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Drivers of Phytochemical Diversity Along Elevation Gradients

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Abstract: Mountains compress steep environmental gradients into short distances, making elevation an ideal natural laboratory for investigating the ecological drivers of phytochemical diversity. While elevational patterns in species richness have been studied extensively, the factors governing phytochemical diversity along mountain slopes remains poorly understood. Through a systematic literature search, we synthesise evidence to evaluate the patterns, drivers and hypotheses of phytochemical diversity across elevation gradients. Reported patterns are mixed, nonlinear, and strongly context-dependent, varying among plant lineages, compound classes, and analytical approaches. Biotic-interaction hypotheses predict declining defensive chemical diversity with elevation, driven by reduced herbivore specialisation and pollinator specificity, while abiotic-stress hypotheses predict increases in stress-related chemicals toward the summit. Community-level patterns further reflect plant species richness, phylogenetic turnover, and scale-dependent sampling effects. We conclude that no universal relationship between phytochemical diversity and elevation can yet be established. Future progress such as community-level studies, manipulative experiments, and causal approaches will advance our understanding on this increasingly urgent dimension of biodiversity under global change.

Keywords: Chemodiversity · Climate change · Ecological drivers · Elevation gradients · Plant-insect interactions

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1. Introduction

Plants are remarkable chemical factories, producing a vast diversity of specialised metabolites (formerly known as secondary metabolites) that mediate their interactions with the physical environment, antagonists, mutualists, competitors, and microbial partners.[1,2] More than 400,000 structurally distinct plant specialised metabolites have been described to date,[3] and this number almost certainly underestimates the true extent of plant chemical diversity.[4] These compounds include alkaloids, terpenoids, phenolics (*e.g.* flavonoids), glucosinolates, cyanogenic glycosides, saponins, and volatile organic compounds, among many others.[5] Their ecological functions span the full range of plant interactions. At the abiotic interface, flavonoids and related phenolics contribute to ultraviolet screening and protection against photooxidative stress, while carotenoids and other antioxidant metabolites help buffer plants against oxidative damage.[6,7] At the biotic interface, alkaloids, glucosinolates, terpenoids, and phenolics can deter herbivores, phytoalexins and antimicrobial metabolites restrict pathogen colonisation, floral scent bouquets mediate pollinator attraction, and herbivore-induced plant volatiles recruit natural enemies of herbivores, thereby mediating indirect defence and tri-trophic interactions.[8] Plant chemistry is therefore not a peripheral attribute of the plant phenotype, but a central ecological currency through which plants respond to and shape their environments.

The ecological importance of plant specialised metabolism lies not only in the presence or abundance of individual compounds, but also in the diversity of metabolites expressed within individuals, populations, species, and communities.[2,4,9] This diversity, often termed phytochemical diversity or chemodiversity, can be quantified across several biological scales, from within-plant chemical richness to among-species turnover in chemical composition and community-level occupation of chemical trait space.[10] Such multidimensional variation matters because most ecological interactions are mediated by complex mixtures rather than single compounds in isolation.[11] Herbivores, pathogens, pollinators, and microbes encounter chemical phenotypes composed of many

metabolites whose effects may be additive, synergistic, antagonistic, or context dependent.[12] Chemically diverse mixtures may reduce the probability that antagonists evolve efficient counteradaptations, broaden the range of consumers or pathogens affected, generate functional redundancy in defence, and increase the information content of chemical cues. At the community scale, plant chemical diversity can influence host-use specialisation, trophic network structure, plant–herbivore-microbe communication, and the assembly of associated faunal and floral communities.[13]

Despite its ecological centrality, phytochemical diversity remains much less well integrated into biodiversity science than taxonomic, phylogenetic, or functional diversity. Chemical ecology has traditionally generated deep mechanistic insight by focusing on specific plant lineages, compound classes, or pairwise interactions between plants and consumers. However, this emphasis has also limited our ability to understand how chemical diversity is distributed across landscapes and which ecological processes maintain it.[9] A plant community may be species-rich but chemically redundant, or relatively species-poor yet chemically distinctive. Similarly, two communities with similar taxonomic composition may differ strongly in their metabolomic profiles because of environmental filtering, phenotypic plasticity, local adaptation, or shifts in biotic interactions. Phytochemical diversity may therefore reveal dimensions of ecological organisation that are not captured by species richness alone, with consequences for plant defence, consumer specialisation, ecosystem functioning, and the conservation of metabolically unique communities.[4]

Mountains provide an especially powerful natural framework for investigating the ecological drivers of phytochemical diversity. Elevational gradients compress steep variation in temperature, season length, ultraviolet radiation, atmospheric pressure, soil development, nutrient availability, moisture regimes, and disturbance over short geographic distances.[14-16] Along the same gradients, plant communities turn over. In parallel, the abundance, richness, phenology, and specialisation of herbivores, pathogens, pollinators, and other interacting organisms may change substantially.[17,18] Thus, as elevation increases, plants are exposed not simply to cooler climates, but to coordinated shifts in abiotic stress, resource limitation, community composition, and biotic interaction regimes. Because each of these factors can influence specialised metabolism, elevational gradients offer a replicated natural experiment for testing whether phytochemical diversity follows predictable spatial patterns and for disentangling the relative roles of environmental stress, species turnover, and interaction intensity.[19]

Several non-mutually exclusive hypotheses can be proposed for how phytochemical diversity should change along elevation. These hypotheses map directly onto the conceptual framework presented in Fig. 1, which distinguishes between biotic drivers that are generally expected to be stronger or more diverse at lower elevations and abiotic drivers that often intensify towards higher elevations.[20] First, if plant chemical diversity is shaped primarily by antagonistic biotic interactions, phytochemical diversity may be highest at low elevations, where warmer temperatures and longer growing seasons are often associated with greater herbivore activity, higher pathogen pressure, and stronger consumer-mediated selection on plant defence.[21] Under this scenario, low-elevation plants or plant communities should experience stronger selection for chemically diverse, redundant, or complementary defensive phenotypes. Second, if phytochemical diversity is shaped primarily by abiotic stress, high-elevation environments may favour increased investment in metabolites involved in photoprotection, antioxidant defence, cold tolerance, and stress signalling, potentially increasing the richness or distinctiveness of particular compound classes at high elevations.[6,22] Third, if phytochemical diversity largely reflects plant species turnover, phylogenetic community structure, or shifts in ecological network composition, chemical patterns may track taxonomic, evolutionary, or interaction beta diversity rather than elevation *per se*.[19] Finally, because the biotic and abiotic drivers illustrated in Fig. 1 covary along mountain slopes and may act simultaneously on the same plant phenotypes, phytochemical diversity may show nonlinear, hump-shaped, or context-dependent responses rather than simple monotonic increases or declines.

Recent empirical work suggests that plant chemistry does vary predictably along elevational gradients, but the direction, magnitude, and mechanisms of these patterns remain incompletely resolved. Studies of plant defence along elevation have reported changes in herbivory, resistance, and secondary metabolite concentrations, yet results differ among systems, plant tissues, compound classes, and analytical approaches. This heterogeneity is consistent with the framework in Fig. 1: depending on the focal system, low-elevation biotic pressure, high-elevation abiotic stress, soil conditions, microbial communities, plant community turnover, or interactions among these factors may dominate the observed chemical response. Some findings are consistent with the classic prediction that stronger low-elevation biotic pressure selects for increased defence, whereas others indicate high-elevation increases in stress-associated metabolites or idiosyncratic responses driven by local conditions. Importantly, recent advances in untargeted metabolomics now make it possible to move beyond single-compound approaches and quantify broad chemical phenotypes across many samples, species, and communities.[4] These approaches allow researchers to test whether plant communities converge or diverge in chemical space along elevation,[23] whether chemical diversity is structured independently of taxonomy,[24] and whether distinct ecological drivers such as those represented in Fig. 1 leave detectable signatures in metabolomic profiles.

Furthermore, the understanding of elevational patterns of phytochemical diversity is increasingly urgent under global change. Mountain ecosystems are experiencing rapid warming, shifts in snow cover, altered water availability, land-use change, and upward movements of plants, insects, and pathogens.[25] These changes are likely to reorganise the abiotic and biotic conditions that shape specialised metabolism, effectively redrawing the elevational balance among ecological drivers summarised in Fig. 1. As species shift their ranges and novel communities assemble, plants may encounter new combinations of herbivores, pathogens, pollinators, competitors, microbial partners, soil conditions, and climatic stressors.[26] Such changes could alter not only where plant species occur, but also which chemical phenotypes are expressed, which metabolites are maintained or lost, and how plant-associated communities are structured. Because specialised metabolites contribute to defence, ecological interactions, ecosystem functioning, and the discovery of bioactive natural products, shifts in phytochemical diversity have implications for biodiversity conservation, ecological forecasting, and bioprospecting.[27]

In this review, we synthesise current knowledge on phytochemical diversity along elevational gradients and evaluate the ecological processes that may generate these patterns. We first summarise empirical evidence for elevational trends in phytochemical diversity, with attention to study systems, plant tissues, chemical classes, and analytical methods. We then examine major abiotic and biotic drivers, including climate, ultraviolet radiation, soil conditions, herbivores, pathogens, pollinators, microbial partners, neighbouring plants, and plant community composition. Finally, we discuss emerging hypotheses, methodological challenges, and future research priorities for linking plant chemical diversity to ecological processes in mountain ecosystems. By integrating chemical ecology, community ecology, and mountain biogeography, we aim to clarify when, where, and why phytochemical diversity changes along elevation and to identify the conceptual and methodological advances needed to make this field more predictive.

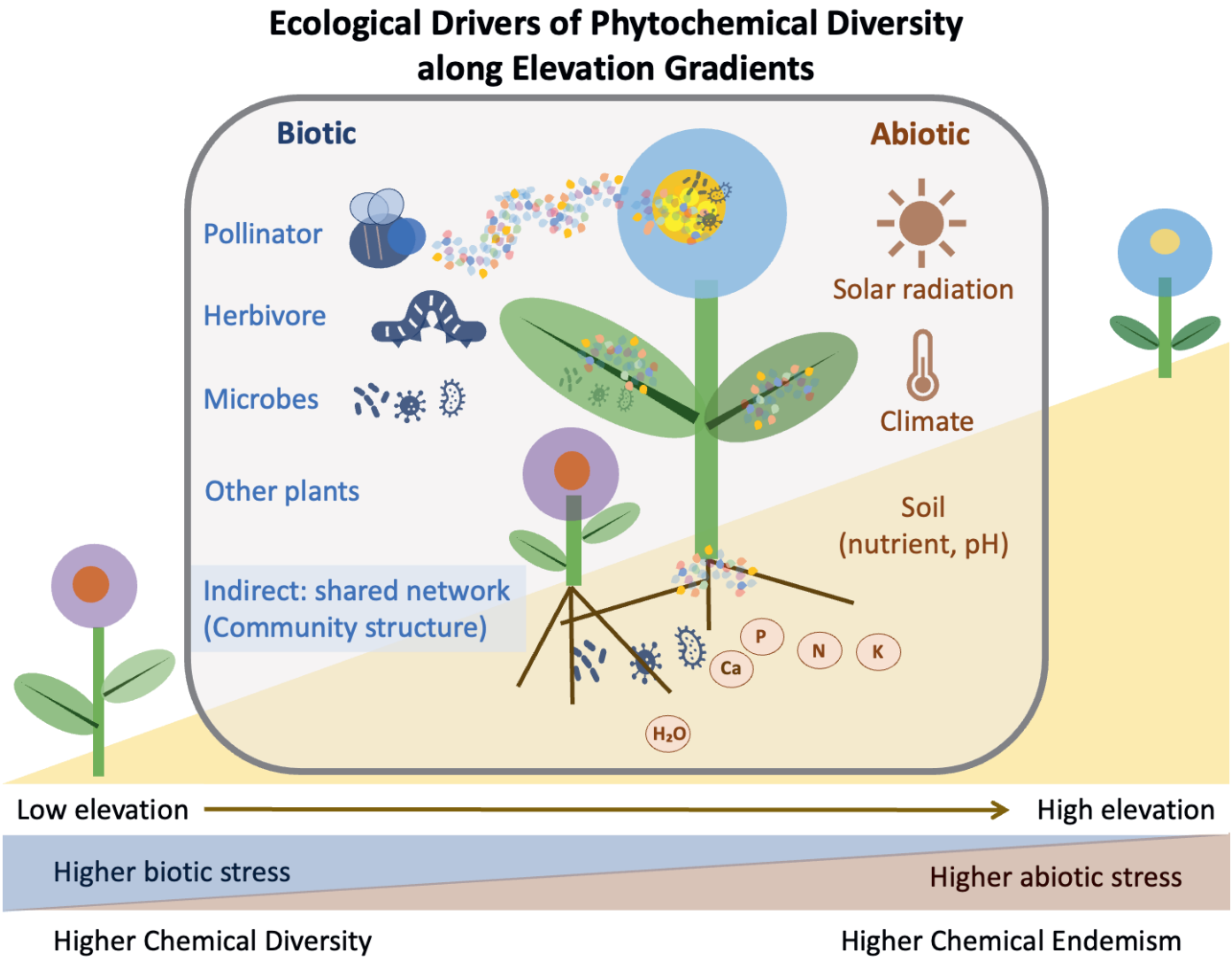

Fig. 1. Ecological drivers of phytochemical diversity along elevational gradients. Conceptual framework illustrating how biotic and abiotic ecological drivers may shape plant phytochemical diversity across mountain environments. Along elevational gradients, plants experience coordinated shifts in interaction regimes and environmental conditions. At lower elevations, warmer climates and longer growing seasons are often associated with stronger biotic pressures, including herbivory, pathogen and microbial interactions, pollinator-mediated selection, competition with neighbouring plants, and indirect effects mediated by shared ecological networks and community structure. These biotic interactions may favour greater phytochemical diversity by selecting for chemically diverse defensive, attractive, signalling, or competitive phenotypes. Toward higher elevations, plants generally experience increasing abiotic stress, including lower temperatures, shorter growing seasons, greater solar and ultraviolet radiation, altered water availability, and changes in soil nutrient status, pH. These conditions may favour chemically distinctive or specialised metabolite profiles associated with photoprotection, antioxidant defence, stress tolerance, and local environmental filtering. The opposing gradients at the bottom of the Fig. summarise the expected shift from stronger biotic stress at low elevation to stronger abiotic stress at high elevation. These processes are not mutually exclusive: biotic and abiotic drivers can act simultaneously, interactively, or indirectly through changes in plant community composition, species turnover, and ecological network structure. As a result, phytochemical diversity may decrease, increase, converge, diverge, or show nonlinear responses along elevation, depending on the relative strength of these drivers and the spatial, taxonomic, and chemical scales considered.

2. Patterns of Phytochemical Diversity Along Elevational Gradients: Literature Review Methodology

To assess the current empirical evidence for patterns of phytochemical diversity along elevational gradients, we conducted a systematic literature search in Scopus on 2nd June 2026. The search strategy was designed to identify studies that explicitly examined plant phytochemical, metabolomic, or chemical diversity in relation to elevation, altitude, or mountain gradients. Because terminology varies across chemical ecology, metabolomics, and community ecology, the query combined three thematic blocks: phytochemical diversity terms, elevational-gradient terms, and plant-organism terms. To increase specificity, phytochemical terms were required to occur within two words of the term 'diversity'. We also excluded studies focused primarily on soils, microbes, fungi, animals, humans, or gut systems, as these fell outside the scope of this review.

The full Scopus search string, applied to titles, abstracts, and keywords, was: TITLE-ABS-KEY((phytochemical OR metabolomic* OR chemical OR 'specialized metabolite*' OR chemodiversity) W/2 diversity) AND TITLE-ABS-KEY(elevation* OR altitud* OR 'mountain gradient*') AND TITLE-ABS-KEY(plant* OR tree* OR shrub* OR herb* OR grass* OR forbs) AND NOT TITLE-ABS-KEY(soil OR microbe* OR bacteri* OR fung* OR microbial OR animal* OR human* OR gut)

The database search returned 52 initial records. Because the term 'animal*' in the exclusion block could in principle also filter out plant–insect interaction studies using 'animal' in a broader ecological sense, we additionally screened the 7 records excluded on this term alone. Moreover, as recommended for systematic review practice, we further complemented the list with 3 additional papers identified through the authors' domain expertise, known to be directly relevant to the topic. This resulted in a total of 62 re-

cords (see Table S1). Records were screened by title and abstract and retained when they met three criteria: (1) a direct empirical focus on phytochemical, metabolomic, or specialised-metabolite diversity, rather than only the concentration of one or a small number of individual compounds; (2) an explicit analysis or sampling design involving elevation, altitude, or mountain gradients; and (3) a plant-focused scope at the population, species, or community level. Studies were excluded when phytochemical diversity was only discussed conceptually, when elevation was not part of the study design or analysis, when the focal system was non-plant, or when methodological information was insufficient to evaluate relevance.

For each retained or potentially relevant record, we extracted information on the study system, geographic region, elevational range, plant tissue, chemical group or metabolomic feature measured, analytical method, and phytochemical diversity metric. We also classified the reported relationship between phytochemical diversity and elevation, where possible, as increasing, decreasing, hump-shaped or otherwise nonlinear, mixed or context dependent, nonsignificant, unclear in direction, or not applicable.

Preliminary scoring of the literature-search corpus revealed substantial heterogeneity in phytochemical responses to elevation (Table S1). Of the 62 records screened, 21 did not provide a usable estimate of phytochemical diversity in relation to elevation or were otherwise classified as not applicable. Among the remaining 41 informative records, the most common outcome was the absence of a clear monotonic relationship, with 14 records reporting no significant, weak, or unclear association between phytochemical diversity and elevation. A further 9 records reported altitude-associated chemical variation but without sufficient information to determine whether diversity increased or decreased. Nine records indicated mixed, nonlinear, hump-shaped, or context-dependent responses, including cases where different compounds, tissues, diversity metrics, or ecological settings produced contrasting patterns. Only a minority of records supported simple monotonic trends: 5 suggested increasing phytochemical diversity or related chemical traits with elevation, whereas 4 suggested decreasing diversity with elevation.

Overall, these preliminary results indicate that phytochemical diversity does not follow a single dominant elevational trajectory across studies. Instead, the available evidence points to strong context dependence, likely reflecting variation among plant taxa, tissues, chemical classes, analytical methods, diversity metrics, and the relative influence of the biotic and abiotic drivers summarised in Fig. 1. This heterogeneity also highlights a major gap in the field: although many studies document changes in plant chemistry along elevation, relatively few explicitly quantify phytochemical diversity in a way that allows direct comparison across systems.

3. Process: Potential Ecological Drivers of Phytochemical Diversity

The heterogeneous elevational patterns identified in the literature review suggest that phytochemical diversity is unlikely to be controlled by a single mechanism. Instead, it probably emerges from the combined influence of abiotic and biotic drivers that covary along mountain slopes and operate across scales, from within-species plasticity and local adaptation to community turnover and interaction networks. Table 1 summarises these drivers, their expected elevational trends, predicted effects on phytochemical diversity, evidence strength, and proposed mechanisms.

Abiotic stressors generally intensify toward higher elevations, where plants experience lower temperatures, shorter growing seasons, higher irradiance, stronger ultraviolet radiation, more frequent freeze–thaw events, and often poorer or shallower soils. Declining temperature may constrain plant growth, enzyme kinetics, and biosynthetic capacity, potentially reducing overall phytochemical diversity or favouring a narrower set of cold-associated metabolites. This expectation is consistent with the growth-differentiation balance hypothesis, which links secondary metabolism to the balance between growth limitation and resource allocation.[29,42] However, as highlighted in Table 1, temperature effects are unlikely to be uniform across compound classes: low temperatures may reduce broad metabolite diversity while favouring specific metabolites involved in cold tolerance, cryoprotection, osmotic adjustment, or stress signalling.

Other high-elevation stressors may instead increase diversity within distinct functional groups (Table 1). Ultraviolet-B radiation increases with elevation and strongly promotes photoprotective compounds, especially flavonoids, hydroxycinnamic acids, and anthocyanins.[6,30] Oxidative stress generated by high irradiance, freeze-thaw cycles, and reactive oxygen species may similarly favour antioxidant phenolics, carotenoids, and related metabolites.[32] Soil nutrient limitation may also promote investment in carbon-based secondary metabolites, such as terpenoids and tannins, as predicted by the resource availability, carbon-nutrient balance, and growth-differentiation balance hypotheses.[31] Thus, abiotic drivers may increase some components of phytochemical diversity while decreasing others, helping to generate the context-dependent patterns observed across studies.

Biotic drivers are generally expected to weaken with elevation, although patterns vary across regions and systems. Herbivores provide the strongest empirical basis for a biotic-interaction hypothesis. Herbivore richness, abundance, and diet specialisation often decline with elevation, although exceptions occur.[17,18,34] Diverse herbivore assemblages can impose diversifying selection on plant chemistry because consumers differ in host preference, detoxification capacity, and sensitivity to particular compounds. Consequently, low-elevation communities may maintain broader or more heterogeneous chemical arsenals, whereas reduced herbivore richness and specialisation at high elevation may relax selection for chemically diverse defence. The evidence summarised in Table 1 supports this mechanism particularly for herbivore richness, herbivore specialisation, and inducible chemical defence.[16,33]

Inducible chemical defences provide a related mechanism. If high-elevation plants experience lower or less predictable herbivore pressure, selection for inducible defence may weaken, reducing chemical plasticity within individuals and populations. Elevational studies suggest that both direct and indirect chemical defences can become less inducible (*i.e.* compounds are produced and/or released only after herbivore damage) at higher elevation.[35] This is important because many studies measure only constitutive chemistry, potentially underestimating the role of inducible diversity in plant–consumer interactions.

Other biotic drivers are less well tested but may also influence phytochemical diversity. Pathogen pressure may decline at high elevation because cold, dry, and UV-rich conditions limit many fungal and bacterial pathogens, potentially weakening selection for antimicrobial compounds.[36] Pollinators may shape floral volatile bouquets, pigments, and nectar-associated chemistry, so declining pollinator diversity could reduce diversifying selection on floral chemical traits.[43] Plant-plant competition and allelopathy may also structure chemical diversity, but their roles along elevation remain largely theoretical.[40,44]

Finally, plant community composition may be a major driver of community-level phytochemical diversity. Species turnover, phylogenetic structure, and plant richness influence community chemical space because each lineage contributes a distinct biosynthetic history. If plant richness peaks at intermediate elevations or declines toward summits, community-level phytochemical diversity may follow similar patterns, independently of within-species responses. This scale dependence is critical: within species, phytochemical diversity may reflect plasticity, local adaptation, or

Table 1. **Expected abiotic and biotic drivers of phytochemical diversity along elevational gradients**. Factor gradients show the expected direction of change with increasing elevation. Phytochemical diversity patterns indicate the expected or observed response of phytochemical diversity to each driver. ↑, increase; ↓, decrease; ∩, hump-shaped; ~, variable or system dependent. Evidence strength is classified as strong when replicated empirical evidence exists across multiple systems, moderate when evidence is consistent but limited to few systems or compound classes, limited when evidence is sparse, indirect, or restricted to single systems, and theoretical when the mechanism is inferred but not yet tested along elevation gradients.

Factor	Level	Factor gradient	Phytochemical diversity	Evidence	Mechanism / notes	Key Refs.
ABIOTIC DRIVERS						
Temperature	Species & Community	↓	↓	Moderate	Thermal constraint on biosynthetic enzymes reduces overall metabolite diversity; low temperatures limit the growth-differentiation balance (GDBH); narrow class of cold-stress metabolites (cryoprotectants, compatible solutes) may increase.	15, 28, 29
UV-B radiation	Species	↑	↑	Strong	Drives production of UV-screening phenolics (flavonoids, hydroxycinnamic acids, anthocyanins); monotonic abiotic signal counteracting biotic-driven declines in other compound classes; effect confined primarily to this functional group.	6, 30
Soil nutrient availability	Species & Community	↓	↑	Moderate	Resource-poor, shallow soils promote greater investment in carbon-based secondary metabolites (terpenoids, tannins) as predicted by RAH, CNB, and GDBH; effect more pronounced on metabolite quantity than chemical diversity *per se*.	31
Oxidative stress (ROS: UV, freeze-thaw, high irradiance)	Species	↑	↑	Moderate	Multiple ROS stressors intensify with elevation; promotes synthesis of antioxidant phenolics, carotenoids, and ascorbate derivatives; increases diversity within this functional compound group.	32
BIOTIC DRIVERS						
Antagonistic-wise						
Herbivore species richness	Community	↓	↓	Strong	Diverse herbivore assemblages impose diversifying selection on plant chemical phenotypes; declining richness above the treeline reduces the breadth of chemical arsenals maintained by selection; foundational to the biotic interaction hypothesis.	17, 33 18
Herbivore diet specialisation	Community	↓	↓	Strong	Specialist herbivores impose specific, diversifying selection on plant chemistry; progressive replacement by generalists at high elevation reduces specificity of chemical selection pressure and is linked to lower plant resistance.	16, 33, 34
Inducibility of chemical defences	Species	↓	↓	Strong	High-elevation plants show reduced capacity for inducible defence; lower inducibility decreases within-individual and within-population chemical plasticity; both direct and indirect defences simultaneously less inducible at altitude.	35
Pathogen pressure	Species & Community	↓	↓	Limited	Fewer fungal and bacterial pathogens at high elevation reduce selection on antimicrobial compound diversity; cold, dry, UV-rich conditions limit pathogen persistence at altitude; direct empirical evidence is absent.	36
Pollinator-wise						
Pollinator diversity	Community	↓	↓	Limited	Diverse pollinator assemblages drive diversifying selection on floral volatile bouquets and pigment profiles; as pollinator richness declines with altitude, this selective force weakens; effect on non-floral secondary metabolites is indirect and unclear.	34, 37, 38
Plant-wise						
Plant species richness	Community	∩ or ↓	∩ or ↓	Moderate	Greater plant species richness expands community-level chemical space because each species contributes a distinct biosynthetic history; phytochemical diversity expected to covary with plant richness; pattern is strongly scale-dependent.	14, 38, 39
Plant–plant competition (allelopathy)	Community	↓	↓	Theoretical	Less competitive community structure at high elevation reduces selection for allelochemical diversity; novel weapons hypothesis predicts chemical novelty as a product of competitive arms races; entirely untested along elevation gradients.	40, 41
Abbreviations: RAH = Resource Availability Hypothesis | CNB = Carbon-Nutrient Balance hypothesis | GDBH = Growth-Differentiation Balance Hypothesis | ROS = reactive oxygen species | ODT = Optimal Defence Theory						

environmental filtering, whereas at the community level it may primarily reflect species replacement and phylogenetic turnover.

Overall, Table 1 highlights opposing ecological forces along elevational gradients, as also illustrated in Fig. 1. Abiotic stressors such as UV-B radiation, oxidative stress, and nutrient limitation may favour stress-associated chemical diversity at high elevation, whereas declining temperature may constrain overall biosynthetic diversity. In contrast, reductions in herbivore richness, herbivore specialisation, pathogen pressure, pollinator diversity, and competitive interactions may reduce biotically mediated selection for diverse chemical phenotypes. The net pattern of phytochemical diversity should therefore depend on the relative strength of these drivers, the compound classes and tissues considered, and the biological scale of analysis. This framework helps explain why empirical studies reveal mixed, nonlinear, and context-dependent patterns rather than a single dominant elevational trajectory.

4. Hypotheses Related to Phytochemical Diversity Along Elevation

The patterns and processes discussed above point to a central challenge: phytochemical diversity along elevation is unlikely to follow a single universal trajectory. Instead, different ecological theories predict contrasting outcomes depending on whether chemical diversity is shaped mainly by biotic interactions, abiotic stress, plant community turnover, or spatial-scale effects. In this section, we outline a set of non-mutually exclusive hypotheses that can help organise current evidence and guide future tests of phytochemical diversity along elevational gradients.

4.1 The Biotic Interaction Hypothesis

A long-standing expectation in ecology is that biotic interactions should be stronger in warmer, less seasonal environments, leading to more intense consumer pressure and stronger selection on plant defence at lower elevations. Applied to phytochemical diversity, this hypothesis predicts that low-elevation plants and plant communities should maintain broader, more diverse, or more specialised chemical arsenals because they interact with richer and more specialised communities of herbivores and pathogens. Conversely, if herbivore and pathogen pressure decline toward higher elevations, selection for diverse defensive chemistry should weaken, leading to reduced phytochemical diversity or greater chemical similarity among high-elevation plants.[33]

This hypothesis is supported indirectly by broad patterns in insect diversity and herbivory along elevation. Insect richness often declines with increasing altitude, although the strength of this pattern varies among regions, taxa, and sampling designs.[17,34] Moreira *et al*.[18] provide the most comprehensive synthesis of elevational gradients in plant defences and insect herbivory. They show that the classic expectation of stronger herbivore pressure at low elevation is broadly influential but not universally supported. In particular, they argue that plant-herbivore interactions along elevation are embedded in complex ecological contexts involving climate, seasonality, plant identity, herbivore community composition, and local environmental conditions. Thus, while the biotic interaction hypothesis predicts declining phytochemical diversity with elevation, this prediction should be treated as a general expectation rather than a universal rule.

4.2 *The Altitudinal Niche-Breadth Hypothesis*

A more specific version of the biotic interaction hypothesis is provided by the altitudinal niche-breadth hypothesis. This hypothesis proposes that specialisation of plant-feeding insects decreases with elevation because harsher, colder, and more seasonal environments favour broader host use and lower ecological specialisation.[16] If specialist insects impose more precise and diversifying selection on plant chemistry than generalists, then a decline in insect specialisation should reduce selection for complex or highly differentiated chemical phenotypes at higher elevations.

Empirical evidence from plant-insect systems supports this logic. Pellissier *et al.*[33] showed that herbivore specialisation and plant resistance can covary along elevation, with lower levels of herbivore specialisation and reduced plant resistance at higher elevations. From a phytochemical perspective, this implies that low-elevation plants may require more diverse or more finely tuned chemical defences to cope with specialised consumers, whereas high-elevation plants may experience weaker selection for chemically differentiated resistance. This hypothesis therefore predicts a decrease in defensive phytochemical diversity with elevation, especially for compound classes involved in herbivore deterrence, toxicity, digestibility reduction, or induced defence. Analogous reasoning extends beyond herbivory to plant-pollinator interactions. Recent work by Rebollo *et al*.[45] in alpine grassland communities suggested that nectar metabolite profiles in high-elevation flowers converge with more similar nectar metabolomics to attract generalised pollinators (dominated by flies) compared to these in low-elevation flowers (dominated by bees).

4.3 *The Phytochemical Convergence Hypothesis*

Recent metabolomic evidence suggests that elevation may not only change the amount or diversity of plant chemistry but also alter the degree of chemical similarity among species. Bakhtiari *et al.*[46] demonstrated ecological convergence of secondary phytochemicals along elevational gradients, with plants becoming more chemically similar at high elevation, independently of phylogenetic relatedness. This result provides a direct bridge between the herbivore-diversity literature and the study of phytochemical diversity. If high-elevation environments impose weaker or less diverse biotic selection, or stronger abiotic filtering, chemically distinct plant lineages may converge toward a narrower set of metabolite profiles suited to similar ecological conditions.[23]

The phytochemical convergence hypothesis predicts that community-level chemical beta diversity should decline with elevation, even when plant species turnover remains high. In other words, high-elevation communities may contain taxonomically distinct species that nevertheless occupy more similar regions of chemical space. This hypothesis differs from a simple 'diversity decreases with elevation' prediction because it focuses on chemical similarity among species rather than only within-species richness or total metabolite number. It also generates testable predictions: if convergence is driven by reduced biotic pressure, it should be associated with declining herbivore richness, specialisation, or inducibility of defences; if convergence is driven by abiotic filtering, it should be associated with shared stress-related metabolite profiles, such as increased photoprotective or antioxidant compounds.

4.4 *The Abiotic Stress Hypothesis*

While biotic-interaction hypotheses often predict lower phytochemical diversity at high elevation, abiotic-stress hypotheses can predict the opposite for some compound classes. High-elevation plants commonly experience stronger ultraviolet radiation, higher irradiance, freeze–thaw cycles, shorter growing seasons, and nutrient limitation.[47] These conditions may favour increased investment in metabolites involved in photoprotection, antioxidant defence, cold tolerance, and stress signalling. Under this hypothesis, phytochemical diversity should increase with elevation when the measured compounds are functionally linked to abiotic stress tolerance.

This prediction is particularly plausible for phenolics, flavonoids, anthocyanins, carotenoids, and related antioxidant or UV-screening metabolites. However, the abiotic stress hypothesis is unlikely to apply equally to all components of plant chemistry. Rather than increasing total phytochemical diversity, high-ele-

vation stress may increase diversity within particular functional groups while reducing or leaving unchanged other chemical classes. This could help explain why empirical studies report mixed or context-dependent patterns: the observed direction of the relationship depends strongly on which tissues, compound classes, and diversity metrics are measured.

4.5 *The Aboveground–Belowground Interaction Hypothesis*

Phytochemical diversity may also be shaped by interactions that link aboveground and belowground communities. Along elevation, plants experience simultaneous changes in foliar herbivores, root herbivores, soil microbes, mycorrhizal partners, pathogens, and nutrient availability. These aboveground and belowground components are not independent: root-associated organisms can alter foliar chemistry, aboveground herbivory can influence root exudates and belowground defence, and soil microbial communities can affect nutrient acquisition and secondary metabolism.

Kergunteuil *et al.*[20] emphasised that aboveground–belowground interactions along elevation are embedded in eco-evolutionary dynamics. Applied to phytochemical diversity, this perspective predicts that elevational patterns in plant chemistry may depend on the combined structure of aboveground and belowground interaction networks. For example, a decline in foliar herbivory with elevation may be offset by changes in root herbivores, soil pathogens, or microbial symbionts. Similarly, nutrient limitation may alter the costs and benefits of chemical defence. This hypothesis predicts context-dependent phytochemical responses and highlights the need to measure belowground drivers alongside aboveground interactions.

4.6 *The Community Composition and Spatial-Scale Hypothesis*

Not all elevational patterns in phytochemical diversity necessarily reflect direct selection on plant chemistry. At the community level, chemical diversity can also arise from plant species richness, species turnover, and phylogenetic structure.[48] Accordingly, because different plant lineages carry distinct biosynthetic pathways for secondary metabolites production, communities with more species or more phylogenetically diverse species may occupy a broader chemical trait space.

Spatial scale is therefore critical. Nogués-Bravo *et al.*[39] and related mountain biodiversity studies have shown that apparent elevational diversity patterns can be strongly influenced by area effects, sampling extent, habitat heterogeneity, and the geometry of mountain landscapes. These issues also apply to phytochemical diversity. A decline in chemical diversity at high elevation could reflect reduced plant richness or smaller available area rather than direct effects of climate or herbivory. Conversely, a mid-elevation peak in phytochemical diversity could emerge from maximum species turnover or habitat heterogeneity at intermediate elevations. This hypothesis predicts that chemical diversity patterns should be analysed alongside taxonomic and phylogenetic diversity, and that within-species and community-level chemical responses should be separated whenever possible.

Together, these hypotheses show that phytochemical diversity along elevation may decline, increase, converge, or vary nonlinearly depending on the dominant ecological drivers and scale of analysis. Biotic-interaction and altitudinal niche-breadth hypotheses generally predict lower defensive chemical diversity or greater phytochemical convergence at high elevation. Abiotic-stress hypotheses predict increased diversity within stress-related compound classes. Aboveground–belowground and community-composition hypotheses predict context-dependent outcomes driven by interaction networks, species turnover, and spatial scale. A major challenge for future research will be to test these hypotheses simultaneously by combining metabolomics, herbivore and pathogen surveys, plant community data, belowground measurements, and explicit spatial designs across replicated elevational gradients.

5. Conclusion and Future Perspectives

Phytochemical diversity is emerging as an important, but still underexplored dimension of biodiversity along elevational gradients. Current evidence suggests that plant chemical diversity does not follow a single dominant trajectory with elevation. Instead, patterns appear mixed, nonlinear, and strongly context dependent, reflecting differences among plant lineages, tissues, compound classes, analytical methods, diversity metrics, and the relative strength of abiotic and biotic drivers. Although biotic-interaction hypotheses often predict declining defensive chemical diversity with elevation, abiotic-stress hypotheses predict increases in stress-related metabolites at high elevation, and community-level patterns may further reflect plant species richness, phylogenetic turnover, and spatial-scale effects. As in studies of elevational biodiversity more broadly, apparent patterns may also be sensitive to sampling extent, lowland habitat degradation, and geometric constraints imposed by mountain topography.[39,49] Thus, the field is not yet mature enough to support a universal conclusion about the relationship between phytochemical diversity and elevation.

Future progress will require moving from descriptive correlations toward more standardised, comparative, and causal approaches. First, chemical analyses should be made more comparable across studies through clearer reporting of sampling design, tissues analysed, metabolomic pipelines, compound annotation levels, and diversity metrics. Shared databases and harmonised workflows would greatly improve our ability to compare phytochemical diversity across gradients, regions, and plant clades. Second, future studies should explicitly separate within-species plasticity and local adaptation from community-level species turnover, ideally using phylogenetically informed analyses, reciprocal transplants, common gardens, experimental evolution, and manipulative experiments. Third, causal frameworks[50,51] such as structural equation modelling, path analysis, and experiments that manipulate herbivory, nutrients, temperature, or radiation will be needed to disentangle the relative contributions of abiotic stress, biotic interactions, and eco-evolutionary history.

Finally, understanding phytochemical diversity along elevation is increasingly urgent under global change. Mountain ecosystems are being reshaped by climate warming, biological invasions, land-use change, agricultural expansion, and habitat fragmentation, all of which may alter the abiotic and biotic niches that maintain plant chemical diversity. Yet current evidence remains geographically biased, with tropical and subtropical mountains still poorly represented relative to temperate systems. More community-level studies are also needed, because phytochemical diversity can influence plant–insect communication, trophic interactions, and ecological network structure beyond individual species.[13] More than two centuries after Humboldt used mountain gradients to reveal the relationship between climate and plant distributions,[52] elevational gradients remain natural laboratories for understanding how environment shapes biodiversity. The next challenge is to extend this tradition to the chemical dimension of biodiversity, identifying which environmental factors generate, maintain, or erode phytochemical diversity, and how rapidly this valuable resource may change in an increasingly unstable world.

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