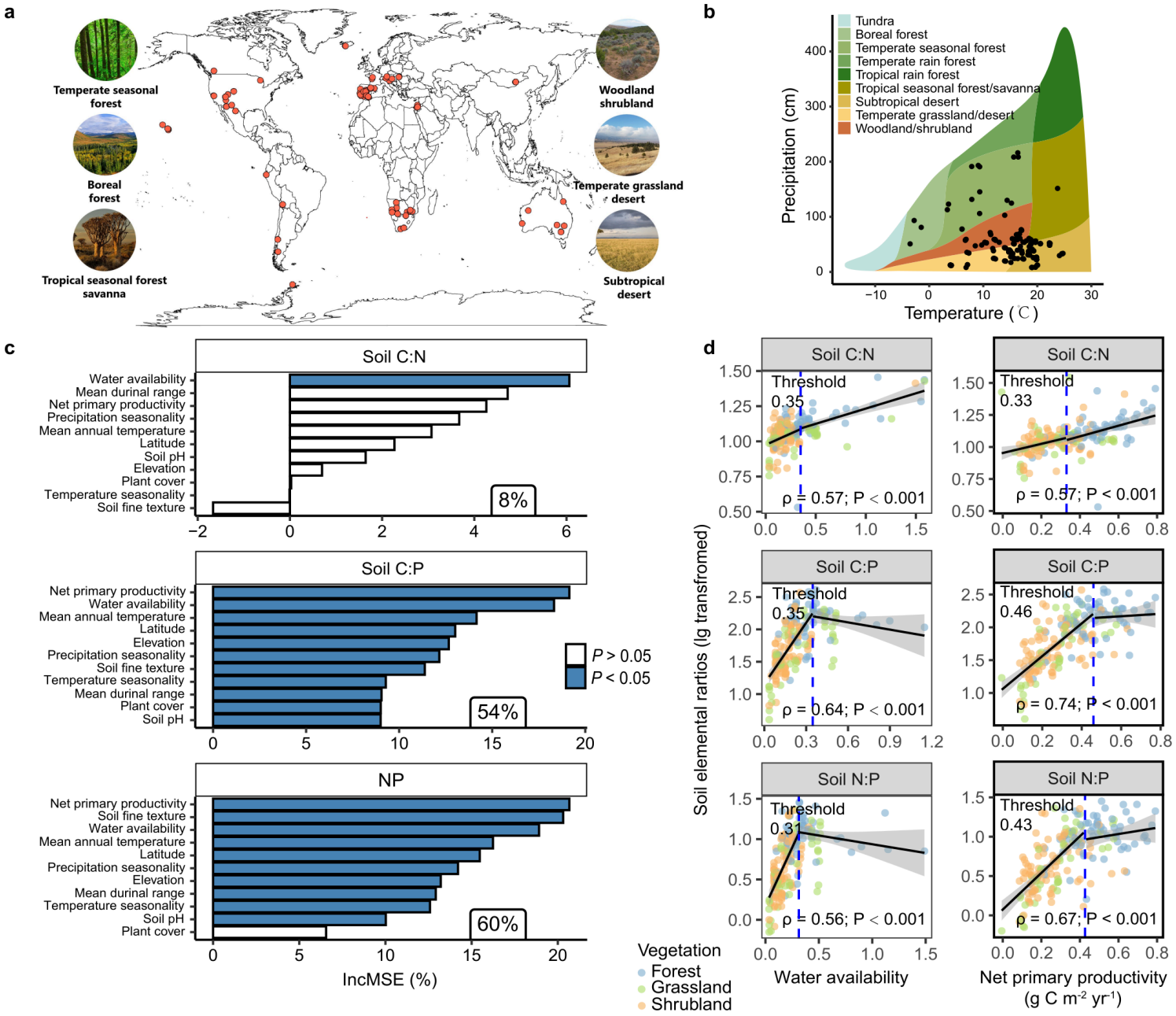

Figure 1

Locations of the 200 sampling sites studied (a). Distribution of sampling sites among climate (sub)zones based on Whittaker biomes (b). Random forest analyses identifying the main environmental factors predicting soil C:N, C:P and N:P ratios (c). Changes of soil C:N, C:P and N:P ratios along main environmental factors such as water availability and net primary productivity (d). Spearman's correlation coefficient is presented in each panel.

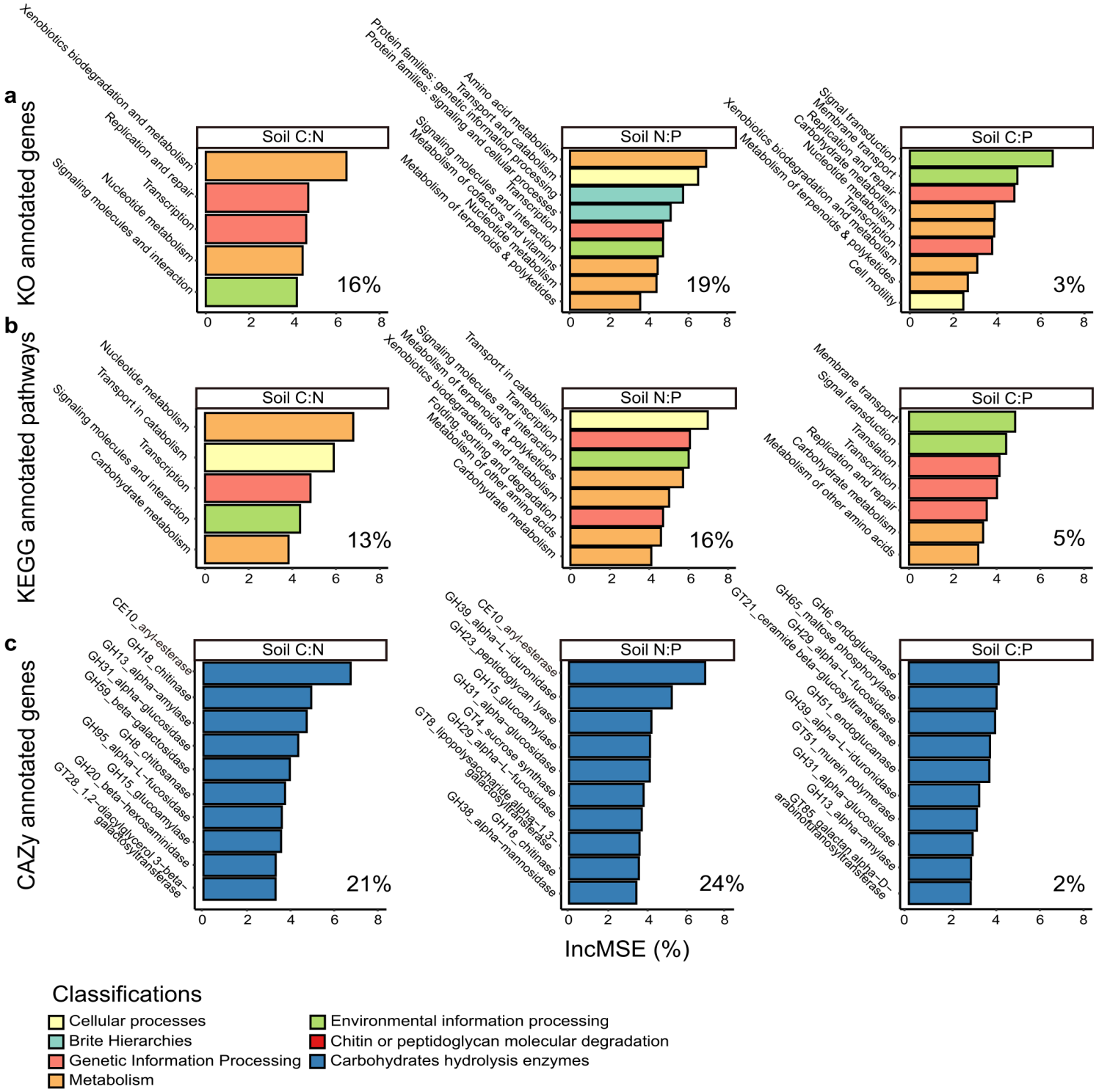

Figure 2

Random forest analyses identifying the key KO-annotated individual genes (a), KEGG-annotated metabolic pathways (b) and Carbohydrate-Active Enzymes -annotated carbohydrates hydrolysis gene modules (c) in response to changes in soil C:N, N:P and C:P ratios. Only well-classified genes that significantly changed (P<0.05) with soil elemental imbalances were represented in each panel.

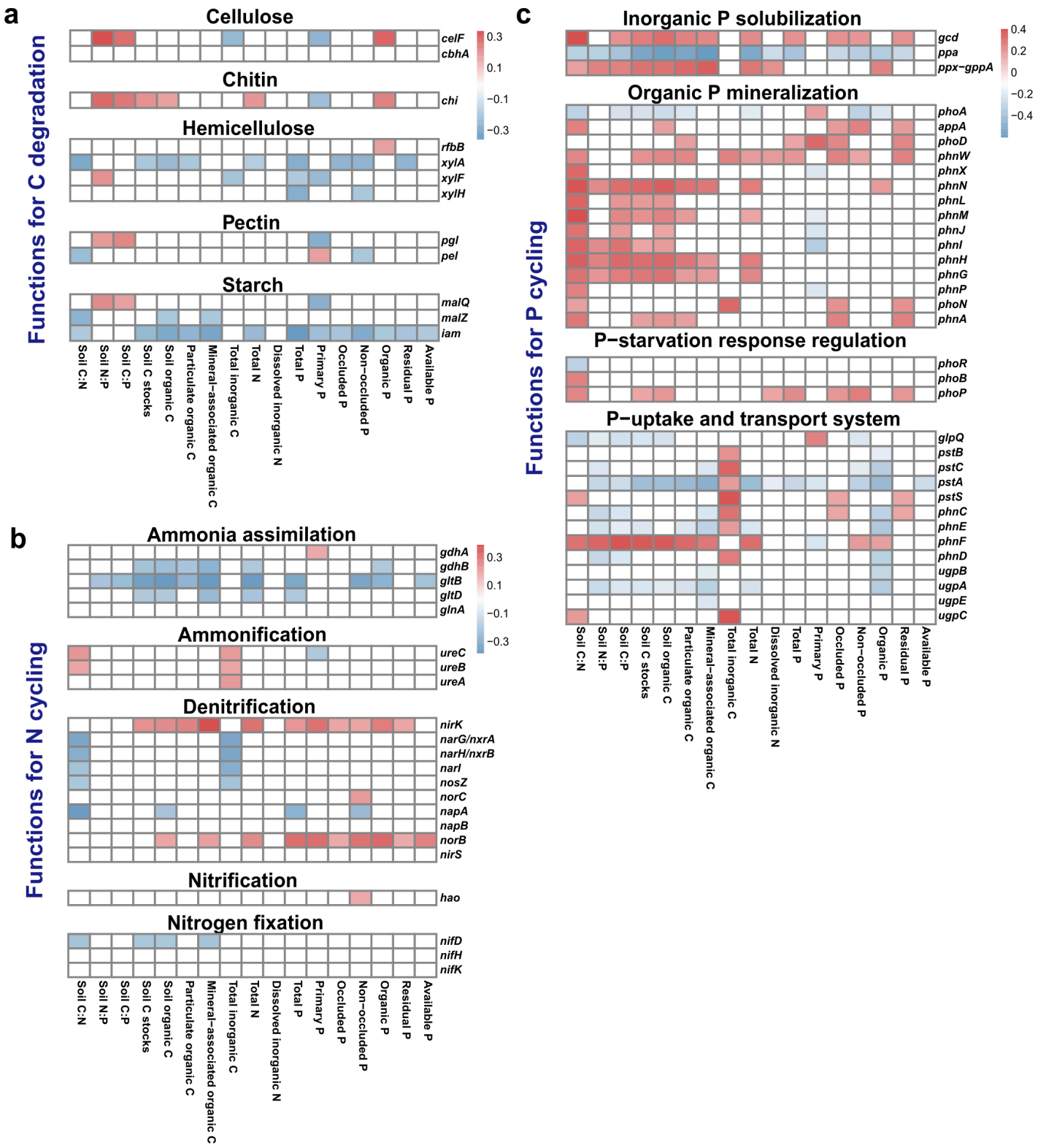

Figure 3

Correlations between the individual KO-annotated genes involved in soil C, N and P pools and contents.Red boxes represent significantly positive relationships ($\rho > 0$, $P < 0.05$), blue boxes represent significantly negative relationships ($\rho < 0$, $P < 0.05$). The blank boxes represent non-significant relationships.

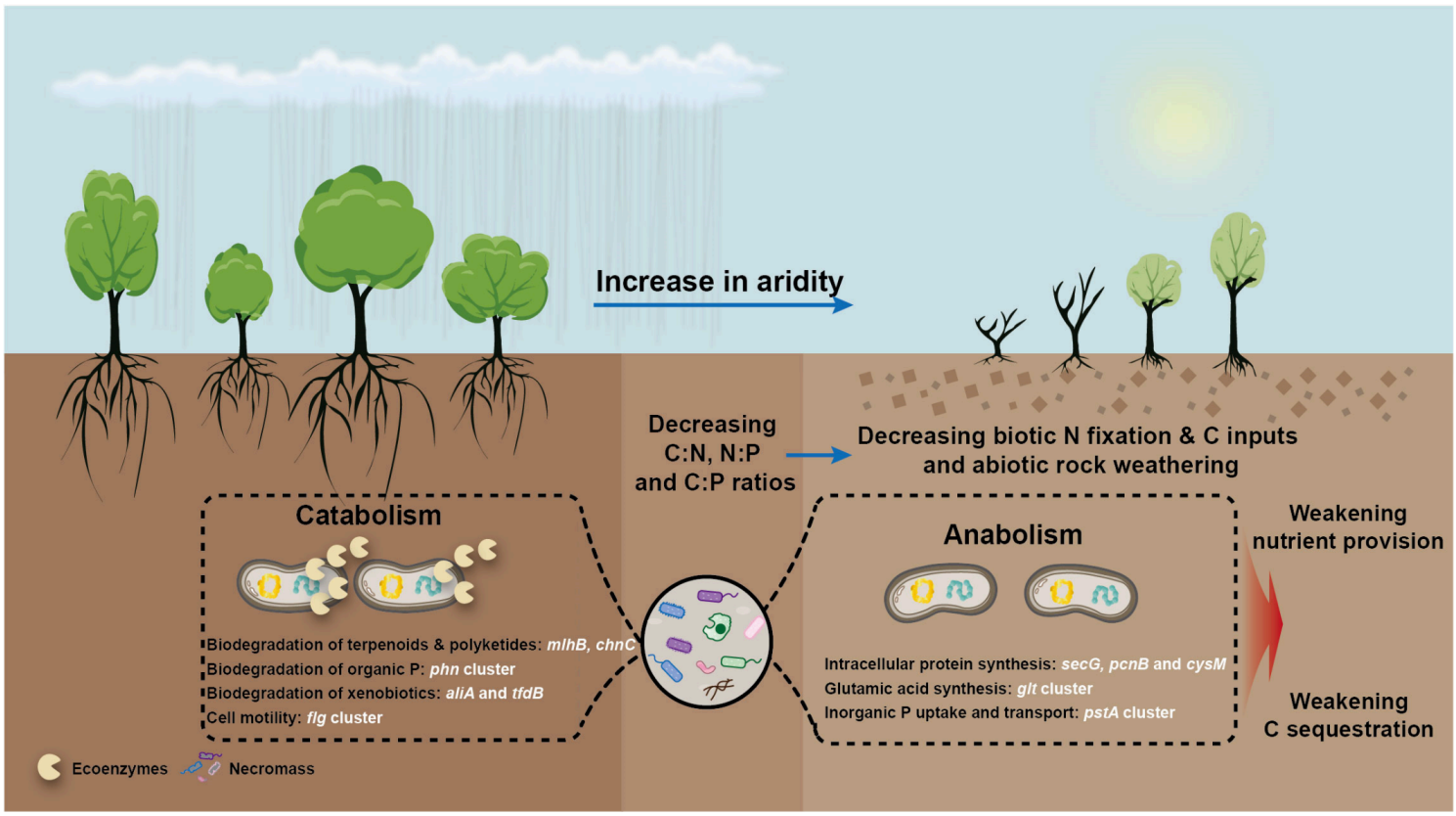

Figure 4

Conceptual diagram summarizing the shift from catabolism to anabolism in terrestrial ecosystems subjected to aridity-driven elemental imbalances. In brief, when water availability and NPP decrease, soil C becomes relatively less available because of the decoupled C, N, and P cycles (represented by decreased soil C:N and C:P ratios). Under such circumstances, the soil microbiome must inhibit catabolic processes by reducing extracellular enzymes to acquire nutrients and energy from organic matter degradation. Instead, their anabolic processes related to drought resistance and survival are promoted. Subsequently, microbial-driven soil nutrient cycling and C sequestration are weakened, thereby threatening ecosystem services under climate change.

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- SupplementaryInformation.pdf