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A phylogenetic approach to bridge the food–medicine continuum at the continental scale

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The relationship between food and medicinal plants is longstanding and complex, with many species serving both roles. This study explores the food–medicine continuum at a continental scale, analysing phylogenetic patterns of plants used for food, medicine and condiments across three ecologically and culturally distinct Eurasian regions: Iberian Peninsula, Caucasus and West Himalaya. We applied an adapted phylogenetic hot node analysis to identify plant lineages significantly rich in useful species across each use category and region, thereby revealing cross-cultural patterns of plant use and enlarging the potential of the method beyond bioprospecting. We found overlap between lineages used for food and medicine, and between condiments and medicine, both across and within regions. Condiments, often classified as food, had a higher overlap with medicinal plants, reinforcing the idea that they play a critical role in bridging nutrition and health. Our results indicate that the food–medicine continuum transcends cultural boundaries and is grounded in shared history. Our study highlights the value of integrating phylogenetic and ethnobotanical approaches to understand multifunctional plant lineages, an approach that can support food security and healthcare amid global environmental and health challenges.

1. Introduction

‘Let food be your medicine; let medicine be your food’. Hippocrates [*ca* 460–370 BC]

Throughout history, humans have relied on a wide variety of plant species for food and medicine. Globally, about 6500 plant species are recognized as food resources, and 24 000 are documented for their medicinal properties [1]. The selection of species is not random, as suggested by the prevalence of specific morphological or organoleptic traits in species used as food or medicine [2]. Plants rich in vitamins or carbohydrates are commonly consumed as food, while those abundant in alkaloids and phenolic compounds are more often

selected as medicine [3–5]. The overlap between medicinal and food uses is often so pronounced that distinguishing between the two can be challenging, a phenomenon known as the ‘food–medicine continuum’ [6,7]. Indeed, many cultures recognize a fluid boundary between food and medicine, where certain plants are consumed for their nutritional value but also for preventive and therapeutic benefits [8,9]. Some authors even argue that selecting resources contributing to both nutrition and disease prevention would have conferred evolutionary advantages to human populations [8]. In contrast, modern diets have become alarmingly limited. Today, just three crops—rice, maize and wheat—account for 60% of the world’s plant-based caloric intake [10], and the consumption of many plants with medicinal and nutritional properties has been abandoned [11].

This growing simplification in contemporary food systems underscores the need for a deeper understanding of the food–medicine continuum. Previous research on this continuum has faced two key limitations. First, nutritional and therapeutic properties have traditionally been studied independently [12]. This separation, common in ethnobotanical and pharmacological work, is not surprising due to different cultural perceptions of these uses; however, it has inevitably led to challenges in classifications, notably for condiments. Added to dishes to enhance flavour, colour and texture, condiments also modify the palatability and digestibility of foods and contribute to their preservation, arguably due to high concentrations of allelochemicals [13]. Although condiments can offer significant benefits to human health and well-being [8], most studies classify them as a type of food, thus hiding their health benefits.

The second limitation of previous studies is their narrower geographical focus, often limited to specific locations or regions, without examining broader cross-cultural patterns [14]. Cross-cultural comparisons of the food–medicine continuum are challenging, since people in different regions interact with distinct floristic environments [15]. This can give the false impression that shared patterns of use do not exist, when, in fact, the underlying floristic environment may simply differ. By leveraging explicit phylogenetic representations of species across regions, it is possible to identify evolutionary lineages consistently used across regions with distinct floristic environments, uncovering cross-cultural patterns in biodiversity use [16–18].

Here, we employed a phylogenetic hot node analysis to identify plant evolutionary lineages significantly contributing to human well-being through the food–medicine continuum at a continental scale. Hot node analysis has its roots in ecophylogenetics, a branch of ecology that emerged about two decades ago. Clades contributing a disproportionate number of species to a plant community were initially identified as hot nodes using the Phylocom software [19]. More recently, it has gained popularity in ethnobotany and has been used to identify highly used plant clades, i.e. groups of related species that contain more useful species than expected by chance, thus pointing to evolutionary patterns in plant use [17,20,21]. While most applications of hot node analysis have focused on identifying promising taxa for drug discovery or resource prospecting (e.g. [22]), in this study, we apply this methodology to explore broader biocultural and ecological patterns in plant use. Specifically, we aim to understand how different cultures interact with food and medicinal plant diversity, and whether these interactions reveal shared evolutionary patterns across distinct floristic and cultural landscapes.

We applied hot node analyses to ethnobotanical datasets from three geographically distinct and environmentally diverse Eurasian regions where ethnobotanical knowledge is relatively well documented: Iberian Peninsula, Caucasus and West Himalaya (figure 1). Despite having distinct floras, these regions share common plant lineages, allowing local cultures to independently prospect similar phylogenetic clades. Additionally, we analyse condiments as a separate category to better understand their role in bridging nutrition and health. Although often classified as food, condiments are frequently valued for their medicinal properties, and our analysis explores whether their evolutionary patterns align more closely with food or medicine. Specifically, our analysis aimed to: (i) assess whether lineages that significantly provide medicinal benefits in a given region also serve as food in the same region (regional continuum), (ii) examine whether lineages associated with medicinal or food uses in one region are similarly used in other regions (continental cross-cultural continuum) and (iii) explore the role of condiments within the continuum, both within and across regions (regional and cross-cultural continuum). To place these patterns in a plant evolutionary context, we also calculated the phylogenetic signal for each use category, assessing the degree to which plant uses are conserved across lineages.

2. Material and methods

(a) Study area

Our study regions were defined based on the botanical countries established by the International Working Group on Taxonomic Databases for Plant Sciences (TDWG) [23]. The ‘Iberian Peninsula’ comprises mainland Portugal, mainland Spain and the Balearic Islands. The ‘Caucasus’ area corresponds to Transcaucasia and North Caucasus (spanning part of Russia, Armenia, Georgia and Azerbaijan). Lastly, ‘West Himalaya’ conforms to a region in the northwest of India (figure 1; electronic supplementary material, table S1). These regions were selected to optimize the trade-off among three key factors: geographic distance to minimize cultural knowledge transfer (although some historical exchange might have occurred, such as via the Silk Route), floral proximity to ensure plant lineages are not drastically different and the availability of robust ethnobotanical data. While the three regions differ in topography and climate, they share a Eurasian native flora and belong to the temperate broadleaf and mixed forests biome, with distinctive features—such as the tropical affinities present in the West Himalaya and the Mediterranean influence in the Iberian Peninsula—that are rare in the other areas.

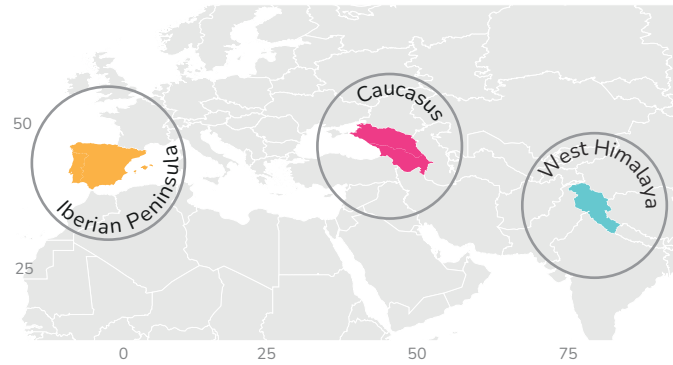


Figure 1. Location of the regions studied on the Eurasian continent.

(b) Data sources

Floristic data for vascular plants from each region were obtained from Plants of the World Online [24]. Native species status was also sourced from POWO [24], which defines plants as native if they have been present in an area since before the Last Glacial Maximum or have naturally colonized the region. Ethnobotanical information was sourced from scientific publications and databases to compile a comprehensive list of food, condiment and medicinal vascular plants from each region (electronic supplementary material, table S1) [25]. Data on the sociocultural groups for which these plants are useful were not consistently available, so unfortunately, we could not consider cultural diversity in our analyses. All species names were harmonized to the World Flora Online taxonomic criteria [26].

In each region, species were classified based on their reported uses into one or more of the following categories: food, condiment, and medicine (see Molina-Venegas *et al.* [27] for an extended description). The category ‘food’ comprises plants consumed by humans (either raw or processed) due to their nutritional value. ‘Food’ includes beverages, such as juices or spirits, that are not intended for medicinal, hallucinogenic or ritual purposes. The category ‘condiments’ comprises plants used for food preservation or to alter the flavour, smell, consistency or appearance of food and beverages. Unlike food plants, condiments are typically consumed in small quantities. Finally, the category ‘medicine’ includes plants used to treat or prevent human diseases or symptoms. Here, ‘useful plants’ are those with one or more uses within the specified categories, regardless of any other uses they may have.

(c) Phylogenetic information

We obtained time-calibrated molecular phylogenies including all native vascular plant species occurring across the three regions ($n = 15\,278$) with the R package V.PhyloMaker [28]. V.PhyloMaker constructs phylogenetic trees from a list of species, leveraging the most extensive species-level mega-phylogeny of vascular plants published (GBOTB.extended; see Jin & Qian [28]). The process involves three stages. First, for each species in the list that is missing in the phylogeny (phylogenetically uncertain taxa, PUTs), the software identifies the largest monophyletic cluster of congeneric species and designates the most recent common ancestor of the species in the cluster as the target crown node for the PUT. Next, the PUTs are incorporated into the phylogeny following one of three possible scenarios. For this work, we selected the second scenario, in which PUTs are attached to a randomly designated node at and below their respective target crown nodes. If the genus is not represented in the phylogeny, the software attaches the PUT to the family-crown node instead. Lastly, the expanded tree is pruned to include only the species in the input list. To account for phylogenetic uncertainty, we repeated this procedure iteratively to generate 1000 different trees [29], which were then pruned to the flora of each region to create 1000 regional trees per region. The creation of a common tree with all species, which is then pruned for each region, is important, as it allows one to maintain the identity of the nodes and thus to be able to compare between regions in the next steps. All analyses were then replicated across the whole set of regional trees.

(d) Hot node analysis

While taxonomic comparisons (e.g. shared genera or families) can provide a preliminary overview of the overlap between use categories, they fail to incorporate evolutionary relatedness among taxa. A phylogenetic approach adds this dimension, uncovering lineage-level patterns that more accurately reflect the evolutionary basis of the food–medicine continuum. Previous research has suggested that species utilized to fulfil specific human needs may be disproportionately concentrated in certain key nodes of the phylogeny [30,31]. While some earlier research studying plant uses from an evolutionary approach has used phylogenetic distance metrics (e.g. [15]), this methodology provides only a general estimate of phylogenetic relatedness and may fail to identify lineages rich in useful species. For example, an ancient clade with several sisters but distantly related useful species will probably not be detected as a cluster due to the long branch lengths [32]. Moreover, distance-based metrics assume gradual trait evolution along branches, which may not reflect the actual distribution of ethnobotanical traits. To overcome these limitations, we opted for the analysis of hot nodes, defined as lineages with significantly more useful species than expected by chance [21,22]. This method is especially suitable for detecting lineage-specific patterns of plant use [33,34]. We identified hot

nodes independently for each region, use category and regional phylogeny, conducting a total of 9000 independent analyses (3 regions \times 3 use categories \times 1000 regional phylogenies). Each analysis returned a non-parametric p -value per node i (excluding the root node) computed as

$$p\text{-value}_i = \text{obs.rank}_i / \text{runs} + 1, \quad (2.1)$$

where 'obs.rank' is the rank of the observed number of useful species descending from node i within a null distribution of null values obtained by shuffling the binary trait 'useful' (1) or 'not useful' (0) across the phylogenetic tips $n = 999$ times (runs). As the p -value approaches 1, the number of useful species descending from the target node increases relative to random expectation. Thus, as previously done by Molina-Venegas *et al.* [21], we have determined as hot nodes those with p -values greater than 0.95 (5% nominal alpha, one-tailed test). The identification as a hot node relies on the relative richness of useful plants of the node, rather than absolute numbers. Therefore, two nodes containing the same number of useful species might not both come as hot, depending on the total number of species for each node. To account for phylogenetic uncertainty, we only kept nodes identified as significantly 'hot' in 950 or more trees (out of the 1000 trees of each region). Here, a node was considered the same across trees only if it included the same set of descendant species, regardless of minor topological differences below the node. Moreover, we only retained hot nodes that included 10 species or more, since previous studies have documented unacceptable rates of statistical errors for smaller lineages [35]. We used the R code provided by Molina-Venegas *et al.* [21], with modifications made to accommodate the computation of p -values [32].

(e) Testing the food–medicine continuum with hot nodes

To assess whether lineages that significantly provide a type of use in a region also serve for a different use within the same region (regional continuum), we calculated the number of overlapping hot nodes between use categories in each region. We then tested whether the degree of overlap was greater than expected by chance by randomizing the hot nodes of each category across all nodes of the corresponding tree 999 times (excluding the root node). For a 5% nominal alpha, a significant overlap is indicated if the observed number of overlapping hot nodes exceeds the number obtained in 95% of the randomizations ($p > 0.95$; equation (2.1)). To evaluate whether lineages provide distinct benefits in different regions (cross-cultural continuum), we calculated the number of overlapping hot nodes across all pairs of categories and regions, using the statistical approach outlined above. In total, we conducted 18 cross-cultural tests, representing all possible pairwise comparisons between the three regions and three types of uses.

The same useful species can contribute to multiple consecutive hot nodes due to the nested structure of phylogenetic trees [36]. As a result, significant overlap—either within or across regions—between hot nodes of two use categories may stem from two distinct patterns: (i) clustering of closely related hot nodes within a single clade (i.e. phylogenetic nesting) or (ii) a more diffuse overlap arising from independent, scattered hot nodes across the phylogeny. Distinguishing between these patterns is crucial to determine whether the observed overlap reflects genuine convergence in ethnobotanical relevance or merely results from phylogenetic proximity. To address this, we performed an additional analysis in which we retained only the most inclusive hot nodes for each use and region, removing all descendant (nested) hot nodes within the same lineage. To avoid excluding a large number of hot nodes solely due to the presence of a few deep (near-root) nodes, we conducted the analysis at two taxonomic levels: family and order. For example, at the order-level analysis, the most inclusive hot node was retained only if it contained species from a single order; nodes spanning multiple orders were excluded. The overlap analysis described above was then repeated using these filtered sets of most inclusive hot nodes—one set at the family level and another at the order level. As calculated for the whole set of hot nodes, for a 5% nominal alpha, a significant overlap of most significant hot nodes is considered when the observed number of overlapping most significant hot nodes exceeds the number obtained in 95% of the randomizations ($p > 0.95$; equation (2.1)).

(f) Phylogenetic signal in plant use categories

We applied the D statistic for binary traits [37] using the `phylo.d` function in the `caper` R package [38] to calculate the phylogenetic signal in each plant use category. While the hot node analysis pinpoints specific clades enriched in useful species, the D statistic captures the evolutionary tendency of plant uses to be shared among related taxa—that is, whether similar uses are concentrated within a few major lineages or independently arise across multiple clades. This complementary approach combines node-level enrichment with a model-based assessment of trait evolution, providing both localized and tree-wide insights into the phylogenetic distribution of plant uses. The D statistic equals 0 when the observed binary trait is evolutionarily conserved, as if it had evolved according to a Brownian motion model, and 1 when trait evolution leads to a random distribution of values across the tips of the phylogeny. Values below 0 and above 1 are also possible, respectively, reflecting a more conserved evolutionary pattern than expected under Brownian motion (values < 0) and greater overdispersion of trait values than expected from pure random evolution (values > 1). Statistical significance was assessed using 1000 permutations of the trait and two p -values, both bounded between 0 and 1: $p\text{-value}_0$ represents the probability that the trait evolved according to Brownian motion or a more conserved model, while $p\text{-value}_1$ reflects the probability that the values of the trait are randomly distributed with respect to the phylogeny or exhibit greater overdispersion than expected from random evolution [37]. Due to computational limitations, this analysis was conducted using 100 randomly selected phylogenies. Nonetheless, we observed minimal phylogenetic uncertainty.

Table 1. Number of overlapping hot nodes, within regions, for each pair of use categories and across all three use categories ($p = 1$ in all comparisons). The percentages indicate the proportion of hot nodes from each region that overlap across that pair of uses or all three uses. Groups of categories are mutually exclusive, and nodes included in the group of three uses (food–condiment–medicine) are different from those considered in the pairs of uses.

	total	Iberian Peninsula	Caucasus	West Himalaya
food–condiment	20	3 (1.2%)	13 (5.2%)	4 (1.4%)
condiment–medicine	55	24 (9.6%)	18 (7.2%)	13 (4.7%)
medicine–food	84	15 (6.0%)	30 (12.0%)	39 (14.0%)
food–condiment–medicine	64	29 (11.6%)	16 (6.4%)	19 (6.8%)

3. Results

The flora of the three regions exhibited similar native species richness (6578, 6092 and 5030 species for Iberian Peninsula, Caucasus and West Himalaya, respectively), totalling 15 278 different species. Of this pool, 2970 species were found in at least one of the three use categories across one or more regions (electronic supplementary material, dataset S1, table S2). The largest category of used species was medicine (2544 species; 86% of all useful species), then food (1236; 42%) and condiments (484; 16%). Many species had multiple uses, with 788 species classified in two categories and 253 in three. Notably, many species documented as condiments ($n = 484$) were also documented as food (283 species) and even more as medicine (422 species).

We identified 777 hot nodes across the three regions and use categories, of which medicinal plants accounted for the highest number ($n = 335$), followed by food ($n = 280$) and condiments ($n = 162$) (electronic supplementary material, figure S1, table S3). Although the proportion of hot nodes for food and medicine was lower than the proportion of useful species in these categories (36 versus 42% for food and 43 versus 86% for medicine), condiments showed the opposite trend: hot nodes were overrepresented relative to the number of species used as condiments (21 versus 16%). To estimate the potential effect of nesting hot nodes, we also identified the most inclusive hot nodes in all regions and use categories (i.e. those containing species from a single family or order, without considering remaining descendant hot nodes; see §2). The most inclusive hot nodes accounted for about 10 and 24% of the hot nodes at the family level and about 13 and 23% at the order level in all regions and use categories (electronic supplementary material, table S4).

Hot nodes from different use categories showed significant overlap within each region analysed ($p = 1$ in all comparisons, i.e. the observed overlap was greater than in 100% of the null distributions; a higher p -value means more useful species descend from the target node relative to random expectation and is significant when $p > 0.95$; see §2). In total, we identified 223 overlapping hot nodes within regions, 29% of which overlapped across the three use categories (table 1; electronic supplementary material, figure S2). About half of the food hot nodes overlapped with medicinal ones and vice versa. In contrast, condiment hot nodes showed a stronger overlap with medicinal (73%) than with food hot nodes (52%). Only 14% of the hot nodes were exclusive to the condiment category. These patterns of hot node overlap were largely consistent across the three regions studied. Most inclusive hot nodes from different use categories also significantly overlapped within regions, both at the family and order level ($p = 1$ in all comparisons) (electronic supplementary material, table S5).

Hot nodes from different use categories also showed significant overlap between regions ($p = 1$ in all comparisons). Food and medicine hot nodes overlapped in a similar and balanced number, with 23 to 37% of the hot nodes in each use category and region overlapping with those from the other category in another region (table 2; electronic supplementary material, figure S3). Consistently, condiment hot nodes most frequently overlapped with medicinal hot nodes in other regions, with overlap ranging from 33 to 75%. The overlap between condiment and food hot nodes across regions was generally lower, ranging from 12 to 55%. Most inclusive hot nodes from different use categories also showed significant overlap across regions (minimum p -value across comparisons = 0.968), with only one comparison failing to reach significance at both family and order levels (electronic supplementary material, table S6).

We identified numerous overlapping hot nodes across one to six cross-regional comparisons (figure 2). The Polygonaceae clade—and several gymnosperm nodes (one uniting Cupressales and Pinales, another Ephedrales)—consistently yielded species with both food and medicinal uses. Likewise, several angiosperm lineages, including Rosales, Saxifragales, Cucurbitales and especially Fagales, recurrently provided food and medicinal uses. Similarly, the same gymnosperm nodes, along with several nodes within Rosales and Sapindales, emerged as dual providers of food and condiments across multiple cross-regional comparisons. Lastly, within Lamiales, several clades emerged—including a key node within the Lamiaceae family—that consistently served as sources of both medicinal and condiment plants. Some of these overlapping hot nodes are nested within other nodes, e.g. several nodes within the order Lamiales. However, we also identified overlap between most inclusive hot nodes at both the family and order level, scattered throughout the phylogeny (see electronic supplementary material, figure S4).

The phylogenetic signal for all plant use categories was significantly higher than expected under pure random evolution (p -value1 < 0.001 for all trees), the hypothesis of Brownian motion evolution was consistently rejected (p -value0 < 0.001 for all trees and plant use categories) and the mean D statistic exceeded 0.75 for each category indicating a weak phylogenetic signal. Specifically, the mean D values were food = 0.7737 [95% CI: 0.7725, 0.7750]; medicine = 0.8138 [95% CI: 0.8127, 0.8148] and condiments = 0.8528 [95% CI: 0.8505, 0.8551].

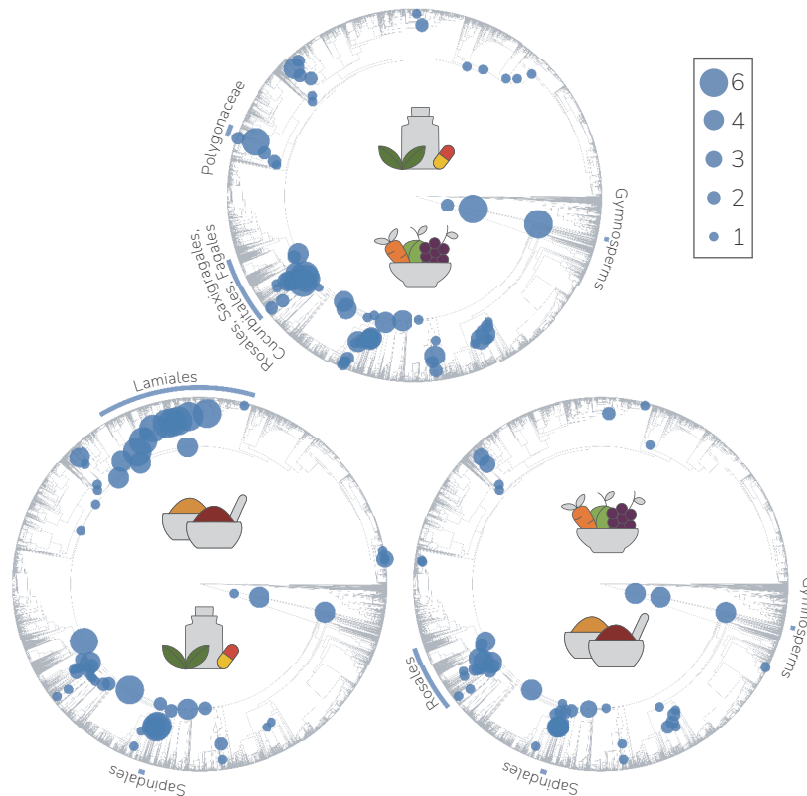


Figure 2. Overlapping hot nodes (blue circles) for each pair of use categories across regional pairwise comparisons. The three graphs are based on the same phylogeny, which includes the native flora of the three regions (15 278 species). Each use category pair can have up to six possible comparisons. For example, for the food–medicine pair, the comparisons are (i) food–Iberia versus medicine–Caucasus, (ii) food–Caucasus versus medicine–Iberia, (iii) food–Caucasus versus medicine–West Himalaya, (iv) food–West Himalaya versus medicine–Caucasus, (v) food–West Himalaya versus medicine–Iberia and (vi) food–Iberia versus medicine–West Himalaya. Circles' size represents the extent of overlap across the six regional pairwise comparisons for each pair of use categories, but there were no cases of five regional comparisons (all $p = 1$). Clades with a high overlap across regions are highlighted with a blue line and their name around the tree.

Table 2. Number of overlapping hot nodes between different use categories and across each pair of regions (in bold), along with the proportion of these overlapping nodes relative to the maximum possible overlap in each case ($p = 1$ in all comparisons).

		Iberian Peninsula		
		food	cond	med
Caucasus	food		24 (36%)	31 (33%)
	cond	10 (18%)		25 (45%)
	med	26 (33%)	37 (56%)	
		Caucasus		
		food	cond	med
West Himalaya	food		21 (38%)	29 (29%)
	cond	17 (43%)		21 (53%)
	med	28 (30%)	27 (48%)	
		West Himalaya		
		food	cond	med
Iberian Peninsula	food		22 (55%)	29 (37%)
	cond	8 (12%)		22 (33%)
	med	24 (23%)	30 (75%)	

4. Discussion

Our study addresses previous challenges in understanding the food–medicine continuum by applying a phylogenetic framework that enables cross-regional comparisons beyond localized cultural or geographic boundaries. While earlier research typically focused on specific regions or communities [39,40], such efforts were constrained by taxonomic differences across

distinct floristic environments, limiting broader generalizations [15]. By identifying shared evolutionary lineages that provide both food and medicine, our analysis demonstrates that the food–medicine continuum operates, at least, at a continental scale. This reveals that cross-cultural plant selection for nutritional and therapeutic purposes has strong evolutionary roots. These findings point to a global evolutionary basis for the multifunctional use of plants, reinforcing the interconnectedness between biological diversity and culture through traditional knowledge (figure 2).

Food and medicinal plant species are largely concentrated within specific, overlapping lineages, such as Rosales and Fagales (figure 2). This pattern holds consistently both within and across regions, suggesting that the food–medicine continuum follows a clear evolutionary scheme in Eurasia, possibly reflecting a deep biochemical and evolutionary link between nutritional and therapeutic properties. Across these lineages, the dual role of food and medicine is evident in plants originally rooted in Eurasian culinary traditions, now gaining global recognition through the concepts of ‘nutraceuticals’ and ‘functional foods’, terms grounded in their chemical composition [4,40,41]. For example, fruits of *Quercus* species (Fagales) are rich in phenolic compounds, triterpenoids and flavonoids that imbue them with anti-inflammatory and antioxidant properties [42]; many *Rumex* species (Polygonaceae), used as leafy vegetables, have high concentrations of anthraquinones and flavonoids, used to treat and prevent inflammatory diseases [43]; and the edible hips of *Rosa* species (Rosales) are packed with vitamins A and C that boost the immune system [44]. Expanding the use of nutraceutical wild plant species in diets, many offering higher nutritional value than their domesticated counterparts [45], has been proposed as a promising strategy for strengthening food system resilience and improving global health [3,46]. There are already several initiatives exploring this potential by investigating wild edible plants as novel crops and innovative foods through agronomic field trials, culinary research, sensory evaluations and market acceptance studies, all aimed at assessing their sustainability and viability for diversifying agroecosystems (e.g. [47,48]). By leveraging phylogenetic and cross-cultural perspectives, we contribute to the understanding of the interconnected food–medicine continuum and identify plant lineages with both nutritional and therapeutic benefits that remain underutilized [49]. Critically, unlocking the value of multifunctional lineages could be instrumental in tackling challenges of an increasingly uncertain climate [50], a priority recognized in the 2030 Agenda for Sustainable Development (SDG 2).

Beyond identifying lineages rich in useful plants, our analysis highlights the pivotal role of condiments in bridging the food–medicine continuum. Condiments often serve as flavour enhancers and health-promoting agents [8,51]. Due to the nested structure of the phylogenetic tree, some hot nodes associated especially with condiment use, such as those within Lamiales, appear aggregated in specific clades (electronic supplementary material, figure S4). These examples could misleadingly suggest that overlapping hot nodes cluster due to the phylogenetic proximity of the useful species. However, analysis of overlap between most inclusive hot nodes at the family and order level reveals that they are widely distributed across the phylogeny for all pairs of use categories. This indicates that the observed overlap is not limited to a few lineages but is instead driven by the multiple use of a broad range of phylogenetically distinct clades (electronic supplementary material, table S6, figure S4). Lineages rich in condiment species frequently also contain food or medicinal plants, while lineages exclusively dominated by condiment uses are comparatively rare. Given that condiments are consumed as part of dishes and beverages, one might expect stronger overlap between condiment- and food-related lineages. However, condiment plants are primarily found within lineages abundant in medicinal plants (table 1), rather than food plants. This evolutionary link between condiments and medicinal uses suggests that condiments may play a more central role in traditional health systems than previously recognized. This reinforces the idea that condiments effectively ‘bring the pharmacy to the plate’, as their biochemical properties connect therapeutic and culinary functions along shared evolutionary trajectories. Rather than serving as a midpoint in a linear food–medicine continuum, condiments appear to close the loop, embodying a dynamic interface where nutrition, flavour, and health converge.

Previous works have typically grouped condiment and food plants together based on their mode of consumption, namely their role in cuisine (e.g. [52]). However, this classification may be obscuring important patterns in plant properties and may underestimate the cultural and therapeutic significance of condiments. As an analogy, it would be akin to grouping plants that provide wood for crafting arrows and those to make poison under a category labelled ‘hunting’: while the use is shared, functions and chemical properties fundamentally differ. Categorizing plants by molecular functionality rather than by use better reflects the true biochemical characteristics and evolutionary relationships that determine the services they provide [53]. This framework offers greater universality and applicability across cultures, fostering interdisciplinary research and forging valuable connections between ethnobotany and pharmacology.

Unlike food plants, condiments are not consumed in large amounts to fill caloric needs. Rather, condiments are consumed in small quantities, and some can even be toxic when consumed in large amounts [54]. This characteristic further aligns condiments with medicinal plants, as both can have harmful effects in high doses. In fact, in cultures such as ancient Greece, the words ‘poison’ and ‘medicine’ were often used interchangeably [55]. In some Amazonian tribes, medicine is seen as something that can ‘kill the evil spirit’ causing the illness [56], just as a poison could kill a person. This highlights the close cultural relationship between medicinal, condiment and toxic properties in plants, reflecting their intertwined roles in traditional healing systems.

Although the phylogenetic patterns examined were highly consistent, some regional variations emerged. For instance, compared to the other two regions, the Iberian Peninsula exhibits a higher proportion of hot nodes across all three uses (table 1). These differences may be shaped by the region’s distinct cultural context and more thoroughly prospected ethnobotanical knowledge (see electronic supplementary material, table S4). The Lamiaceae family, for example, is a key group for both medicinal and condiment uses (figure 2), boasting high diversity in the Mediterranean [57,58] and a long history of medicinal application [59,60]. Regional variations underscore the caution needed in drawing generalizations and the need to expand research to other regions, such as Latin America, where condiments appear to play a lesser role. Broadening the geographical scope of the analysis presented here will be essential to assess the universality of the food–medicine continuum.

Finally, although the phylogenetic signal detected for the three use categories was statistically significant, its low value suggests only a slight tendency towards evolutionary conservatism of the traits that make these plants useful. In other words, the traits underlying the usefulness of wild plants as food, condiments or medicine appear to be somewhat more conserved than expected by chance, yet distributed across multiple small clusters throughout the phylogeny rather than concentrated in a few major clades. This pattern points to a mosaic of independent but recurrent trait emergence across the evolutionary history of the Eurasian flora, reflecting a broad and historically widespread spectrum of plant selection by human cultures. Such selection could stem from a combination of traditional knowledge and ecological availability, with societies drawing on accessible and familiar plants that offer nutritional or therapeutic benefits. This extensive prospecting might reflect a profound, cross-generational understanding of plant diversity, with societies purposefully identifying and potentially preserving plants with valuable properties from a wide range of lineages. However, the low phylogenetic signal may also point to incomplete utilization of multifunctional lineages due to lack of knowledge [61], or intentional non-utilization driven by their cultural significance [62]. This cultural differentiation in the use of wild plants is well illustrated by the contrast between ‘herbophilous’ communities, which actively embrace and eat green vegetables, and communities that associate them with famine foods and barely consume them [63]. Clades may exhibit gaps in utilization because not all cultures across their distributional range have historically used them. Additionally, this type of analysis cannot incorporate frequency of use, which would allow highly consumed plants to carry more weight, as such data are rarely available in ethnobotanical sources. Obtaining reliable information on use frequency and integrating it into future analyses could help refine the interpretation of phylogenetic patterns and better capture the cultural and functional relevance of plant taxa. Moreover, the dynamic nature of traditional knowledge, where species once consumed are no longer used [63], combined with limitations in territorial prospecting [64], can lead to false negatives, further diluting the phylogenetic signal in plant uses. In sum, the low signal may reflect not only the evolutionary complexity of plant traits but also the intricate, context-dependent ways in which human societies have engaged with plant diversity.

5. Concluding remarks

Our study underscores the wide-reaching, cross-regional nature of the food–medicine continuum, demonstrating that dual roles of plants as food and medicine are deeply embedded within shared evolutionary lineages across Eurasian flora. This overlap highlights the sophisticated knowledge that societies have developed to identify and use plants with nutritional and therapeutic value.

At the same time, the weak phylogenetic signal in plant uses points to a complex interplay of factors that shapes plant selection and usage (ecological availability, incomplete knowledge, cultural variation, and the dynamic nature of traditional knowledge). To fully harness the potential of multifunctional plant lineages, further research is needed, particularly in underexplored regions and for phytochemical traits, to fill persistent knowledge gaps and inform strategies for sustainable food and healthcare systems.

Condiments have emerged as key elements within the food–medicine continuum, bridging culinary and medicinal uses. Their strong association with medicinal plants—more so than with food plants—reveals a pattern that, until now, had not been explored from a large regional perspective. Condiments may have long played an evolutionary rooted role in health-related practices, beyond their culinary function. The multifunctional role of condiments suggests an underappreciated route for integrating nutraceutical wild plants into daily diets. Diversifying modern diets with once traditionally used wild plants from multifunctional lineages could enhance both food system resilience and public health, aligning with the Sustainable Development Goals.

Ethics. This work did not require ethical approval from a human subject or animal welfare committee.

Data accessibility. The dataset supporting this study is openly available in Figshare [25]. It consists of a comprehensive species list indicating their ethnobotanical uses (food, condiment and/or medicine) and the regions where these uses occur (Iberian Peninsula, Caucasus and Western Himalaya). The data are provided in a structured format with clear metadata to facilitate reproducibility and reuse in comparative and phylogenetic analyses.

Electronic supplementary material is available online [65].

Declaration of AI use. We have used artificial intelligence to improve the writing, grammar and vocabulary of the text.

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All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interest declaration. We declare we have no competing interests.

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