

Review

Not peer-reviewed version

Towards Understanding the Factors Shaping the Composition and Function of the Noccaea Microbiome in Metal-Contaminated Environments

[Marjana Regvar](#) , [Valentina Bočaj](#) , [Jure Mravlje](#) , [Teja Pelko](#) , [Matevž Likar](#) , [Paula Pongrac](#) ,
[Katarina Vogel-Mikuš](#) *

Posted Date: 1 August 2025

doi: 10.20944/preprints202508.0080.v1

Keywords: Noccaea; plant microbiome; metal hyperaccumulation; phytoremediation; Thlaspi; Brassicaceae



Preprints.org is a free multidisciplinary platform providing preprint service that is dedicated to making early versions of research outputs permanently available and citable. Preprints posted at Preprints.org appear in Web of Science, Crossref, Google Scholar, Scilit, Europe PMC.

Copyright: This open access article is published under a Creative Commons CC BY 4.0 license, which permit the free download, distribution, and reuse, provided that the author and preprint are cited in any reuse.

Review

Towards Understanding the Factors Shaping the Composition and Function of the *Noccaea* Microbiome in Metal-Contaminated Environments

Marjana Regvar ¹, Valentina Bočaj ¹, Jure Mravlje ^{1,2}, Teja Pelko ¹, Matevž Likar ¹, Paula Pongrac ^{2,1} and Katarina Vogel-Mikuš ^{1,2*}

¹ Biotechnical Faculty, University of Ljubljana, Jamnikarjeva 101, SI-1000 Ljubljana

² Jozef Stefan Institute, Jamova 39, SI-1000 Ljubljana

* Correspondence: katarina.vogelmikus@bf.uni-lj.si

Abstract

Noccaea species (formerly *Thlaspi*) are Brassicaceae plants renowned for their capacity to hyperaccumulate zinc (Zn), cadmium (Cd), and nickel (Ni), which has made them model systems in studies of metal tolerance, phytoremediation, and plant adaptation to extreme environments. While their physiological and genetic responses to metal stress are relatively well characterised, the extent to which these traits influence microbiome composition and function remains largely unexplored. These species possess compact genomes shaped by ancient whole-genome duplications and rearrangements, and such genomic traits may influence microbial recruitment through changes in secondary metabolism, elemental composition, and tissue architecture. Here, we synthesise current findings on how genome size, metal hyperaccumulation, structural adaptations, and glucosinolate diversity affect microbial communities in *Noccaea* roots and leaves. We review evidence from bioimaging, molecular profiling, and physiological studies, highlighting interactions with bacteria and fungi adapted to metalliferous soils. While mycorrhizal associations remain debated, data suggest functional colonisation by selected fungal taxa. Taken together, these insights indicate that multiple plant traits interact to shape microbiome assembly and activity in *Noccaea* species. Understanding these dynamics offers new perspectives on plant–microbe co-adaptation, ecological resilience, and the optimisation of microbiome-assisted strategies for sustainable phytoremediation.

Keywords: *Noccaea*; *Thlaspi*; plant microbiome; metal hyperaccumulation; Brassicaceae; phytoremediation

1. Introduction

The plant microbiome—the diverse community of microorganisms associated with plant tissues—plays a crucial role in plant health, nutrient uptake, stress tolerance, and adaptation to extreme environments [1]. Recent research has revealed that microbiome composition is not random but shaped by a variety of intrinsic plant traits, including genome size, secondary metabolite production, and tissue structure [2,3]. Yet, the genetic and physiological determinants of microbiome assembly in non-model and stress-adapted plants remain poorly understood.

One such group of interest is the genus *Noccaea* (formerly part of *Thlaspi*), which includes several species capable of thriving in metal-contaminated soils and hyperaccumulating high concentrations of zinc (Zn), cadmium (Cd), and nickel (Ni)—at concentrations that are toxic to most organisms [4]. These species represent models for studying heavy metal tolerance and phytoremediation, and at the same time offer a unique opportunity to explore how extreme plant adaptations influence microbial colonisation in roots and leaves.

Noccaea belongs to the Brassicaceae, a family of one of the most diverse lineages of flowering plants, comprising 338 genera and 3,709 species [5,6]. The family likely originated around 19 million

years ago in the open, dry grasslands of the eastern Mediterranean [7]. Its evolutionary success has been linked to an ancient polyploidisation event and subsequent processes such as chromosome rearrangements, gene loss or silencing, genome downsizing, and diploidisation [8,9]. These events have conferred genomic plasticity and increased mutational robustness, enhancing adaptability to environmental stress [10,11]. As a result, many Brassicaceae, including *Noccaea*, can colonise harsh, nutrient-poor, and metal-polluted habitats. Based on nuclear transcriptomic markers, the family is currently divided into six major clades (A–F), with *Noccaea*, *Thlaspi*, and *Brassica* species grouped within clade B [12].

Species of *Noccaea* have small genomes, specialised root and leaf structures, and diverse glucosinolate profiles—traits that may significantly influence the structure and function of their microbiomes. For example, small genome size has been hypothesised to enhance ecological adaptability and may affect microbial recruitment by altering metabolic and signalling networks [13]. Secondary metabolites such as glucosinolates, which are prominent in Brassicaceae, have known antimicrobial properties and may act as chemical filters for microbial colonisation [14,15]. Moreover, structural features like peri-endodermal thickenings and epidermal lignification may impose spatial and biochemical constraints on microbial entry and survival [16].

Despite increasing attention to plant–microbe interactions, the *Noccaea* microbiome remains underexplored. Even fundamental questions—such as the mycorrhizal status of these species—remain controversial [17]. While *Noccaea* has long been considered non-mycorrhizal, evidence suggests that under certain conditions, specific fungal symbionts, including Glomeromycota, can colonise their roots, potentially contributing to nutrient cycling and metal tolerance [18–21].

This review synthesises current knowledge on the genomic, physiological, and ecological traits of *Noccaea* species that influence microbiome assembly and function. We discuss how genome evolution, metal hyperaccumulation, secondary metabolism, and tissue structure interact with microbial communities in the rhizosphere and phyllosphere. By highlighting emerging evidence and identifying key gaps, we aim to provide a framework for future research on plant–microbiome co-adaptation and its relevance for phytoremediation and resilience in metal-stressed environments.

2. Phylogenetic Relationships within *Noccaea* (Formerly *Thlaspi*) Species

The genus *Thlaspi* L., once considered one of the largest genera in the Brassicaceae, comprised approximately 75 species primarily distributed across Eurasia [6]. However, molecular phylogenetic studies have revealed that *Thlaspi sensu lato* (s.l.) is polyphyletic. This hypothesis was first raised by Meyer in 1973, but gained wide acceptance only after the advent of molecular systematics. Subsequent analyses of nuclear genes and internal transcribed spacer (ITS) regions provided strong evidence for multiple evolutionary lineages, ultimately supporting the taxonomic reorganisation of *Thlaspi s.l.* into distinct monophyletic genera—*Thlaspi sensu stricto*, *Noccaea*, *Microthlaspi*, *Noccidium*, and others [12,22,23].

Among these, *Noccaea* has emerged as a genus of particular ecological and physiological interest. Al-Shehbaz (2014) presented a comprehensive monograph of *Noccaea*, describing 128 species, many of which are adapted to extreme edaphic conditions [6]. Notably, the genus includes several metal hyperaccumulators, such as *N. caerulescens*, *N. cepeaefolia*, *N. goesingensis*, and *N. praecox*, that thrive on naturally and/or anthropogenically metal-rich soils. These species can accumulate extraordinary concentrations of Zn, Cd, and Ni, metals that are typically toxic to most organisms even at trace levels [4].

Noccaea caerulescens, the most widely studied species of the genus, has become a model system for research in metal homeostasis, adaptation to metalliferous environments, and plant–microbe interactions [24,25]. Its close relative, *N. praecox*, also exhibits extreme metal tolerance and accumulation traits, especially to Cd [19,26,27]. Phylogenetic reconstruction based on ITS rDNA has shown a 99% sequence similarity between these two species, suggesting a recent divergence in the early Pleistocene, approximately 1.2 million years ago [28]. This divergence occurred in parallel with

the expansion and diversification of perennial *Noccaea* species in North America from Eurasian ancestors [29].

Nuclear gene phylogenies across Brassicaceae support a pattern of nested radiation and convergent morphological evolution [12]. This evolutionary plasticity is reflected in the repeated emergence of metal tolerance traits and compact genome sizes in several Brassicaceae lineages. The genomic simplification observed in *Noccaea* may result from ancient polyploidy followed by genome downsizing, rearrangements, and diploidisation [8,9]. These processes, though complicating phylogenetic reconstruction, are also thought to have enhanced mutational robustness and ecological adaptability of Brassicaceae [10,11].

Understanding the evolutionary history of *Noccaea* is thus essential for interpreting its extraordinary physiological traits, including metal hyperaccumulation, compact genome size, tissue-specific structural adaptations, and unique secondary metabolite profiles. These characteristics likely shape its ability to establish highly selective interactions with root- and leaf-associated microbiota. Phylogenetic insights provide a valuable framework for exploring the ecological and functional consequences of these plant traits, especially in the context of microbiome assembly, stress adaptation, and phytoremediation.

3. The Large Genome Size Constraint Hypothesis

Although several whole-genome duplication (WGD) events have occurred in the Brassicaceae [9,30–32], this has not led to a proportional increase in genome size [8]. Compared to other angiosperms—with more than an eight-fold range in DNA content, or 4.4-fold when excluding allotetraploids—the genomes of most Brassicaceae are relatively small [33], with genome sizes of the metal hyperaccumulators *Arabidopsis halleri* (255 Mbp) and *Noccaea caerulea* (267 Mbp) even smaller than those of *Thlaspi arvense* (539 Mbp), *Sinapis alba* (553 Mbp), and *Caulanthus heterophyllus* (686 Mbp) [33,34].

The Large Genome Size Constraint Hypothesis suggests that species with small genomes are more adaptable and capable of colonising diverse environments. In contrast, large-genome species, enriched in non-coding DNA, may face limitations due to slower cell division, lower metabolic efficiency, and reduced tolerance to stress, which could make them more prone to extinction [35]. In metal-polluted environments, where physiological plasticity and efficient stress response mechanisms are critical, a small genome size may confer a particular advantage [36,37]. This may explain why metal hyperaccumulators like *Noccaea* exhibit small and stable genomes, supporting their ecological success under extreme edaphic conditions.

According to data from the Plant DNA C-values Database [38] Brassicaceae species in clades E and F have the highest average DNA contents (1.98 pg/1C and 1.05 pg/1C, respectively) (Figure 1; Table A1), while clade B—home to *Noccaea*, *Thlaspi*, and *Brassica*—has the smallest (0.57 pg/1C) [12]. Interestingly, species retained in genus *Thlaspi* have a higher average DNA amount (0.43 pg/1C) than those assigned to *Noccaea* (0.34 pg/1C). Within *Noccaea*, *N. alpestris* and *N. praecox* have the smallest average DNA contents (0.24 and 0.26 pg/1C, respectively). For comparison, average DNA content in *Arabidopsis thaliana* ranges from 0.16 to 0.44 pg/1C.

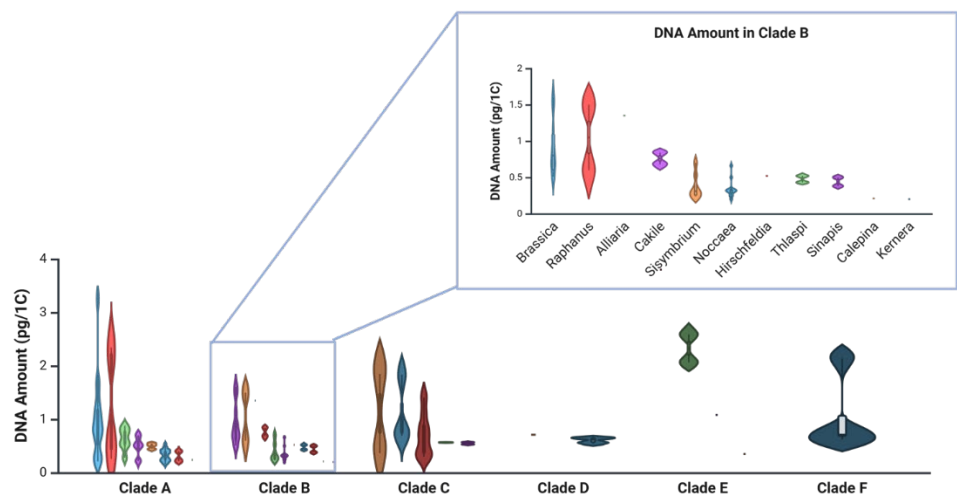


Figure 1. Violin plots representing DNA amounts available at the Plant DNA C-values database [38] of the Brassicaceae clades [12]. Enlarged is clade B with *Noccaea* species (formerly *Thlaspi*) data corrected according to Flora Europaea (The Euro+Med Plantbase Project, <https://www2.bgbm.org/EuroPlusMed/query.asp>). Dots indicate mean values, whiskers represent minimum and maximum, and kernel density outlines the distribution. The figure was prepared by Biorender.

Recent metagenomic work has shown that microbial genome size is shaped by environmental context and trophic strategies [39]. Metal hyperaccumulator plants, with their chemically and structurally complex tissues, can be viewed as unique microecosystems. Hence, host genome size may also influence the structure and function of associated microbial communities. Genome size in plants varies dramatically (0.065–152.23 pg/1C) [40,41] and correlates with traits like cell size, cell cycle control, and metabolic activity [42,43], all of which may influence microbial colonisation.

Genome size may also modulate plant-microbe interactions through secondary metabolism. Expansion of specific gene families during WGD may alter secondary metabolite production and defence signalling [44], thereby affecting microbial recruitment. However, direct testing of the link between host genome size and microbial colonisation remains limited.

One approach is to estimate root fungal colonisation levels in species with known genome sizes [38]. In *Noccaea* species collected from various polluted and non-polluted sites in Central Europe, the root fungal colonisation levels were generally low [45], supporting the hypothesis that small-genome species may restrict or tightly regulate microbial entry. When plotted against their corresponding genome size (**Figure 2**), it seems species with medium genome sizes may develop the highest root fungal colonisation levels.

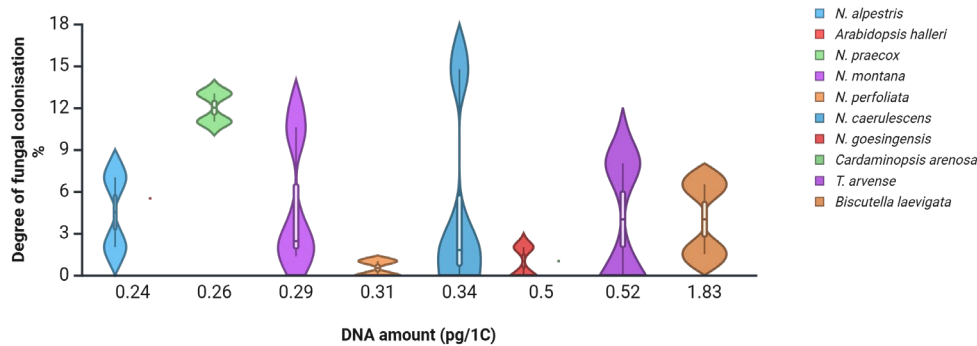


Figure 2. Degree of root fungal colonisation levels of several Brassicaceae species collected in polluted and non-polluted environments [45], plotted against nuclear DNA content (pg/1C) [38]. Dots indicate species averages; whiskers and kernel plots indicate distribution. The figure was prepared by Biorender.

Similar findings were reported from a two-year study on vegetation at a metal-polluted site in Slovenia [20]. Plants with moderate genome sizes tended to support higher levels of mycorrhizal colonisation (Figure 3). Nevertheless, some species remained free of colonisation across all sampling periods (e.g., *Biscutella laevigata*, *Minuartia gerardii*), although *B. laevigata* collected at heavy metal polluted sites in Poland was reported to host arbuscular mycorrhiza (AM) [46], suggesting that factors beyond genome size—such as environmental filtering or chemical defence—may also play significant roles. To date, mycorrhizal status in Brassicaceae still remains controversial [17].



Figure 3. Heatmap of mycorrhizal colonisation parameters of species from a metal-polluted site in Slovenia [20], arranged according to their corresponding DNA content (pg/1C). Data were collected in two seasons over two consecutive years (N = 3–20). AM was assessed according to Trouvelot et al. [47]. F%, mycorrhizal frequency; M%, mycorrhizal intensity; m%, mycorrhizal intensity of colonised root fragments; A%, arbuscular richness; a%, arbuscular richness of colonised root fragments; V%, vesicular richness; v%, vesicular richness of colonised root fragments.

Species identity is one of the main drivers of plant microbiome composition, followed by the presence of the metal hyperaccumulation trait [48]. The extent to which genome size impacts colonisation by beneficial microbes remains unclear, but circumstantial evidence is growing. For example, Brassicaceae-associated bacteria often have larger genomes than their free-living relatives, with enriched gene sets for secretion, pongracngraccarbohydrate metabolism, and stress tolerance—adaptations essential for colonising chemically complex hosts [49]. Similarly, fungal root endophytes tend to have larger genomes than foliar endophytes or saprotrophs [13], likely reflecting their need for genomic flexibility in navigating plant immunity and nutritional signals.

Collectively, the data support the hypothesis that small genome size in *Noccaea* and related Brassicaceae species may confer a selective advantage under environmental stress, particularly in metal-polluted habitats. This advantage may be mediated through more efficient growth and physiological plasticity and via modulation of plant–microbe interactions. While direct mechanistic links between genome size and microbiome assembly remain to be fully resolved, mounting evidence suggests that genome size influences microbial compatibility, colonisation patterns, and symbiotic potential. Future research should integrate genome-scale, metabolomic, and microbiome data to untangle these complex relationships and better understand how genome size acts as both a constraint and an opportunity in shaping plant–microbe co-evolution.

4. Genetic Requirements of Metal Hyperaccumulation and Impacts on the Microbiome in *Noccaea* Species

Brassicaceae hosts the greatest number of metal hyperaccumulating species among dicotyledons, with 103 species currently listed in the Global Hyperaccumulator Database [4]. The thresholds defining hyperaccumulation are 100 mg kg⁻¹ for Cd, 1000 mg kg⁻¹ for Ni, and 10,000 mg kg⁻¹ (1%) for zinc Zn in dry leaf tissue. According to these criteria, 23 *Noccaea* species are known to hyperaccumulate Ni, 10 species Zn, and three Cd [4,50].

The evolution of metal hyperaccumulation is driven by a combination of natural selection on cis-regulatory regions and gene copy number expansions [51]. In *A. halleri*, tandem triplication of the HMA4 gene (Heavy Metal ATPase 4) facilitates enhanced root-to-shoot metal transport and plays a key role in metal homeostasis, enabling colonisation of Zn- and Cd-contaminated sites [51,52]. In *N. caerulescens*, a tandem quadruplication of HMA4—arising independently from that in *A. halleri*, despite their shared ancestry over 40 Mya, suggests convergent evolution of Zn and Cd hyperaccumulation in Brassicaceae [53].

Importantly, HMA4 copy number in *N. caerulescens* is variable among ecotypes, contributing to intraspecific differences in Cd uptake, xylem loading, and translocation [54]. Additional genomic mechanisms, such as gene inversion events enhancing expression of HMA4 and ZIP6, as well as expanded gene families related to nicotianamine biosynthesis and transport (NAS2, YSL3, ZIFL1), further contribute to the distinct metal accumulation profiles in *Noccaea* species [34].

At the physiological level, hyperaccumulation and hypertolerance involve several key processes: i) enhanced metal uptake by roots, ii) efficient symplastic transfer to the vascular tissue, iii) accelerated root-to-shoot transport via the xylem, and iv) metal sequestration in leaf vacuoles [55,56]. For example, the NcNramp1 transporter shows high expression in roots of the Ganges ecotype, facilitating increased Cd uptake across the endodermal membrane [57]. Similarly, NcHMA4 is pivotal for Zn and Cd xylem loading and is considered a central regulator of both hyperaccumulation and tolerance [51,54]. In the shoots, vacuolar sequestration of Zn is mediated by constitutive expression of NcMTP1, encoding a Zn transporter that mitigates cytoplasmic toxicity [58]. Transcriptome analysis of the Ganges ecotype further revealed the presence of numerous isotigs encoding metal homeostasis-related proteins, including an extra copy of Metallothionein 3 [59], a protein that binds metal ions and contributes to detoxification.

Besides plant genetics, microbial partners play an increasingly recognised role in metal accumulation and tolerance. Several fungal endophytes isolated from metalliferous sites were shown to enhance Ni uptake and biomass production in *N. caerulescens*, indicating a functional synergy between host and microbiome [60]. Comparative studies of *Noccaea* populations from metal-rich and metal-poor soils show that bacterial and fungal community composition is shaped by both edaphic factors and host genotype [61,62]. Microbial communities associated with *Noccaea* roots in metalliferous environments often harbour unique taxa with adaptations to high metal loads and show reduced antagonistic interactions, likely due to the selective pressure imposed by the toxic environment [61].

The capacity for metal hyperaccumulation in *Noccaea* species is underpinned by a complex network of genetic adaptations, including gene duplications, regulatory mutations, and physiological innovations in metal uptake, transport, and sequestration. These traits enable survival in metalliferous environments and shape the composition and function of the associated microbiome. Fungal and bacterial partners contribute to nutrient acquisition, stress mitigation, and enhanced metal tolerance, suggesting a tightly co-evolved relationship between host and microbiota. The observed intraspecific and interspecific variability in both metal-handling capacity and microbial assemblages underscores the importance of integrating genomics, ecology, and microbiome research to fully understand plant adaptation to extreme environments. Future work focusing on functional metagenomics, transcriptomics, and controlled inoculation studies will be essential to unravel the causal links between host genotype, microbial function, and environmental stress resilience in *Noccaea* and other metal-tolerant plants.

5. Bioimaging Techniques Reveal Adaptation Mechanisms in the Leaves of *Noccaea* Species

To withstand the “metal tsunami” posed by excessive levels of Zn, Cd, and Ni in their environment, hyperaccumulating *Noccaea* species have evolved remarkable structural and physiological adaptations. These adaptations are often tissue- and cell-specific and can be visualised with high-resolution bioimaging techniques. Since the tip of the leaf matures first [63] it becomes the primary site of Zn accumulation in *N. caerulescens*, whereas Ni shows a more homogeneous distribution throughout the leaf. This spatial pattern was clearly demonstrated using Laser Ablation Inductively Coupled Plasma Mass Spectrometry (LA-ICP-MS) [64] underscoring the combined influence of developmental gradients and elemental properties on the metal distribution at the organ level.

Advanced synchrotron-based bioimaging techniques have revealed significant tissue-specific biochemical specialisation in the leaves of hyperaccumulating *Noccaea* species. For instance, Synchrotron Radiation Fourier Transform Infrared (SR-FTIR) spectroscopy and Low-Energy X-ray Fluorescence (LEXRF) microscopy demonstrated that, besides vacuoles [65], Zn is also sequestered in the thickened cell walls of epidermal cells in *N. praecox*, where it is co-localised with lignin and pectin [66]. These findings support the “egg-box” model of pectin–metal binding [67]. Meanwhile, Cd preferentially accumulates in the mesophyll at high soil Zn levels, as confirmed by micro-Particle Induced X-ray Emission (μ -PIXE) [26,68] and in vacuoles in low Zn environment as seen by Synchrotron micro-X-ray Fluorescence (SR- μ -XRF) [27]. These contrasting accumulation patterns suggest that mesophyll tissues serve as key sinks for Cd, while specialised epidermal compartments help to immobilise Zn, thereby limiting its cytotoxic effects.

Importantly, the spatial organisation of these metals and associated biochemical barriers, such as lignified or pectin-enriched walls, likely plays a dual role—not only in metal detoxification but also in shaping the leaf microbiome. Recent studies indicate that physical and chemical leaf traits such as pH, stomatal density, trichome presence, and even surface roughness can significantly influence microbial colonisation on leaf surfaces [69]. In *N. caerulescens* growing in metalliferous soils, highly specialised strains of *Pseudomonas* have been found to dominate the phyllosphere microbiome [70]. These findings suggest that the micro-environmental conditions created by metal compartmentalisation may act as a spatial and chemical filter, permitting colonisation only by metal-tolerant or symbiotically adapted microbes.

Despite compelling physiological and ecological evidence, the relationship between leaf elemental microarchitecture and microbiome spatial distribution remains unexplored. No published studies have yet integrated spatially resolved metagenomics or Fluorescence In Situ Hybridisation (FISH) with metal mapping to examine how localised chemical environments influence microbial community structure in the phyllosphere of hyperaccumulators. Such research could provide critical insights into the co-adaptive strategies of plants and microbes under extreme environmental pressures.

Future directions should include the use of correlative imaging approaches, such as X-ray computed tomography (XCT), SR- μ -XRF, LA-ICP-MS, and confocal Raman microscopy, alongside high-resolution microbiome profiling. Integrating these tools could help uncover how micro-niches within leaves facilitate or restrict microbial colonisation, leading to a better understanding of plant–microbe–metal interactions in hyperaccumulating systems.

6. Specific Features in the Roots of *Noccaea* Species Affect Microbial Composition and Metal Uptake

Roots of *N. caerulescens* exhibit distinct anatomical specialisations, including peri-endodermal cell wall thickenings that form on the radial and inner tangential walls of cells adjacent to the endodermis. These structures, which resemble a “half-moon” or letter “C”, were first described by Zelko et al 2008 [71] and later characterised using Raman spectroscopy as being rich in cellulose and

lignin, with inner surfaces enriched in pectin [16]. In addition to providing mechanical support, these thickened cell walls likely function as a selective barrier, immobilising excess metals and restricting their movement toward the central vascular tissues.

Fungal entry into roots is further limited by suberin lamellae in the endodermis. However, in *A. thaliana*, it has been demonstrated that beneficial colonisation by *Colletotrichum tofieldiae* under phosphate-deficient conditions depends on the presence of unsubsized endodermal passage cells [72]. These passage cells primarily facilitate the movement of elements and signalling molecules between root layers [73,74] and may also serve as entry points for endophytic microbes. Remarkably, some evidence suggests that internalised microbes can be digested within root cells to release nitrogen that is then transported to the shoots [75].

Plant-microbe interactions in the rhizosphere are shaped by structural traits as well as by hormonal signalling. Specific bacteria can suppress abscisic acid signalling, altering the development of root diffusion barriers and indirectly influencing microbiome composition and plant stress responses [76,77]. In Brassicaceae roots, dominant fungal taxa typically belong to Ascomycota and Basidiomycota, while Glomeromycotina are generally present at low abundance [78]. Notably, fungal communities associated with metal hyperaccumulating *N. caerulescens* and *N. goesingensis* include members of Dothideomycetes, Sordariomycetes, Eurotiomycetes, and Leotiomycetes, many of which promote plant growth and nickel accumulation [60].

Comparative studies show that the root-associated microbiomes of *N. praecox* and *N. caerulescens*, even when collected from the same metalliferous site, exhibit no significant differences in overall structure, implying that local soil microbial communities heavily influence microbiome assembly [61]. However, *Noccaea brachypetala*, another hyperaccumulator, displays increased bacterial species richness and relative abundance of taxa associated with metal tolerance, suggesting microbial co-selection for both phytoremediation support and enhanced nutrient acquisition [58].

The mycorrhizal status of *Noccaea* species—and Brassicaceae more broadly—remains controversial, primarily because genomic analyses have revealed a consistent absence or degeneration of key genes required for AM symbiosis [17,79]. Although occasional root colonisation by AM fungi has been observed under specific conditions, these associations are typically rudimentary or facultative and often lack functional arbuscule formation. The Brassicaceae family, including *A. thaliana*, is known to lack several essential components of the canonical “symbiosis toolkit” likely due to gene loss or pseudogenisation following ancient whole-genome duplication events [80]. Additionally, the presence of glucosinolate biosynthesis pathways—which produce antimicrobial compounds—further inhibits functional mycorrhisation in this lineage. Consequently, while some *Noccaea* species may occasionally host AM fungi, e.g. during the flowering period [81,82], the majority of research supports the classification of this group as primarily non-mycorrhizal. A recent high-throughput sequencing, however, identified Glomeromycetes in the roots of *N. caerulescens* and *N. praecox*, comprising up to 9% of fungal taxa [61]. These results were supported by successful colonisation of inoculated roots with monospore Glomeromycotina cultures and subsequent elemental shifts under controlled conditions [21,83], pointing to a context-dependent facultative mycorrhizal relationship.

In *Noccaea* species, specialised anatomical features such as peri-endodermal thickenings and endodermal suberisation influence metal sequestration as well as microbial entry and community structure. Root-associated microbiota are shaped by intrinsic plant traits, environmental filtering in metalliferous soils, and potential symbiotic dynamics involving both fungi and bacteria. The ambiguous but emerging role of mycorrhizal fungi in *Noccaea* highlights the need for integrated approaches—combining structural imaging, metagenomics, and functional assays—to unravel the multifaceted interactions between roots, metals, and microbes. Such insights are pivotal for leveraging plant-microbe partnerships in sustainable phytoremediation and adaptation to extreme edaphic conditions.

7. Glucosinolates

Genome expansion in plants has been associated with alterations in secondary metabolite pathways, which can impact both microbial recruitment and defence signalling. In Brassicaceae, whole-genome duplication events followed by the silencing or loss of duplicated gene copies are believed to have facilitated gene neofunctionalisation, accelerating the evolution of glucosinolate biosynthesis genes [8,12,84]. Glucosinolates, a hallmark group of secondary metabolites in Brassicaceae, play a central role in defence against pathogens and herbivores by producing toxic isothiocyanates upon hydrolysis [85,86].

In *N. caerulescens*, significant intraspecific variation in both glucosinolate composition and concentration has been reported [87], with seasonal patterns showing increased shoot and decreased root glucosinolate levels during flowering [82,88]. In *N. praecox*, indolyl-glucosinolates dominate in the shoots, whereas roots contain approximately equal proportions of indolyl- and alkyl-glucosinolates [89]. These chemotypes may influence microbial colonisation in a tissue-specific manner.

Recent studies indicate that glucosinolates shape microbial communities through selective pressures. For example, allyl-glucosinolates have been shown to enrich specific bacterial taxa in the phyllosphere of *A. thaliana* [90]. Moreover, the indolic glucosinolate pathway has been implicated in suppressing AM colonisation in non-host Brassicaceae [91]. In this context, the expression of transcription factors regulating aliphatic, but not indolic, glucosinolate biosynthesis in the roots of *N. caerulescens* ecotype Ganges may be a key factor in shaping its rhizosphere microbial community [59].

Beyond plant-driven biosynthesis, microbial interactions with glucosinolates further shape community structure. Bacterial myrosinase specificity influences glucosinolate breakdown and can affect community composition, especially when coupled with metabolic cross-feeding between microbial taxa [90]. Some fungal endophytes and soil fungi can metabolise siringin as a carbon source, although they remain sensitive to isothiocyanates [92]. Additionally, *Sclerotinia sclerotiorum* was recently found to detoxify isothiocyanates using a specific hydrolase, suggesting microbial adaptation to these potent compounds [93].

Glucosinolates in *Noccaea* species serve as potent chemical defences and as ecological gatekeepers that modulate microbial colonisation in a genotype-, tissue-, and environment-specific manner. Their biosynthesis is shaped by genome evolution and selective pressures, resulting in structurally diverse compounds with distinct effects on microbial communities. Recent studies show that specific glucosinolate classes—particularly aliphatic and indolic types—can differentially influence bacterial and fungal assemblages in roots and leaves [90,91]. However, the mechanistic pathways underlying these interactions remain largely unresolved. To fully understand how glucosinolates structure the microbiome, future research should integrate metabolomic profiling, transcriptomics, and spatially resolved microbial community analyses. Such interdisciplinary approaches will elucidate how secondary metabolites mediate plant-microbe interactions, particularly under the extreme conditions of metal-rich soils.

8. Conclusions and Further Directions

Noccaea species provide a powerful model to explore how genomic, structural, and chemical traits of plants influence microbial assembly in extreme environments such as metal-contaminated soils. Their small genome size, metal hyperaccumulation capacity, specialised leaf and root anatomy, and glucosinolate profiles act in concert to modulate root and leaf microbiomes, potentially selecting for metal-tolerant and functionally beneficial microbes. Although evidence supports a tight coupling between plant traits and microbial composition, the precise mechanisms—particularly the roles of spatial metal distribution, facultative mycorrhisation, and glucosinolate specificity—remain poorly understood. Future research should adopt integrative, multidisciplinary approaches combining genomics, bioimaging, metabolomics, and spatially resolved microbiome profiling to uncover the

dynamic interplay between plant adaptation and microbial community structure, with implications for phytoremediation and ecological resilience.

Author Contributions: Conceptualisation, MR; writing—original draft preparation, MR, VB, JM, ML, PP, TP, KVM; writing—review and editing, KVM.; visualisation, MR; supervision, MR, KVM; project administration, MR, KVM; funding acquisition, MR, KVM All authors have read and agreed to the published version of the manuscript

Funding: The authors receive financial support from the Slovenian Research and Innovation Agency: research core funding No. P1-0212, project funding (J1-3014, J1-50014, J7-60126, J4-3091, N4-0346) and Young researcher projects, Valentina Bočaj and Teja Pelko.

Data Availability Statement: Plant names were adopted according to Flora Europaea (<https://ww2.bgbm.org/EuroPlusMed/query.asp>). Information on DNA amount was drawn from the Plant DNA C-value database, Royal Botanical Gardens, Kew (<https://ww2.bgbm.org/EuroPlusMed/query.asp>). Data on mycorrhizal colonisation is contained in the articles (Regvar et al., 2003, 2006). The final table is provided in the Appendix. The images were prepared by Biorender. AI was used to find references (Elicit) and for text editing (Grammarly, ChatGPT).

Acknowledgements: The manuscript is dedicated to Prof. Hermann Bothe.

Conflicts of Interest: “The authors declare no conflicts of interest. The funders had no role in the design of the study; in the collection, analyses, or interpretation of data; in the writing of the manuscript; or in the decision to publish the results”.

Abbreviations

The following abbreviations are used in this manuscript:

AM	Arbuscular mycorrhiza
DNA	Deoxyribonucleic Acid
FTIR	Fourier Transform Infrared Spectroscopy
HMA4	Heavy Metal ATPase 4
LA-ICP-MS	Laser Ablation Inductively Coupled Plasma Mass Spectrometry
LEXRF	Low-Energy X-Ray-Fluorescence
NAS2	Nicotianamine Synthase 2
NcHMA4	<i>Noccaea caerulea</i> Heavy Metal ATPase 4
NcMTP1	<i>Noccaea caerulea</i> Metal Tolerance Protein 1
PIXE	Particle-Induced X-ray Emission
SR-μ-XRF	Synchrotron micro X-Ray-Fluorescence
YSL3	Yellow Stripe-Like 3
XCT	X-ray computed tomography
WDG	whole-genome duplication
ZIFL1	Zinc-Induced Facilitator-Like 1

Appendix A

Appendix A.1

Table A1. Brassicaceae clades [12] with their corresponding DNA amounts, available at the Plant DNA C-values database [38]. Data corrected according to Flora Europaea (The Euro+Med Plantbase Project, <https://ww2.bgbm.org/EuroPlusMed/query.asp>).

No	Clade	Genus	Species	DNA Amount	Original Reference See https://ww2.bgbm.org/EuroPlusMed/query.asp	Clade average DNA Amount
				1C (pg)		1C (pg)
1	Clade A	<i>Capsella</i>	<i>rubella</i>	0.22	Lysák et al.,2009	
2	Clade A	<i>Capsella</i>	<i>bursa-pastoris</i>	0.4	Lysák et al.,2009	
3	Clade A	<i>Pachycladon</i>	<i>exilis</i>	0.44	Lysák et al.,2009	
4	Clade A	<i>Pachycladon</i>	<i>fastigiata</i>	0.51	Lysák et al.,2009	
5	Clade A	<i>Pachycladon</i>	<i>novae-zelandiae</i>	0.55	Lysák et al.,2009	
6	Clade A	<i>Turritis</i>	<i>glabra</i>	0.24	Lysák et al.,2009	
7	Clade A	<i>Arabidopsis</i>	<i>thaliana</i>	0.16	Bennett et al.,2003	
8	Clade A	<i>Arabidopsis</i>	<i>arenosa</i>	0.2	Lysák et al.,2009	
9	Clade A	<i>Arabidopsis</i>	<i>neglecta</i>	0.2	Lysák et al.,2009	
10	Clade A	<i>Arabidopsis</i>	<i>halleri</i>	0.24	Lysák et al.,2009	
11	Clade A	<i>Arabidopsis</i>	<i>korshynskyi</i>	0.25	Nagl et al.,1983	
12	Clade A	<i>Arabidopsis</i>	<i>lyrata</i>	0.25	Lysák et al.,2009	
13	Clade A	<i>Arabidopsis</i>	<i>cebenensis</i>	0.29	Lysák et al.,2009	
14	Clade A	<i>Arabidopsis</i>	<i>pumila</i>	0.34	Houben et al.,2003	

15	Clade A	<i>Arabidopsis suecica</i>	0.35	Lysák et al.,2009
16	Clade A	<i>Arabidopsis arenosa</i>	0.39	Lysák et al.,2009
17	Clade A	<i>Arabidopsis wallichii</i>	0.4	Houben et al.,2003
18	Clade A	<i>Arabidopsis neglecta</i>	0.4	Lysák et al.,2009
19	Clade A	<i>Arabidopsis thaliana</i>	0.44	Schmuths et al.,2004
20	Clade A	<i>Arabidopsis lyrata</i>	0.45	Dart et al.,2004
21	Clade A	<i>Arabidopsis kamchatica</i>	0.52	Wolf et al.,2014
22	Clade A	<i>Physaria gracilis</i>	0.26	Lysák et al.,2009
23	Clade A	<i>Physaria ovalifolia</i>	0.43	Lysák et al.,2009
24	Clade A	<i>Physaria arctica</i>	0.69	Lysák et al.,2009
25	Clade A	<i>Physaria didymocarpa</i>	2.23	Lysák et al.,2009
26	Clade A	<i>Physaria bellii</i>	2.34	Lysák et al.,2009
27	Clade A	<i>Erysimum sylvestre</i>	0.28	Vidic et al.,2009
28	Clade A	<i>Erysimum duriaei</i>	0.47	Loureiro et al.,2013
29	Clade A	<i>Erysimum scoparium</i>	0.54	Suda et al.,2003
30	Clade A	<i>Erysimum bicolor</i>	0.58	Suda et al.,2003
31	Clade A	<i>Erysimum goniocaulon</i>	0.69	Bou Dagher-Kharrat et al.,2013
32	Clade A	<i>Erysimum bicolor</i>	0.76	Lysák et al.,2009
33	Clade A	<i>Erysimum cheiranthoides</i>	0.83	Lysák et al.,2009
34	Clade A	<i>Erysimum diffusum</i>	0.88	Pustahija et al.,2013

35	Clade A	Rorippa	lipizensis	0.22	Vallès et al.,2014
36	Clade A	Rorippa	sylvestris	0.48	Pustahija et al.,2013
37	Clade A	Rorippa	palustris	0.54	Lysák et al.,2009
38	Clade A	Rorippa	nasturtium-aquaticum	0.7	Kenton and Owens,1988
39	Clade A	Cardamine	impatiens	0.21	Johnston et al.,2005
40	Clade A	Cardamine	hirsuta	0.23	Johnston et al.,2005
41	Clade A	Cardamine	amara	0.24	Hanson et al.,2002
42	Clade A	Cardamine	glauca	0.28	Pustahija et al.,2013
43	Clade A	Cardamine	chelidonia	0.36	Kubešová et al.,2010
44	Clade A	Cardamine	schinziana	0.68	Marhold et al.,2010
45	Clade A	Cardamine	yezoensis	0.7	Marhold et al.,2010
46	Clade A	Cardamine	amaraeiformis	0.71	Marhold et al.,2010
47	Clade A	Cardamine	valida	0.71	Marhold et al.,2010
48	Clade A	Cardamine	yezoensis	0.87	Marhold et al.,2010
49	Clade A	Cardamine	flexuosa	0.9	Mowforth and Grime,1989
50	Clade A	Cardamine	yezoensis	0.99	Marhold et al.,2010
51	Clade A	Cardamine	schinziana	1	Marhold et al.,2010
52	Clade A	Cardamine	torrentis	1.13	Marhold et al.,2010
53	Clade A	Cardamine	yezoensis	1.24	Marhold et al.,2010
54	Clade A	Cardamine	asarifolia	1.34	Lihova et al.,2006

55	Clade A	Cardamine	diphylla	1.62	Sonnier,2016	
56	Clade A	Cardamine	pratensis	1.70	Band,1984	
57	Clade A	Cardamine	concatenata	3.25	Bai et al.,2012	0.67
1	Clade B	Raphanus	sativus	0.6	Dolezel et al.,1992	
2	Clade B	Raphanus	sativus	1.50	Olszewska and Osiecka,1983	
3	Clade B	Hirschfeldia	incana	0.52	Lysák et al.,2009	
4	Clade B	Brassica	hirta	0.51	Arumuganathan and Earle,1991	
5	Clade B	Brassica	tournefortii	0.6	Nagpal et al.,1996	
6	Clade B	Brassica	campestris	0.6	Bennett et al.,1976	
7	Clade B	Brassica	nigra	0.8	Verma and Rees,1974	
8	Clade B	Brassica	oleracea	0.8	Olszewska and Osiecka,1983	
9	Clade B	Brassica	rapa	0.8	Ingle et al.,1975	
10	Clade B	Brassica	napus	1.10	Greilhuber,1988	
11	Clade B	Brassica	junceae	1.50	Verma and Rees,1974	
12	Clade B	Brassica	carinata	1.60	Verma and Rees,1974	
13	Clade B	Sinapis	arvensis	0.38	Arumuganathan and Earle,1991	
14	Clade B	Sinapis	alba	0.50	Bennett MD, Smith JB, Heslop-Harrison,1982	
15	Clade B	Cakile	maritima	0.68	Lysák et al.,2009	
16	Clade B	Cakile	edentula	0.84	Bai et al.,2012	
17	Clade B	Sisymbrium	officinale	0.24	Lysák et al.,2009	

18	Clade B	<i>Sisymbrium</i>	<i>loeselii</i>	0.24	Kubešová et al.,2010
19	Clade B	<i>Sisymbrium</i>	<i>altissimum</i>	0.26	Kubešová et al.,2010
20	Clade B	<i>Sisymbrium</i>	<i>orientale</i>	0.31	Johnston et al.,2005
21	Clade B	<i>Sisymbrium</i>	<i>austriacum</i>	0.36	Lysák et al.,2009
22	Clade B	<i>Sisymbrium</i>	<i>irio</i>	0.53	Johnston et al.,2005
23	Clade B	<i>Sisymbrium</i>	<i>strictissimum</i>	0.7	Kubešová et al.,2010
24	Clade B	<i>Thlaspi</i>	<i>ceratocarpum</i>	0.43	Lysák et al.,2009
25	Clade B	<i>Thlaspi</i>	<i>arvense</i>	0.52	Lysák et al.,2009
26	Clade B	<i>Alliaria</i>	<i>petiolata</i>	1.35	Barow & Meister,2003
27	Clade B	<i>Calepina</i>	<i>irregularis</i>	0.21	Lysák et al.,2009
28	Clade B	<i>Noccaea</i>	<i>alpestris</i>	0.24	Lysák et al.,2009
29	Clade B	<i>Noccaea</i>	<i>alpestris</i>	0.2	Band,1984
30	Clade B	<i>Noccaea</i>	<i>caerulescens</i>	0.34	Peer et al.,2006
31	Clade B	<i>Noccaea</i>	<i>montana</i>	0.29	Peer et al.,2006
32	Clade B	<i>Noccaea</i>	<i>goesingensis</i>	0.5	Siljak-Yakovlev et al.,2010
33	Clade B	<i>Noccaea</i>	<i>oxyceras</i>	0.34	Peer et al.,2003
34	Clade B	<i>Noccaea</i>	<i>praecox</i>	0.26	Temsch et al.,2010
35	Clade B	<i>Noccaea</i>	<i>perfoliata</i>	0.31	Peer et al.,2006
36	Clade B	<i>Noccaea</i>	<i>rosularis</i>	0.32	Peer et al.,2003
37	Clade B	<i>Noccaea</i>	<i>tymphaea</i>	0.32	Peer et al.,2006

38	Clade B	<i>Noccaea</i>	<i>tymphaea</i>	0.66	Peer et al.,2006	
39	Clade B	<i>Noccaea</i>	<i>violascens</i>	0.31	Peer et al.,2003	
40	Clade B	<i>Kernera</i>	<i>saxatilis</i>	0.2	Lysák et al.,2009	0.57
1	Clade C	<i>Iberis</i>	<i>sempervirens</i>	0.56	Lysák et al.,2009	
2	Clade C	<i>Iberis</i>	<i>gibraltarica</i>	0.57	Lysák et al.,2009	
3	Clade C	<i>Lobularia</i>	<i>libyaca</i>	0.53	Lysák et al.,2009	
4	Clade C	<i>Lobularia</i>	<i>canariensis</i>	0.57	Suda et al.,2003	
5	Clade C	<i>Cochlearia</i>	<i>aucheri</i>	0.3	Peer et al.,2003	
6	Clade C	<i>Cochlearia</i>	<i>sempervivum</i>	0.33	Peer et al.,2003	
7	Clade C	<i>Cochlearia</i>	<i>pyrenaica</i>	0.4	Krisai and Greilhuber,1997	
8	Clade C	<i>Cochlearia</i>	<i>danica</i>	0.7	Lysák et al.,2009	
9	Clade C	<i>Cochlearia</i>	<i>officinalis</i>	0.75	Lysák et al.,2009	
10	Clade C	<i>Cochlearia</i>	<i>tatrae</i>	1.04	Kochjarova et al.,2006	
11	Clade C	<i>Cochlearia</i>	<i>borzaeana</i>	1.41	Kochjarova et al.,2006	
12	Clade C	<i>Lunaria</i>	<i>rediviva</i>	0.37	Pustahija et al.,2013	
13	Clade C	<i>Lunaria</i>	<i>biennis</i>	1.85	Zonneveld et al.,2005	
14	Clade C	<i>Biscutella</i>	<i>auriculata</i>	0.69	Lysák et al.,2009	
15	Clade C	<i>Biscutella</i>	<i>didyma</i>	0.79	Peer et al.,2003	
16	Clade C	<i>Biscutella</i>	<i>laevigata</i>	1.83	Temsch et al.,2010	0.79
1	Clade D	<i>Alyssum</i>	<i>saxatile</i>	0.65	Lysák et al.,2009	

2	Clade D	<i>Alyssum markgrafii</i>	0.54	Pustahija et al.,2013	
3	Clade D	<i>Alyssum murale</i>	0.58	Siljak-Yakovlev et al.,2010	
4	Clade D	<i>Alyssum saxatile</i>	0.65	Lysák et al.,2009	
5	Clade D	<i>Berteroa incana</i>	0.71	Lysák et al.,2009	0.63
1	Clade E	<i>Parrya nudicaulis</i>	1.08	Lysák et al.,2009	
2	Clade E	<i>Chorispora tenella</i>	0.35	Lysák et al.,2009	
3	Clade E	<i>Bunias erucago</i>	2.07	Greilhuber and Obermayer,1999	
4	Clade E	<i>Bunias orientalis</i>	2.59	Greilhuber and Obermayer,1999	
5	Clade E	<i>Hesperis matronalis</i>	3.8	Kubešová et al.,2010	1.98
1	Clade F	<i>Aethionem a saxatile</i>	0.62	Pustahija et al.,2013	
2	Clade F	<i>Aethionem a grandifloru m</i>	0.71	Lysák et al.,2009	
3	Clade F	<i>Aethionem a schistosum</i>	0.71	Lysák et al.,2009	
4	Clade F	<i>Aethionem a cordifolium</i>	2.14	Bou Dagher-Kharrat et al.,2013	1.05

References

1. Turner, T.R.; James, E.K.; Poole, P.S. The Plant Microbiome. *Genome Biol* **2013**, *14*, 1–10. <https://doi.org/10.1186/GB-2013-14-6-209/FIGURES/1>.

2. Trivedi, P.; Leach, J.E.; Tringe, S.G.; Sa, T.; Singh, B.K. Plant–Microbiome Interactions: From Community Assembly to Plant Health. *Nature Reviews Microbiology* **2020**, *18*, 607–621. <https://doi.org/10.1038/s41579-020-0412-1>.

3. Fitzpatrick, C.R.; Salas-González, I.; Conway, J.M.; Finkel, O.M.; Gilbert, S.; Russ, D.; Teixeira, P.J.P.L.; Dangl, J.L. The Plant Microbiome: From Ecology to Reductionism and Beyond. *Annu Rev Microbiol* **2020**, *74*, 81–100. <https://doi.org/10.1146/ANNUREV-MICRO-022620-014327/CITE/REFWORKS>.

4. Reeves, R.D.; Baker, A.J.M.; Jaffré, T.; Erskine, P.D.; Echevarria, G.; van der Ent, A. A Global Database for Plants That Hyperaccumulate Metal and Metalloid Trace Elements. *New Phytologist* **2018**, *218*, 407–411. <https://doi.org/10.1111/NPH.14907>.

5. Al-Shehbaz, I.A.; Beilstein, M.A.; Kellogg, E.A. Systematics and Phylogeny of the Brassicaceae (Cruciferae): An Overview. *Plant Systematics and Evolution* **2006**, *259*, 89–120. <https://doi.org/10.1007/S00606-006-0415-Z/METRICS>.

6. Al-Shehbaz, I.A. A Synopsis of the Genus *Noccaea* (Coluteocarpeae, Brassicaceae). *Harv Pap Bot* **2014**, *19*, 25–51. <https://doi.org/10.3100/HPIB.V19ISS1.2014.N3>.
7. Franzke, A.; German, D.; Al-Shehbaz, I.A.; Mummenhoff, K. Arabidopsis Family Ties: Molecular Phylogeny and Age Estimates in Brassicaceae. *Taxon* **2009**, *58*, 425–437. <https://doi.org/10.1002/TAX.582009>.
8. Hohmann, N.; Wolf, E.M.; Lysak, M.A.; Koch, M.A. A Time-Calibrated Road Map of Brassicaceae Species Radiation and Evolutionary History. *Plant Cell* **2015**, *27*, 2770–2784. <https://doi.org/10.1105/TPC.15.00482>.
9. Mandáková, T.; Joly, S.; Krzywinski, M.; Mummenhoff, K.; Lysak, M.A. Fast Diploidization in Close Mesopolyploid Relatives of Arabidopsis. *Plant Cell* **2010**, *22*, 2277–2290. <https://doi.org/10.1105/TPC.110.074526>.
10. Kagale, S.; Robinson, S.J.; Nixon, J.; Xiao, R.; Huebert, T.; Condie, J.; Kessler, D.; Clarke, W.E.; Edger, P.P.; Links, M.G.; et al. Polyploid Evolution of the Brassicaceae during the Cenozoic Era. *Plant Cell* **2014**, *26*, 2777–2791. <https://doi.org/10.1105/TPC.114.126391>.
11. Van De Peer, Y.; Mizrachi, E.; Marchal, K. The Evolutionary Significance of Polyploidy. *Nature Reviews Genetics* **2017**, *18*, 411–424. <https://doi.org/10.1038/nrg.2017.26>.
12. Huang, C.H.; Sun, R.; Hu, Y.; Zeng, L.; Zhang, N.; Cai, L.; Zhang, Q.; Koch, M.A.; Al-Shehbaz, I.; Edger, P.P.; et al. Resolution of Brassicaceae Phylogeny Using Nuclear Genes Uncovers Nested Radiations and Supports Convergent Morphological Evolution. *Mol Biol Evol* **2016**, *33*, 394–412. <https://doi.org/10.1093/MOLBEV/MSV226>.
13. Zhang, H.; Liu, H.; Han, X. Traits-Based Approach: Leveraging Genome Size in Plant–Microbe Interactions. *Trends Microbiol* **2024**, *32*, 333–341. <https://doi.org/10.1016/J.TIM.2023.10.004>.
14. Sotelo, T.; Lema, M.; Soengas, P.; Cartea, M.E.; Velasco, P. In Vitro Activity of Glucosinolates and Their Degradation Products against Brassica-Pathogenic Bacteria and Fungi. *Appl Environ Microbiol* **2015**, *81*, 432–440. https://doi.org/10.1128/AEM.03142-14/SUPPL_FILE/ZAM999105920SO1.PDF.
15. Abdel-Massih, R.M.; Debs, E.; Othman, L.; Attieh, J.; Cabrerizo, F.M. Glucosinolates, a Natural Chemical Arsenal: More to Tell than the Myrosinase Story. *Front Microbiol* **2023**, *14*, 1130208. <https://doi.org/10.3389/FMICB.2023.1130208/XML>.
16. Kováč, J.; Lux, A.; Soukup, M.; Weidinger, M.; Gruber, D.; Lichtscheidl, I.; Vaculík, M. A New Insight on Structural and Some Functional Aspects of Peri-Endodermal Thickenings, a Specific Layer in *Noccaea Caerulescens* Roots. *Ann Bot* **2020**, *126*, 423–434. <https://doi.org/10.1093/AOB/MCAA069>.
17. Trautwig, A.N.; Jackson, M.R.; Kivlin, S.N.; Stinson, K.A. Reviewing Ecological Implications of Mycorrhizal Fungal Interactions in the Brassicaceae. *Front Plant Sci* **2023**, *14*, 1269815. <https://doi.org/10.3389/FPLS.2023.1269815/BIBTEX>.
18. Pongrac, P.; Sonjak, S.; Vogel-Mikuš, K.; Kump, P.; Nečemer, M.; Regvar, M. Roots of Metal Hyperaccumulating Population of *Thlaspi Praecox* (Brassicaceae) Harbour Arbuscular Mycorrhizal and Other Fungi under Experimental Conditions. *Int J Phytoremediation* **2009**, *11*, 347–359. <https://doi.org/10.1080/15226510802565527>.
19. Vogel-Mikuš, K.; Drobne, D.; Regvar, M. Zn, Cd and Pb Accumulation and Arbuscular Mycorrhizal Colonisation of Pennycress *Thlaspi Praecox* Wulf. (Brassicaceae) from the Vicinity of a Lead Mine and Smelter in Slovenia. *Environmental Pollution* **2005**, *133*, 233–242. <https://doi.org/10.1016/j.envpol.2004.06.021>.
20. Regvar, M.; Vogel-Mikuš, K.; Kugonič, N.; Turk, B.; Batič, F. Vegetational and Mycorrhizal Successions at a Metal Polluted Site: Indications for the Direction of Phytostabilisation? *Environmental Pollution* **2006**, *144*, 976–984. <https://doi.org/10.1016/j.envpol.2006.01.036>.
21. Vogel-Mikuš, K.; Pongrac, P.; Kump, P.; Nečemer, M.; Regvar, M. Colonisation of a Zn, Cd and Pb Hyperaccumulator *Thlaspi Praecox* Wulfen with Indigenous Arbuscular Mycorrhizal Fungal Mixture

- Induces Changes in Heavy Metal and Nutrient Uptake. *Environmental Pollution* **2006**, *139*, 362–371. <https://doi.org/10.1016/j.envpol.2005.05.005>.
22. Zunk, K.; Mummenhoff, K.; Koch, M.; Hurka, H. Phylogenetic Relationships of *Thlaspi* s.l. (Subtribe Thlaspidinae, Lepidieae) and Allied Genera Based on Chloroplast DNA Restriction- Site Variation. *Theoretical and Applied Genetics* **1996**, *92*, 375–381. <https://doi.org/10.1007/BF00223682/METRICS>.
 23. Koch, M.; Mummenhoff, K. *Thlaspi* s.str. (Brassicaceae) versus *Thlaspi* s.l.: Morphological and Anatomical Characters in the Light of ITS nrDNA Sequence Data. *Plant Systematics and Evolution* **2001**, *227*, 209–225. <https://doi.org/10.1007/S006060170049/METRICS>.
 24. Krämer, U. Metal Hyperaccumulation in Plants. *Annu Rev Plant Biol* **2010**, *61*, 517–534. <https://doi.org/10.1146/ANNUREV-ARPLANT-042809-112156/CITE/REFWORKS>.
 25. Fasani, E.; Zamboni, A.; Sorio, D.; Furini, A.; DalCorso, G. Metal Interactions in the Ni Hyperaccumulating Population of *Noccaea Caerulescens* Monte Prinzer. *Biology (Basel)* **2023**, *12*, 1537. <https://doi.org/10.3390/BIOLOGY12121537/S1>.
 26. Vogel-Mikuš, K.; Regvar, M.; Mesjasz-Przybyłowicz, J.; Przybyłowicz, W.J.; Simčič, J.; Pelicon, P.; Budnar, M. Spatial Distribution of Cadmium in Leaves of Metal Hyperaccumulating *Thlaspi Praecox* Using Micro-PIXE. *New Phytologist* **2008**, *179*, 712–721. <https://doi.org/10.1111/j.1469-8137.2008.02519.x>.
 27. Koren, Š.; Arčon, I.; Kump, P.; Nečemer, M.; Vogel-Mikuš, K. Influence of CdCl₂ and CdSO₄ Supplementation on Cd Distribution and Ligand Environment in Leaves of the Cd Hyperaccumulator *Noccaea (Thlaspi) Praecox*. *Plant Soil* **2013**, *370*, 125–148. <https://doi.org/10.1007/s11104-013-1617-0>.
 28. Likar, M.; Pongrac, P.; Vogel-Mikuš, K.; Regvar, M. Molecular Diversity and Metal Accumulation of Different *Thlaspi Praecox* Populations from Slovenia. *Plant Soil* **2010**, *330*, 195–205. <https://doi.org/10.1007/S11104-009-0192-X/TABLES/3>.
 29. Koch, M.; Al-Shehbaz, I.A. Taxonomic and Phylogenetic Evaluation of the American “*Thlaspi*” Species: Identity and Relationship to the Eurasian Genus *Noccaea* (Brassicaceae). *Syst Bot* **2004**, *29*, 375–384. <https://doi.org/10.1600/036364404774195566>.
 30. Mandáková, T.; Li, Z.; Barker, M.S.; Lysak, M.A. Diverse Genome Organization Following 13 Independent Mesopolyploid Events in Brassicaceae Contrasts with Convergent Patterns of Gene Retention. *The Plant Journal* **2017**, *91*, 3–21. <https://doi.org/10.1111/TPJ.13553>.
 31. Lysak, M.A.; Koch, M.A.; Pecinka, A.; Schubert, I. Chromosome Triplication Found across the Tribe Brassiceae. *Genome Res* **2005**, *15*, 516–525. <https://doi.org/10.1101/GR.3531105>.
 32. Vision, T.J.; Brown, D.G.; Tanksley, S.D. The Origins of Genomic Duplications in Arabidopsis. *Science (1979)* **2000**, *290*, 2114–2117. <https://doi.org/10.1126/SCIENCE.290.5499.2114/ASSET/D8275032-A6D3-4203-B7CA-04032F721F31/ASSETS/GRAPHIC/SE4909059002.JPEG>.
 33. Johnston, J.S.; Pepper, A.E.; Hall, A.E.; Chen, Z.J.; Hodnett, G.; Drabek, J.; Lopez, R.; Price, H.J. Evolution of Genome Size in Brassicaceae. *Ann Bot* **2005**, *95*, 229–235. <https://doi.org/10.1093/AOB/MCI016>.
 34. Mandáková, T.; Singh, V.; Krämer, U.; Lysak, M.A. Genome Structure of the Heavy Metal Hyperaccumulator *Noccaea Caerulescens* and Its Stability on Metalliferous and Nonmetalliferous Soils. *Plant Physiol* **2015**, *169*, 674–689. <https://doi.org/10.1104/PP.15.00619>.
 35. Knight, C.A.; Molinari, N.A.; Petrov, D.A. The Large Genome Constraint Hypothesis: Evolution, Ecology and Phenotype. *Ann Bot* **2005**, *95*, 177–190. <https://doi.org/10.1093/AOB/MCI011>.
 36. Temsch, E.M.; Temsch, W.; Ehrendorfer-Schratt, L.; Greilhuber, J. Heavy Metal Pollution, Selection, and Genome Size: The Species of the Žerjav Study Revisited with Flow Cytometry. *J Bot* **2010**, *2010*, 596542. <https://doi.org/10.1155/2010/596542>.

37. Vidic, T.; Greilhuber, J.; Vilhar, B.; Dermastia, M. Selective Significance of Genome Size in a Plant Community with Heavy Metal Pollution. *Ecological Applications* **2009**, *19*, 1515–1521. <https://doi.org/10.1890/08-1798.1>.
38. Leitch IJ, J.E.P.J.H.O.B.M. release 7. 1, A. 2019 Plant DNA C-Values Database | Royal Botanic Gardens, Kew Available online: <https://cvalues.science.kew.org/> (accessed on 29 July 2025).
39. Rodríguez-Gijón, A.; Nuy, J.K.; Mehrshad, M.; Buck, M.; Schulz, F.; Woyke, T.; Garcia, S.L. A Genomic Perspective Across Earth's Microbiomes Reveals That Genome Size in Archaea and Bacteria Is Linked to Ecosystem Type and Trophic Strategy. *Front Microbiol* **2022**, *12*, 761869. <https://doi.org/10.3389/FMICB.2021.761869/BIBTEX>.
40. Greilhuber, J.; Borsch, T.; Müller, K.; Worberg, A.; Porembski, S.; Barthlott, W. Smallest Angiosperm Genomes Found in Lentibulariaceae, with Chromosomes of Bacterial Size. *Plant Biol (Stuttg)* **2006**, *8*, 770–777. <https://doi.org/10.1055/S-2006-924101>.
41. Pellicer, J.; Fay, M.F.; Leitch, I.J. The Largest Eukaryotic Genome of Them All? *Botanical Journal of the Linnean Society* **2010**, *164*, 10–15. <https://doi.org/10.1111/J.1095-8339.2010.01072.X>.
42. Francis, D.; Davies, M.S.; Barlow, P.W. A Strong Nucleotypic Effect on the Cell Cycle Regardless of Ploidy Level. *Ann Bot* **2008**, *101*, 747–757. <https://doi.org/10.1093/AOB/MCN038>.
43. D'Ario, M.; Tavares, R.; Schiessl, K.; Desvoves, B.; Gutierrez, C.; Howard, M.; Sablowski, R. Cell Size Controlled in Plants Using DNA Content as an Internal Scale. *Science* **2021**, *372*, 1176–1181. <https://doi.org/10.1126/SCIENCE.ABB4348>.
44. Segraves, K.A. The Effects of Genome Duplications in a Community Context. *New Phytologist* **2017**, *215*, 57–69. <https://doi.org/10.1111/NPH.14564>.
45. Regvar, M.; Vogel, K.; Irgel, N.; Hildebrandt, U.; Wilde, P.; Bothe, H. *Colonization of Pennycresses (Thlaspi Spp.) of the Brassicaceae by Arbuscular Mycorrhizal Fungi*; 2003; Vol. 160.
46. Orłowska, E.; Zubek, S.; Jurkiewicz, A.; Szarek-Lukaszewska, G.; Turnau, K. Influence of Restoration on Arbuscular Mycorrhiza of *Biscutella laevigata* L. (Brassicaceae) and *Plantago lanceolata* L. (Plantaginaceae) from Calamine Spoil Mounds. *Mycorrhiza* **2002**, *12*, 153–159. <https://doi.org/10.1007/S00572-001-0155-4>.
47. Trouvelot, A.; Kough, J.L.; Gianinazzi-Pearson, V. Du Taux de Mycorhization VA d'un Système Radiculaire. Recherche de Méthodes d'estimation Ayant Une Signification Fonctionnelle. *Mycorhizes: Physiologie et génétique* **1986**.
48. Ancousture, J.; Durand, A.; Blaudez, D.; Benizri, E. A Reduced but Stable Core Microbiome Found in Seeds of Hyperaccumulators. *Science of The Total Environment* **2023**, *887*, 164131. <https://doi.org/10.1016/J.SCITOTENV.2023.164131>.
49. Levy, A.; Salas Gonzalez, I.; Mittelviefhaus, M.; Clingenpeel, S.; Herrera Paredes, S.; Miao, J.; Wang, K.; Devescovi, G.; Stillman, K.; Monteiro, F.; et al. Genomic Features of Bacterial Adaptation to Plants. *Nature Genetics* **2017**, *50*, 138–150. <https://doi.org/10.1038/s41588-017-0012-9>.
50. van der Ent, A.; Spiers, K.M.; Brueckner, D.; Echevarria, G.; Aarts, M.G.M.; Montargès-Pelletier, E. Spatially-Resolved Localization and Chemical Speciation of Nickel and Zinc in *Nocca Tymphaea* and *Bornmuellera emarginata*. *Metallomics* **2019**. <https://doi.org/10.1039/c9mt00106a>.
51. Hanikenne, M.; Talke, I.N.; Haydon, M.J.; Lanz, C.; Nolte, A.; Motte, P.; Kroymann, J.; Weigel, D.; Krämer, U. Evolution of Metal Hyperaccumulation Required Cis-Regulatory Changes and Triplication of HMA4. *Nature* **2008**, *453*, 391–395. <https://doi.org/10.1038/nature06877>.

52. Roux, C.; Castric, V.; Pauwels, M.; Wright, S.I.; Saumitou-Laprade, P.; Vekemans, X. Does Speciation between *Arabidopsis Halleri* and *Arabidopsis Lyrata* Coincide with Major Changes in a Molecular Target of Adaptation? *PLoS ONE* **2011**, *6*, e26872. <https://doi.org/10.1371/JOURNAL.PONE.0026872>.
53. Ó Lochlainn, S.; Bowen, H.C.; Fray, R.G.; Hammond, J.P.; King, G.J.; White, P.J.; Graham, N.S.; Broadley, M.R. Tandem Quadruplication of HMA4 in the Zinc (Zn) and Cadmium (Cd) Hyperaccumulator *Noccaea Caerulescens*. *PLoS ONE* **2011**, *6*, e17814. <https://doi.org/10.1371/JOURNAL.PONE.0017814>.
54. Craciun, A.R.; Meyer, C.L.; Chen, J.; Roosens, N.; De Groodt, R.; Hilson, P.; Verbruggen, N. Variation in HMA4 Gene Copy Number and Expression among *Noccaea Caerulescens* Populations Presenting Different Levels of Cd Tolerance and Accumulation. *J Exp Bot* **2012**, *63*, 4179–4189. <https://doi.org/10.1093/JXB/ERS104>.
55. Clemens, S.; Palmgren, M.G.; Krämer, U. A Long Way Ahead: Understanding and Engineering Plant Metal Accumulation. *Trends Plant Sci* **2002**, *7*, 309–315. [https://doi.org/10.1016/S1360-1385\(02\)02295-1](https://doi.org/10.1016/S1360-1385(02)02295-1).
56. Hanikenne, M.; Nouet, C. Metal Hyperaccumulation and Hypertolerance: A Model for Plant Evolutionary Genomics. *Curr Opin Plant Biol* **2011**, *14*, 252–259. <https://doi.org/10.1016/J.PBI.2011.04.003>.
57. Milner, M.J.; Mitani-Ueno, N.; Yamaji, N.; Yokosho, K.; Craft, E.; Fei, Z.; Ebbs, S.; Clemencia Zambrano, M.; Ma, J.F.; Kochian, L. V. Root and Shoot Transcriptome Analysis of Two Ecotypes of *Noccaea Caerulescens* Uncovers the Role of NcNramp1 in Cd Hyperaccumulation. *The Plant Journal* **2014**, *78*, 398–410. <https://doi.org/10.1111/TPJ.12480>.
58. Martos, S.; Gallego, B.; Sáez, L.; López-Alvarado, J.; Cabot, C.; Poschenrieder, C. Characterization of Zinc and Cadmium Hyperaccumulation in Three *Noccaea* (Brassicaceae) Populations from Non-Metalliferous Sites in the Eastern Pyrenees. *Front Plant Sci* **2016**, *7*, 173623. <https://doi.org/10.3389/FPLS.2016.00128/BIBTEX>.
59. Lin, Y.F.; Severing, E.I.; te Lintel Hekkert, B.; Schijlen, E.; Aarts, M.G.M. A Comprehensive Set of Transcript Sequences of the Heavy Metal Hyperaccumulator *Noccaea Caerulescens*. *Front Plant Sci* **2014**, *5*, 78115. <https://doi.org/10.3389/FPLS.2014.00261/BIBTEX>.
60. Ważny, R.; Rozpądek, P.; Domka, A.; Jędrzejczyk, R.J.; Nosek, M.; Hubalewska-Mazgaj, M.; Lichtscheidl, I.; Kidd, P.; Turnau, K. The Effect of Endophytic Fungi on Growth and Nickel Accumulation in *Noccaea* Hyperaccumulators. *Science of The Total Environment* **2021**, *768*, 144666. <https://doi.org/10.1016/J.SCITOTENV.2020.144666>.
61. Bočaj, V.; Pongrac, P.; Grčman, H.; Šala, M.; Likar, M. Rhizobiome Diversity of Field-Collected Hyperaccumulating *Noccaea* Sp. *BMC Plant Biol* **2024**, *24*, 1–14. <https://doi.org/10.1186/S12870-024-05605-4/FIGURES/5>.
62. Durand, A.; Sterckeman, T.; Gonnelli, C.; Coppi, A.; Bacci, G.; Leglize, P.; Benizri, E. A Core Seed Endophytic Bacterial Community in the Hyperaccumulator *Noccaea Caerulescens* across 14 Sites in France. *Plant Soil* **2021**, *459*, 203–216. <https://doi.org/10.1007/S11104-020-04743-6/FIGURES/5>.
63. Wolters, H.; Jürgens, G. Survival of the Flexible: Hormonal Growth Control and Adaptation in Plant Development. *Nature Reviews Genetics* **2009**, *10*, 305–317. <https://doi.org/10.1038/nrg2558>.
64. Callahan, D.L.; Hare, D.J.; Bishop, D.P.; Doble, P.A.; Roessner, U. Elemental Imaging of Leaves from the Metal Hyperaccumulating Plant *Noccaea Caerulescens* Shows Different Spatial Distribution of Ni, Zn and Cd. *RSC Adv* **2015**, *6*, 2337–2344. <https://doi.org/10.1039/C5RA23953B>.
65. Vázquez, M.D.; Barceló, J.; Poschenrieder, Ch.; Mádico, J.; Hatton, P.; Baker, A.J.M.; Cope, G.H. Localization of Zinc and Cadmium in *Thlaspi Caerulescens* (Brassicaceae), a Metallophyte That Can Hyperaccumulate Both Metals. *J Plant Physiol* **1992**, *140*, 350–355. [https://doi.org/10.1016/S0176-1617\(11\)81091-6](https://doi.org/10.1016/S0176-1617(11)81091-6).

66. Regvar, M.; Eichert, D.; Kaulich, B.; Gianoncelli, A.; Pongrac, P.; Vogel-Mikuš, K. Biochemical Characterization of Cell Types within Leaves of Metal-Hyperaccumulating *Noccaea Praecox* (Brassicaceae). *Plant Soil* **2013**, *373*, 157–171. <https://doi.org/10.1007/s11104-013-1768-z>.
67. Braccini, I.; Pérez, S. Molecular Basis of Ca²⁺-Induced Gelation in Alginates and Pectins: The Egg-Box Model Revisited. *Biomacromolecules* **2001**, *2*, 1089–1096. <https://doi.org/10.1021/BM010008G/ASSET/IMAGES/LARGE/BM010008GF00007.JPEG>.
68. Pongrac, P.; Vogel-Mikuš, K.; Vavpetič, P.; Tratnik, J.; Regvar, M.; Simčič, J.; Grlj, N.; Pelicon, P. Cd Induced Redistribution of Elements within Leaves of the Cd/Zn Hyperaccumulator *Thlaspi Praecox* as Revealed by Micro-PIXE. *Nucl Instrum Methods Phys Res B* **2010**, *268*, 2205–2210. <https://doi.org/10.1016/j.nimb.2010.02.089>.
69. Smets, W.; Chock, M.K.; Walsh, C.M.; Vanderburgh, C.Q.; Kau, E.; Lindow, S.E.; Fierer, N.; Koskella, B. Leaf Side Determines the Relative Importance of Dispersal versus Host Filtering in the Phyllosphere Microbiome. *mBio* **2023**, *14*, e0111123. <https://doi.org/10.1128/MBIO.01111-23>.
70. Fones, H.N.; McCurrach, H.; Mithani, A.; Smith, J.A.C.; Preston, G.M. Local Adaptation Is Associated with Zinc Tolerance in *Pseudomonas* Endophytes of the Metal-Hyperaccumulator Plant *Noccaea Caerulescens*. *Proceedings of the Royal Society B: Biological Sciences* **2016**, *283*. <https://doi.org/10.1098/RSPB.2016.0648>.
71. Zelko, I.; Lux, A.; Czibula, K. Difference in the Root Structure of Hyperaccumulator *Thlaspi Caerulescens* and Non-Hyperaccumulator *Thlaspi Arvense*. *Int J Environ Pollut* **2008**, *33*, 123–132. <https://doi.org/10.1504/IJEP.2008.019387>.
72. Hiruma, K.; Gerlach, N.; Sacristán, S.; Nakano, R.T.; Hacquard, S.; Kracher, B.; Neumann, U.; Ramírez, D.; Bucher, M.; O'Connell, R.J.; et al. Root Endophyte *Colletotrichum Tofieldiae* Confers Plant Fitness Benefits That Are Phosphate Status Dependent. *Cell* **2016**, *165*, 464–474. <https://doi.org/10.1016/J.CELL.2016.02.028>.
73. Andersen, T.G.; Naseer, S.; Ursache, R.; Wybouw, B.; Smet, W.; De Rybel, B.; Vermeer, J.E.M.; Geldner, N. Diffusible Repression of Cytokinin Signalling Produces Endodermal Symmetry and Passage Cells. *Nature* **2018**, *555*, 529–533. <https://doi.org/10.1038/nature25976>.
74. Holbein, J.; Shen, D.; Andersen, T.G. The Endodermal Passage Cell – Just Another Brick in the Wall? *New Phytologist* **2021**, *230*, 1321–1328. <https://doi.org/10.1111/NPH.17182>.
75. Paungfoo-Lonhienne, C.; Rentsch, D.; Robatzek, S.; Webb, R.I.; Sagulenko, E.; Näsholm, T.; Schmidt, S.; Lonhienne, T.G.A. Turning the Table: Plants Consume Microbes as a Source of Nutrients. *PLoS ONE* **2010**, *5*, e11915. <https://doi.org/10.1371/JOURNAL.PONE.0011915>.
76. Durr, J.; Reyt, G.; Spaepen, S.; Hilton, S.; Meehan, C.; Qi, W.; Kamiya, T.; Flis, P.; Dickinson, H.G.; Feher, A.; et al. A Novel Signaling Pathway Required for Arabidopsis Endodermal Root Organization Shapes the Rhizosphere Microbiome. *Plant Cell Physiol* **2021**, *62*, 248–261. <https://doi.org/10.1093/PCP/PCAA170>.
77. Salas-González, I.; Reyt, G.; Flis, P.; Custódio, V.; Gopaulchan, D.; Bakhoun, N.; Dew, T.P.; Suresh, K.; Franke, R.B.; Dangl, J.L.; et al. Coordination between Microbiota and Root Endodermis Supports Plant Mineral Nutrient Homeostasis. *Science* **2021**, *371*. <https://doi.org/10.1126/SCIENCE.ABD0695>.
78. Maciá-Vicente, J.G.; Nam, B.; Thines, M. Root Filtering, Rather than Host Identity or Age, Determines the Composition of Root-Associated Fungi and Oomycetes in Three Naturally Co-Occurring Brassicaceae. *Soil Biol Biochem* **2020**, *146*, 107806. <https://doi.org/10.1016/J.SOILBIO.2020.107806>.
79. Sharma, A.; Sinharoy, S.; Bisht, N.C. The Mysterious Non-Arbuscular Mycorrhizal Status of Brassicaceae Species. *Environ Microbiol* **2023**, *25*, 917–930. <https://doi.org/10.1111/1462-2920.16339>.
80. Delaux, P.M.; Radhakrishnan, G. V.; Jayaraman, D.; Cheema, J.; Malbreil, M.; Volkening, J.D.; Sekimoto, H.; Nishiyama, T.; Melkonian, M.; Pokorny, L.; et al. Algal Ancestor of Land Plants Was Preadapted for

- Symbiosis. *Proc Natl Acad Sci U S A* **2015**, *112*, 13390–13395. https://doi.org/10.1073/PNAS.1515426112/SUPPL_FILE/PNAS.1515426112.SD03.XLS.
81. Pongrac, P.; Vogel-Mikuš, K.; Poschenrieder, C.; Barceló, J.; Tolrà, R.; Regvar, M. *Arbuscular Mycorrhiza in Glucosinolate-Containing Plants: The Story of the Metal Hyperaccumulator Noccaea (Thlaspi) Praecox (Brassicaceae)*; 2013;.
 82. Pongrac, P.; Vogel-Mikuš, K.; Regvar, M.; Tolrà, R.; Poschenrieder, C.; Barceló, J. Glucosinolate Profiles Change during the Life Cycle and Mycorrhizal Colonization in a Cd/Zn Hyperaccumulator *Thlaspi Praecox* (Brassicaceae). *J Chem Ecol* **2008**, *34*, 1038–1044. <https://doi.org/10.1007/s10886-008-9502-7>.
 83. Bočaj, V.; Regvar, M.; Pongrac, P. Linking Microbiome and Hyperaccumulation in Plants. **2025**. <https://doi.org/10.2024/Accepted>.
 84. Yang, J.; Song, N.; Zhao, X.; Qi, X.; Hu, Z.; Zhang, M. Genome Survey Sequencing Provides Clues into Glucosinolate Biosynthesis and Flowering Pathway Evolution in Allotetrapolyploid *Brassica Juncea*. *BMC Genomics* **2014**, *15*, 1–9. <https://doi.org/10.1186/1471-2164-15-107/FIGURES/5>.
 85. Grubb, C.D.; Abel, S. Glucosinolate Metabolism and Its Control. *Trends Plant Sci* **2006**, *11*, 89–100. <https://doi.org/10.1016/J.TPLANTS.2005.12.006>.
 86. Agerbirk, N.; Olsen, C.E. Glucosinolate Structures in Evolution. *Phytochemistry* **2012**, *77*, 16–45. <https://doi.org/10.1016/J.PHYTOCHEM.2012.02.005>.
 87. De Graaf, R.M.; Krosse, S.; Swolfs, A.E.M.; Te Brinke, E.T.; Prill, N. Te; Leimu, R.; Van Galen, P.M.; Wang, Y.; Aarts, M.G.M.; Van Dam, N.M. Isolation and Identification of 4- α -Rhamnosyloxy Benzyl Glucosinolate in *Noccaea Caerulescens* Showing Intraspecific Variation. *Phytochemistry* **2015**, *110*, 166–171. <https://doi.org/10.1016/J.PHYTOCHEM.2014.11.016>.
 88. Jeon, B.W.; Oh, M.H.; Kim, H.S.; Kim, E.O.; Chae, W.B. Glucosinolate Variation among Organs, Growth Stages and Seasons Suggests Its Dominant Accumulation in Sexual over Asexual-Reproductive Organs in White Radish. *Sci Hortic* **2022**, *291*, 110617. <https://doi.org/10.1016/J.SCIENTA.2021.110617>.
 89. Tolrà, R.; Pongrac, P.; Poschenrieder, C.; Vogel-Mikuš, K.; Regvar, M.; Barceló, J. Distinctive Effects of Cadmium on Glucosinolate Profiles in Cd Hyperaccumulator *Thlaspi Praecox* and Non-Hyperaccumulator *Thlaspi Arvense*. *Plant Soil* **2006**, *288*, 333–341. <https://doi.org/10.1007/s11104-006-9124-1>.
 90. Unger, K.; Raza, S.A.K.; Mayer, T.; Reichelt, M.; Stuttmann, J.; Hielscher, A.; Wittstock, U.; Gershenzon, J.; Agler, M.T. Glucosinolate Structural Diversity Shapes Recruitment of a Metabolic Network of Leaf-Associated Bacteria. *Nature Communications* **2024**, *15*. <https://doi.org/10.1038/S41467-024-52679-7>.
 91. Anthony, M.A.; Celenza, J.L.; Armstrong, A.; Frey, S.D. Indolic Glucosinolate Pathway Provides Resistance to Mycorrhizal Fungal Colonization in a Non-Host Brassicaceae. *Ecosphere* **2020**, *11*, e03100. <https://doi.org/10.1002/ECS2.3100>.
 92. Szucs, Z.; Plaszkó, T.; Cziáky, Z.; Kiss-Szikszai, A.; Emri, T.; Bertóti, R.; Sinka, L.T.; Vasas, G.; Gonda, S. Endophytic Fungi from the Roots of Horseradish (*Armoracia Rusticana*) and Their Interactions with the Defensive Metabolites of the Glucosinolate - Myrosinase - Isothiocyanate System. *BMC Plant Biol* **2018**, *18*, 1–15. <https://doi.org/10.1186/S12870-018-1295-4/FIGURES/6>.
 93. Chen, J.; Ullah, C.; Reichelt, M.; Beran, F.; Yang, Z.L.; Gershenzon, J.; Hammerbacher, A.; Vassão, D.G. The Phytopathogenic Fungus *Sclerotinia Sclerotiorum* Detoxifies Plant Glucosinolate Hydrolysis Products via an Isothiocyanate Hydrolase. *Nature Communications* **2020**, *11:1* **2020**, *11*, 1–12. <https://doi.org/10.1038/s41467-020-16921-2>.

Disclaimer/Publisher's Note: The statements, opinions and data contained in all publications are solely those of the individual author(s) and contributor(s) and not of MDPI and/or the editor(s). MDPI and/or the editor(s)

disclaim responsibility for any injury to people or property resulting from any ideas, methods, instructions or products referred to in the content.