

## **The evolutionary link between food, condiments and medicine**

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### **(a) The food-medicine continuum**

The deep relationship between humans and plants is of great interest to ethnobotanists, human ecologists, and evolutionary biologists. Humans have incorporated thousands of plant species into both traditional medicine and our diets, as foods and condiments. Many of these provide not only calories but also micronutrients and other bioactive compounds that contribute to health [1]. The boundaries between these categories (food, medicine, and condiments) are therefore somewhat blurred, and many plants have multiple uses. This overlap, and the relationships between groupings, have been widely discussed in ethnobotanical research. A recent article by Mateo-Martín et al. explores this continuum using a statistical phylogenetic framework, sampling three cultures and 3,000 used plants across Europe [2].

The idea that food and medicine are linked predates modern ethnobotanical investigation. Across ancient ecological knowledge traditions, including Graeco-Roman medicine, Ayurveda and Traditional Chinese Medicine, flavour and sensory experience play a central role in deciding which plants are used to treat illness. The Greek philosopher Theophrastus explicitly attributed physiological powers to different tastes. Sweet flavours smoothen, astringent flavours desiccate and solidify, pungent flavours relieve heat, and bitter flavours melt and irritate [3]. These ideas reflect the humoral medical framework, in which sensory qualities were believed to act directly on the body. Although humoral medicine has long been replaced by modern biomedicine, recent work shows that people can indeed infer medicinal potential from taste [4]. Bitterness often signals detoxifying or purgative effects; pungency is associated with stimulation and digestion; and cooling sensations are linked to anti-inflammatory action. Across diverse cultures, these sensory cues provided a shared framework for evaluating plant efficacy long before plant chemistry could be formally characterised, revealing the underlying biology behind the incorporation of plants of traditional knowledge.

Condiment plants are an important link in the food-medicine tradition, but have remained relatively unexplored in modern investigations at large scales. Commonly used to add flavour, many herbs and spices possess antimicrobial, digestive, and tonic properties that influence the body beyond the minimal calories they provide. Well-known examples include garlic (*Allium sativum*), ginger (*Zingiber officinale*) and mints (*Mentha* spp.), all of which have established health impacts beyond anecdotal traditions. Taste

and chemosensation are therefore deeply embedded in traditional healing systems, blurring the boundary between food, medicine and flavouring.

Despite these interesting links, most modern ethnobotanical studies have tended to separate food and medicine and to focus on relatively small geographic scales, limiting the range of human ecological behaviour examined. Recently, Mateo-Martín et al. [2] addressed this gap by exploring the food–medicine continuum across three culturally and floristically distinct regions of Eurasia. Using a statistical evolutionary framework, they compared patterns of relatedness of plants used as foods, medicines and condiments, rather than studying how plants of these categories cluster in isolation, or neglecting condiments entirely and focussing solely on food and medicine. Curiously, they found that condiment plants cluster more closely with medicinal plants than with food plants. This suggests that condiments act as a bridge between nutrition and health, likely reflecting the bioactive properties shared by many flavouring species. In this sense, condiments consistently “bring the pharmacy to the plate” across distant cultures, offering evidence that the food–medicine continuum may reflect a broadly shared feature of human ecological behaviour.

By comparing plants used as food, medicine and condiments within a statistical evolutionary framework, Mateo-Martín et al. [2] contribute to an important idea in ethnobotany. Their results align with recent work showing that ancient links between flavour, bioactivity and medicine are reflected in evolutionary history and deeply rooted patterns of human behaviour [4].

In this commentary, I discuss the importance of these findings in the broader context of evolutionary ethnobotany, a field that has rapidly evolved in recent decades.

### **(b) Non-random selection of medicinal plants**

Long before evolutionary frameworks became standard tools in ethnobotanical research, researchers recognised that medicinal plant use is not random. Certain taxonomic lineages are selected more than others, such as families Asteraceae, Lamiaceae, Fabaceae and Solanaceae. Early comparative work, notably by Daniel Moerman, showed statistically that certain lineages contain more medicinally used plants than expected by chance [5]. This reflects a foundational principle of evolution beyond ethnobotany, that closely related species are more similar than distantly related species due to shared ancestry, and is described as phylogenetic signal [6]. It is the reason why phylogenetic frameworks are used so widely in ethnobotany, as the effects of shared ancestry must be controlled for statistically.

Beyond revealing patterns in the plants themselves, these non-random phylogenetic distributions suggested another important evolutionary principle underlies ethnobotanical knowledge. Patterns of plant lineage selection are often shared across cultures, even those which are distant and whose local floras do not strongly overlap at the species level [7–10] (Figure 1). This insight is powerful, given the major differences between distant floras at the species level; distant cultures do not have access to the exact same set of species, but independently converged on the same higher lineages for medicinal uses. When the same features evolve independently, we describe this as convergent evolution, and when features evolve convergently, it provides strong evidence for the forces behind evolutionary changes [11]. In contrast, when an evolutionary feature evolves only once in a lineage (or a small number of times), we lack the power to identify the ecological forces driving this.

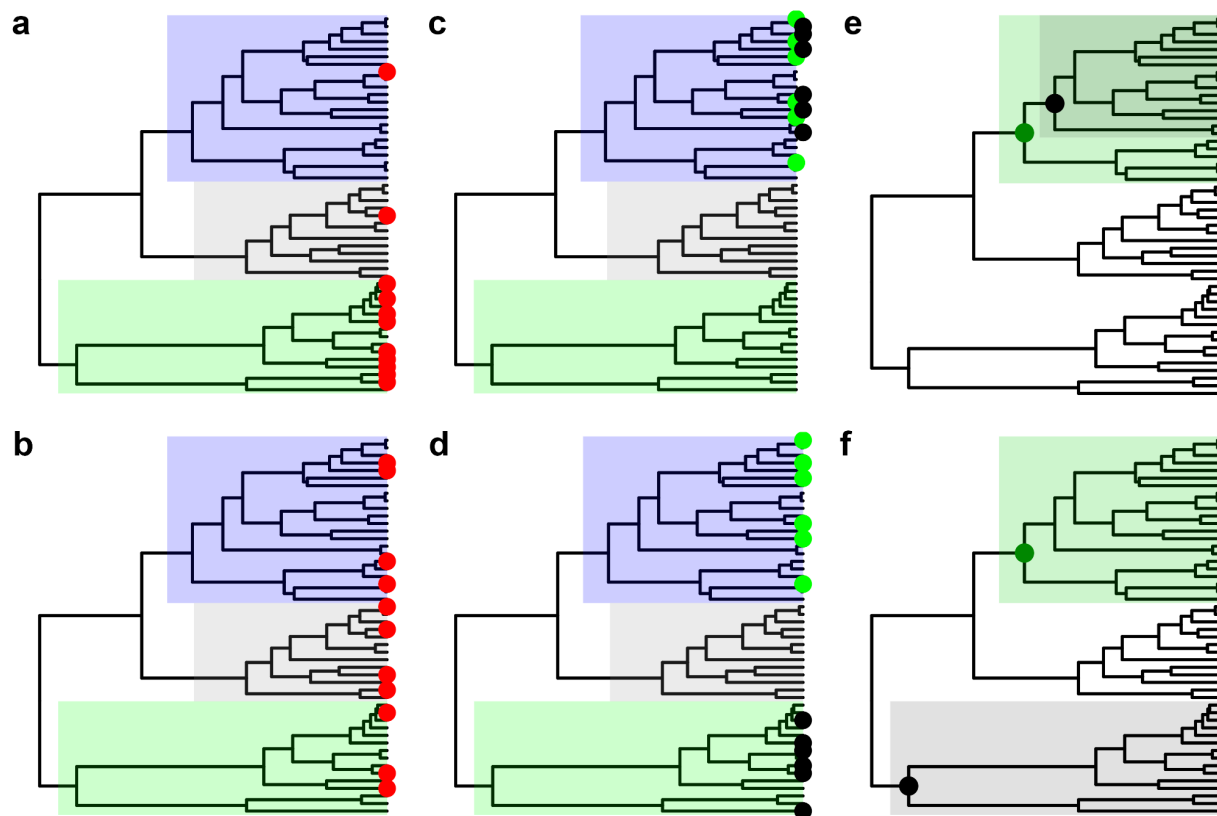
In ethnobotany, the more convergence of plant uses with particular lineages that we identify in distant cultures, the more strongly we can ascribe drivers of knowledge acquisition and identify unifying ecological behaviours [12]. With the staggering diversity of plant species available in the world, and variation in the plants available to distant cultures, repeated discovery of useful higher lineages supports several important patterns; (1) medicinal traits and compounds are lineage specific, and (2) cultures independently identify discover useful plants from related lineages. These two assertions are important as they underlie assumptions of the research by Mateo-Martín et al. [2].

### **(c) The evolution of evolutionary methods in ethnobotany**

The rise of molecular phylogenetics in the early 2000s transformed ethnobotany from a largely qualitative discipline and provided a statistical framework to test a number of different hypotheses [13]. As phylogenetic trees became available, researchers tested for non-random patterns of medicinal compounds [14], ethnomedicinal plant uses [7,9], and drivers of convergence of knowledge [15]. Researchers such as Rønsted and colleagues mapped secondary metabolites such as alkaloids, and their activity, to phylogenetic trees [14]. Results suggested that there is a weak but significant level of phylogenetic signal, indicating that a mixture of evolutionary conservatism and other sources of variation shaped phytochemical diversity. In parallel, researchers such as Hawkins and Saslis-Lagoudakis used phylogenies to explore plant uses and cross-cultural patterns, which extended the scope beyond phytochemistry to inform human behaviour and cultural evolution [7,9].

A critical development was the adoption of the “hot nodes” statistical method, originally developed to identify biological lineages with more descendants possessing a particular trait [16] (Figure 1). Given the principles of phylogenetic signal and ethnobotanical

convergence, it was argued that plant lineages with a higher proportion of medicinally used plants are likely to harbour undiscovered drug compounds [17]. By identifying these, bioprospecting could be accelerated beyond the random screening approaches (e.g. those used by Spjut et al. [18]). The hot nodes approach has seen widespread use and has been applied to numerous systems, including individual genera [9], cross-cultural comparisons of entire floras [7,19], plants used for psychoactive applications [19], reproductive health [20], and cancer [8]. While we are yet to test this approach empirically in a laboratory setting, initial predictive work suggests that it can effectively whittle the number of plants to bioprospect [20,21], thus supporting the efficacy of the hot nodes method. Recent work has scrutinised the statistical assumptions underlying hot nodes and tested their robustness across phylogenetic scales [22].



**Figure 1: A simulated phylogeny of three plant families showing different phylogenetic distributions.** (a) Phylogenetic signal of medicinal plant use (red dots), showing clustering of useful species within a family (green clade). (b) No phylogenetic signal. Used species (red dots) are randomly distributed across the phylogeny. (c) Ethnobotanical convergence. Two cultures (green and black dots) independently select different species within the same family (blue clade). (d) No ethnobotanical convergence. Cultures select species from different families. (e) Nested hot nodes

inferred from the distribution of species (shaded branches). Here, the hot nodes overlap. (f) Distinct hot nodes. When cultures select plants from different families, the resulting hot nodes (shaded branches) do not overlap.

#### **(d) The evolutionary link between food, condiments and medicine**

Mateo-Martín et al. [2] used these phylogenetic approaches to investigate evolutionary clustering among plants used for medicine, food, and condiments across three geographic regions in Eurasia, following similar comparative frameworks sampling different regions to improve non-independence [7,9,10]. These are the Iberian Peninsula, the Caucasus, and the West Himalaya, and they were chosen for their floristic and cultural differences. Although the plant uses were regional and not culture-specific, the cultures in these regions are geographically and historically distant, which helps isolate convergence from simply borrowing. Together, they provide a large dataset of ~15,000 native plant species, of which ~3,000 are used ethnobotanically, which Mateo-Martín et al. classified into food, condiment, and medicine, or any combination of the three. Using a large molecular phylogeny, and adding species without molecular data according to taxonomy, they created 1,000 phylogenetic frameworks sampling all plant species present in each region. Analysing multiple phylogenies, which differ in the placement of species and branch lengths, is good practice in comparative biology, as phylogenies suffer from many sources of uncertainty. Using each phylogeny, Mateo-Martín et al. [2] identified hot nodes for each combination of use category and region, and calculated phylogenetic signal. By doing this, they created a robust framework for comparative research into the food, condiment and medicine continuum.

Across all three regions, food, medicine and condiment uses show weak but statistically significant phylogenetic signal. The plants used for these purposes are not randomly distributed across the plant Tree of Life, yet they are not deeply conserved across long evolutionary timescales. Useful species are clustered at shallow taxonomic levels, and are drawn from diverse plant lineages. This is consistent with the earlier phylogenetic studies of medicinal plant use. Evolutionary history constrains human selection to some degree, but cultural exploration and experimentation still draw on diverse plants from across the local flora [15,23]. Patterns in human use of plants reflect a mix of knowledge conservation and adaptive change [24].

These usage patterns have been linked to the biology of the plants. The properties making plants edible, flavoursome and medicinal arise from biosynthetic pathways that are themselves structured by shared ancestry [25]. Plants produce a staggeringly diverse array of secondary metabolites, including alkaloids, terpenoids, flavonoids and phenolic compounds. Classes of secondary metabolites frequently show phylogenetic

signal, reflecting deeply conserved biochemical pathways [25]. But, similar compounds evolve convergently in distantly related lineages, such as caffeine in Rubiaceae (the family containing coffee) and Theaceae (containing tea). The secondary metabolites produced by these chemical pathways are often invoked to explain ethnobotanical patterns, as cultures are assumed to have discovered the useful chemistry as they honed their knowledge throughout time. This has also been used to argue for the efficacy of ethnomedicinal plant use, which underlies the hot nodes approach by revealing the predictivity of traditional knowledge [7]. However, it must be noted that ethnobotanical knowledge does not precisely predict bioactive plant chemistry. Local plant abundance and availability also shape human choices [15,23,26], as do historical and ritual uses.

Similarly, the properties making plants edible also evolve from a balance of phylogenetic signal and convergence. Nutrient and sugar-rich fruits, starch-heavy underground organs, and seeds rich in lipids and proteins also emerge from conserved developmental pathways. Yet these traits have also evolved convergently across distant lineages. Condiments occupy an interesting position in this framework. Unlike staple foods, they contribute very little calorific value, but their desirable properties emerge from their biochemistry. Many aromatic herbs and spices derive their flavours from compounds such as terpenoids and polyphenols, which evolved primarily as anti-herbivore or antimicrobial defences. Having established that plant uses have a medium level of phylogenetic signal, Mateo-Martín et al. [2] then compared overlap among use categories within each region. As expected, plants in food and medicinal hot nodes overlap significantly. The link between the sensory and nutritional properties of food and medicinal plants is ancient and very strong [4]. As demonstrated by previous work on plants used to manage cancer, many medicinal lineages are characterised by broad-spectrum activity across general health issues, which is likely explained by nutritional factors rather than anti-tumour-specific bioactive chemistry [8].

Curiously, condiment hot nodes have greater overlap with medicinal hot nodes than with food hot nodes. Condiments, often considered to be simple additions to a plate, are more closely related to medicinal plants than food plants. Condiments appear to cluster within lineages with higher metabolically active chemistry, and are evolutionarily closer to medicinal plants than to staple food plants. This suggests that condiments may represent an evolutionary bridge between nutrition and healing, structured by shared biochemistry and driven by human sensory perception. From the anthropological perspective, this pattern hints at a recurrent and innate pathway in cultural evolution, where flavour-driven experimentation drives the incorporation of foods into medicinal knowledge systems.

The authors strengthen this finding by comparing the hot nodes between regions. Despite species-level floristic differences across the Iberian Peninsula, the Caucasus, and the West Himalaya, similar higher-level taxonomic lineages emerged as hot nodes for food, condiments, and medicine. This cross-regional agreement provides evidence for ethnobotanical convergence and suggests that the selection of food, condiment and medicinal plants is influenced by shared evolutionary constraints. Lineages rich in bioactive compounds are selected repeatedly in both culinary and medicinal traditions. The food–medicine continuum may transcend cultural boundaries, and is driven by the shared evolutionary history of plants, and also in the biology of human perception.

### **(e) Future work**

Although insightful, the work of Mateo-Martín et al. [2] leaves some questions unanswered. First, although geographically distinct, these three Eurasian regions share long histories of migration, exchange and cultural contact. Millennia of interactions along spice trade networks moved not only plants, many of which were condiments and medicinal, but also knowledge, blurring evidence of independent convergence. Similar phylogenetic patterns may therefore reflect horizontal transmission, and future work should disentangle this from independent discovery [24]. Extending analyses to more isolated regions and integrating demographic, societal, and historical predictors of cultural variation would help distinguish convergence driven by plant evolution from similarity shaped by shared human history. Second, the mechanism underlying phylogenetic clustering remains unresolved. Do hot nodes identify lineages genuinely enriched in bioactive chemistry, or do they simply reflect plants that are widespread and locally abundant? Ecological opportunity and availability may shape plant selection as strongly as, or even more strongly than, phytochemistry [15,23,26], a hypothesis long emphasised in ethnobotanical research [27]. Furthermore, although Mateo-Martín et al. [2] invoke shared biochemical properties, likely detected through flavour, as the bridge between food, condiments and medicine, this mechanism remains to be tested explicitly.

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