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3 **The human fingerprint of medicinal plant species diversity**
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29 **Medicinal plants have long been crucial to human civilizations, supporting both**
30 **traditional and modern healthcare systems. However, the processes influencing the**
31 **global diversity and distribution of medicinal plants remain underexplored. Their**
32 **diversity, like that of other species groups, is shaped by abiotic and biotic influences,**
33 **which include, in unique ways, human ecological (including cultural) practices. Here,**
34 **we investigate and compare these influences on the distribution and diversity of**
35 **32,460 medicinal plant species and on global vascular plant distributions. We**
36 **identify significant regional variation in medicinal plant diversity, including**
37 **"hotspots" (India, Nepal, Myanmar, and China) and "coldspots" (Andes, New Guinea,**
38 **Madagascar, the Cape Provinces, and Western Australia) of unrealized diversity.**
39 **Human migratory timelines have significant influence on medicinal plant diversity**
40 **and distributions, underscoring the likely importance of accumulated**
41 **ethnobotanical knowledge over time. Regions with long histories of human**
42 **settlement typically boast more diverse medicinal floras than expected. In contrast,**
43 **language diversity, an indicator of cultural diversity, appears to have a limited direct**
44 **effect on medicinal plant diversity, but its indirect effects warrant further**
45 **exploration. Our study emphasizes the need for integrated conservation strategies**
46 **that incorporate both standard ecological factors and human ecological dimensions;**
47 **the latter are critical for preserving medicinal plant resources and enhancing global**
48 **healthcare solutions.**

49 Medicinal plants have been integral to human cultures for millennia and have played a
50 central role in the development and expansion of societies (1). These plants represent a
51 global biodiversity heritage that is essential for both traditional and modern healthcare
52 systems. Medicinal plants are pivotal for ongoing pharmaceutical research and drug
53 development (1-3), contribute to ecosystem health (4), and support myriad cultural
54 traditions and the global economy (4-6). Notably, around 80% of the Global South relies
55 exclusively on medicinal plants, and approximately 25% of Western pharmaceuticals are
56 derived or inspired by plants and fungi (3, 7).

57 The sustainable use and conservation of medicinal plants depend heavily on precise
58 species distribution data and a comprehensive understanding of their spatial patterns and
59 related abiotic and biotic influences. Conservation of medicinal plants also depends on the
60 survival of indigenous cultures and the traditional knowledge they contain. Indigenous
61 peoples currently steward over 25% of the world's land surface and 37% of remaining
62 natural lands (8). Ethnobotanical studies demonstrate that a large share of vernacular
63 names and known medicinal uses of plants may be found only in indigenous languages
64 which are themselves endangered (9-12). Thus, both scientific and traditional knowledge
65 are crucial for maintaining biodiversity, protecting ecosystem services, and unlocking the
66 benefits of medicinal plants for future advancements in healthcare (1, 4). Despite their
67 importance, however, a systematic understanding of the broad distribution of medicinal
68 plants and the processes influencing their diversity and distribution remains in its infancy.

69 In a recent ground-breaking investigation, Pironon *et al.* (13) identified a strong correlation
70 between vascular plant diversity and the diversity of plant species used by humans,
71 including medicinal species. Their findings demonstrated that medicinal plant diversity
72 largely mirrors overall plant diversity, with regions rich in vascular plants also boasting

73 significant medicinal plant diversity. However, drivers of the diversity and distribution of
74 medicinal plants involve not only abiotic factors, traits, and interspecific interactions, but
75 also human ecological practices. For example, cultural norms and knowledge systems
76 found in Indigenous languages are known to influence plant use and its diversity (14, 15);
77 regions with high cultural diversity for which linguistic diversity may serve as a proxy (16,
78 17) often also have diverse medicinal plant practices. However, global and regional
79 assessments of medicinal plant diversity rarely include the likely influence of human
80 sociocultural dynamics (16-23).

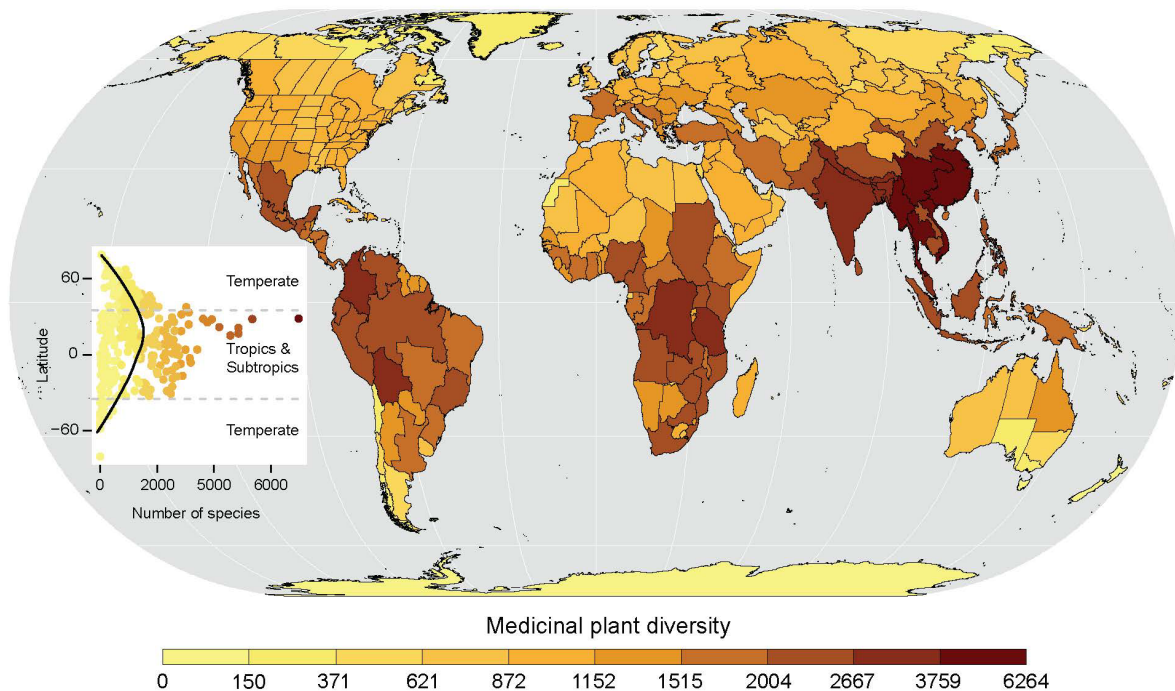
81 A key unexplored topic is whether variation in the duration of human interactions with a
82 flora has influenced regional heterogeneity in medicinal plant knowledge and diversity.
83 Different regions have been inhabited by modern humans (*Homo sapiens*) for different
84 lengths of time (24); Africa, for example, was occupied \approx 200,000–150,000 years ago (25),
85 whereas *H. sapiens* arrived in the Americas \approx 16,000–15,000 years ago (26, 27). Such
86 differences may have impacted the extent to which medicinal plants were experimentally
87 discovered, used, and integrated into traditional knowledge systems in different regions.
88 For instance, South African Zulu healers use 1,142 medicinal plants (12, 28), whereas
89 Belizean Mayan healers use 659 medicinal plants (9).

90 Our central hypothesis is that longer human occupancy fosters a greater accumulation of
91 traditional knowledge and cultural use of local plant species for healing purposes, leading
92 to higher medicinal plant diversity. To our knowledge, the imprint of regional occupancy
93 times on current medicinal plant knowledge and diversity remains untested.

94 Here, our primary objectives are to [i.] identify broad patterns in medicinal plant diversity
95 and examine their correlation with vascular plant distributions at regional and global
96 scales and [ii.] investigate how medicinal plant diversity patterns are related to two key
97 human ecological factors: cultural diversity (using language diversity as a proxy) and the
98 duration of human occupancy. Our aim is to enhance understanding of the complex
99 interplay between climate, overall vascular plant diversity, and human ecology in shaping
100 the global distribution and diversity of medicinal plants. Such knowledge is crucial for
101 recognizing the impacts of environmental and cultural changes on biodiversity, and for the
102 conservation and sustainable use of medicinal plants in improving human health.

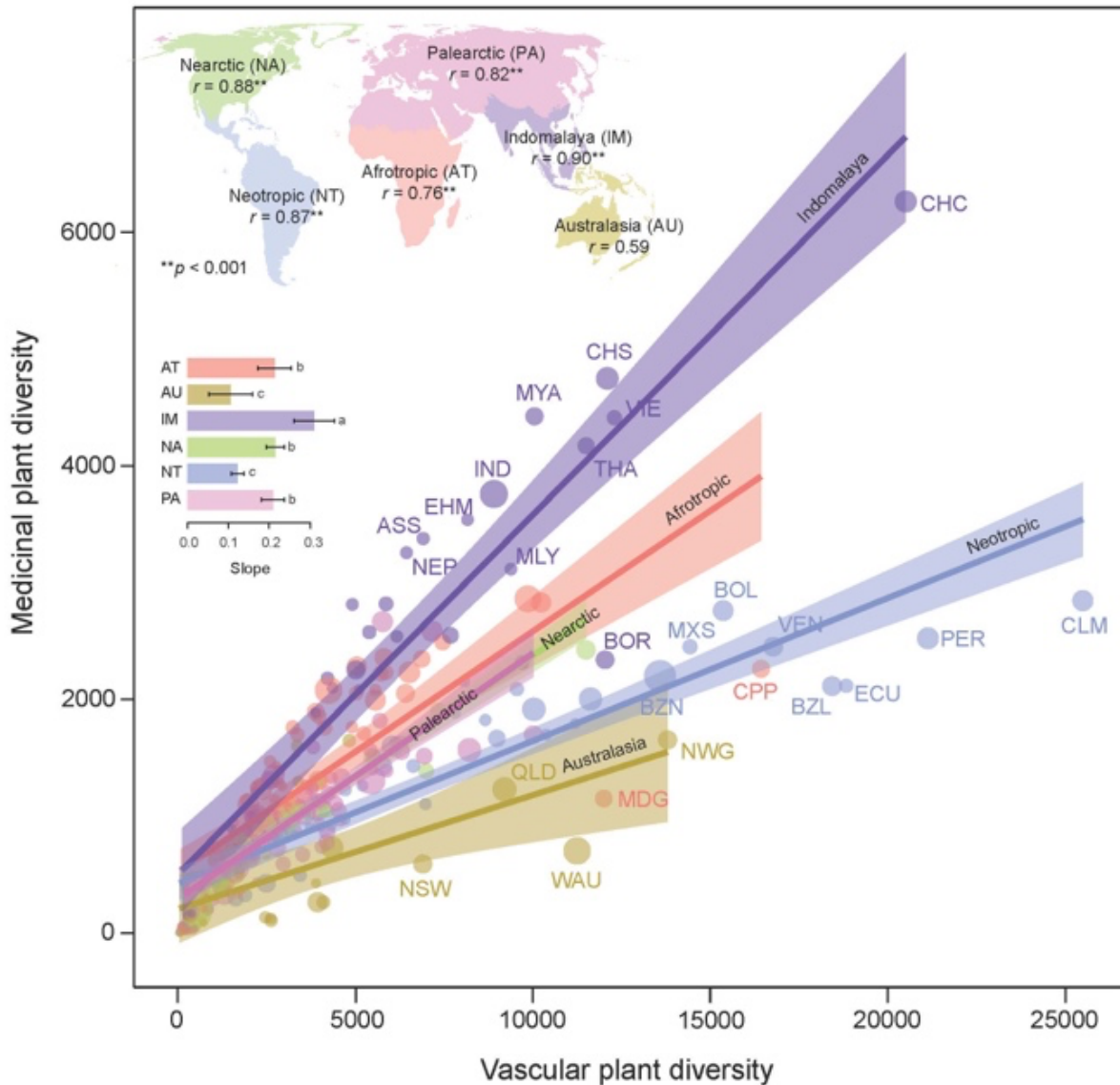
103 **Uncovering substantial regional variation in medicinal plant diversity**

104 We conducted a comprehensive analysis of global medicinal (N = 32,460) and vascular
105 plant species (N = 357,008), mapping their diversities across 369 botanical countries
106 (spatial units defined by the World Geographical Scheme for Recording Plant Distributions
107 (29), table S1). Plant species data were sourced from the Medicinal Plant Names Services
108 (MPNS) version 12 (<https://mpns.science.kew.org/>) and the World Checklist of Vascular
109 Plants (WCVP)(30). Consistent with Pironon *et al.* (13), our results demonstrate that
110 medicinal plant diversity generally aligns with the latitudinal distribution of vascular
111 plants, peaking in tropical regions (figs. 1 and S1) (20, 31). However, there are intriguing
112 departures from this general trend. The well-documented very high vascular plant
113 diversity is accompanied by unusually low medicinal plant diversity in both New Guinea
114 (with the highest language diversity in the world (fig. s2)) and Madagascar (with low
115 language diversity) (figs. 1 and S1).



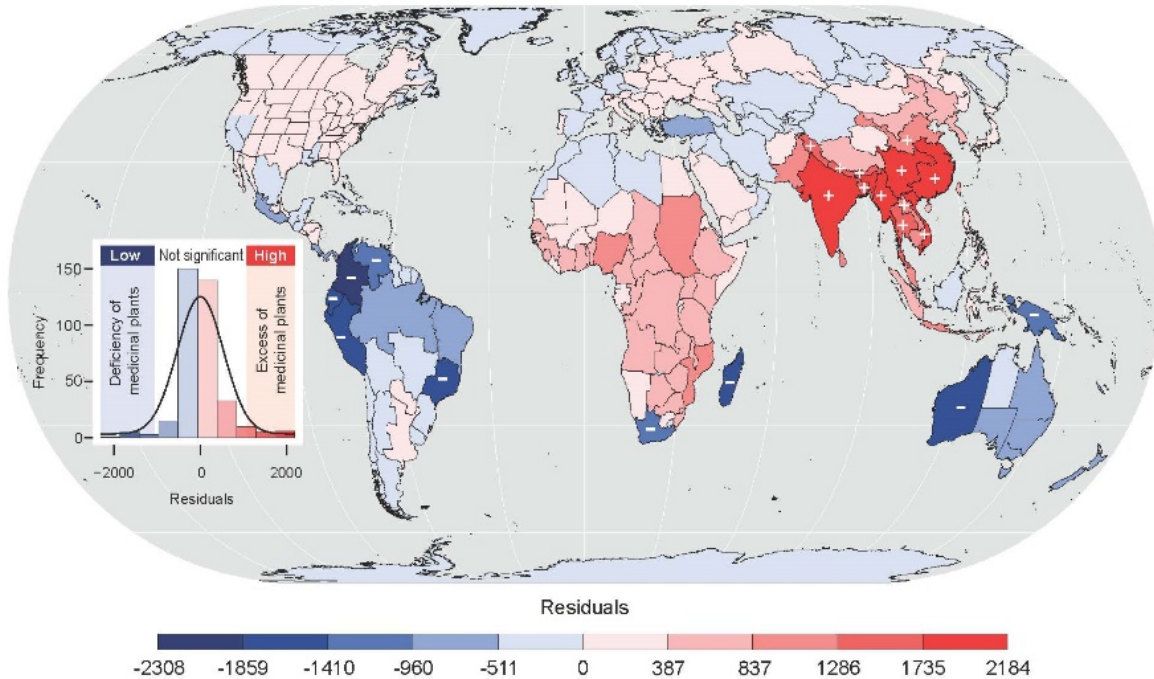
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 117 **Figure 1. Global distribution of medicinal plant species.** The map illustrates medicinal plant species
 118 diversity, with darker shades representing higher diversity and lighter shades indicating lower diversity
 119 levels. The inset depicts the latitudinal trend, highlighting the highest species diversity in tropical regions,
 120 consistent with the latitudinal diversity gradient. The black solid line represents a locally weighted
 121 scatterplot smoothing (LOWESS) regression. The map is presented using an Eckert IV projection.

122 To further assess regional variations, we analyzed medicinal plant diversity across
 123 botanical countries grouped into six widely accepted phytogeographic regions (25):
 124 Afrotropic, Australasia, Indomalaya, Nearctic, Neotropic, and Palearctic. Our one-way
 125 ANOVA results indicated significant regional variation in medicinal plant diversity ($F_{5,327} =$
 126 $22.82, P < 0.001$), with Tukey's HSD post-hoc tests revealing notable differences between
 127 regions (fig. S3). Indomalaya, despite comparable vascular plant diversity to the Neotropics
 128 (fig. S1), exhibits significantly higher medicinal plant diversity ($P < 0.05$) (fig. S3),
 129 underscoring that vascular plant diversity alone does not account for observed differences
 130 (13). Our linear model (medicinal plant diversity as the response variable and vascular
 131 plant diversity as the predictor), which included phytogeographic region as an interaction
 132 term, revealed a significant interaction effect between vascular plant diversity and region
 133 ($F_{5,326} = 28.62, P < 0.001$), implying that region *per se* has a notable influence on the
 134 relationship between vascular and medicinal plant diversity. Our regional models
 135 corroborated this finding, further revealing significant differences in the strength of the
 136 relationship between vascular and medicinal plant diversity across regions (fig. 2). The
 137 Indomalaya region exhibits the steepest slope between vascular and medicinal diversity
 138 (fig. 2), indicating that an increase in vascular plant diversity results in greater medicinal
 139 diversity gains in Indomalaya compared to other regions. In contrast, Australasia exhibits
 140 the least steep slope, indicating lower overall medicinal diversity gains compared to other
 141 regions.



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 143 **Figure 2. Comparative analysis of vascular and medicinal plant diversity across biogeographic realms.**
 144 Each dot's size reflects the area of six color-coded phylogeographic regions, with larger dots indicating larger
 145 areas of botanical countries. The three-letter codes next to each dot represent botanical countries (refer to
 146 table S1 for details). Pearson's correlation coefficients (r) for the relationship between vascular and medicinal
 147 plant diversities are displayed for each realm. The bar on the left illustrates the slopes and 95% confidence
 148 intervals of this relationship across the six realms. Bars with different letters (a, b, c) indicate significant
 149 differences ($p < 0.05$), determined using Bonferroni correction for pairwise comparisons.

150 Our investigation into deviations from predicted medicinal plant diversity revealed
 151 “hotspots” and “coldspots” of medicinal plant diversity (fig. 3). Regions like India, Nepal,
 152 Myanmar, and China show higher than predicted diversity (two-tailed test, $P < 0.05$). At the
 153 same time, the Andes, Cape Provinces, Madagascar, Western Australia, and New Guinea
 154 demonstrate lower than expected medicinal plant diversity (two-tailed test, $P < 0.05$) (fig.
 155 3).



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 157 **Figure 3. Residual analysis of medicinal versus vascular plant diversity.** The map displays residuals from
 158 the linear regression comparing medicinal plant diversity to vascular plant diversity. Red indicates positive
 159 residuals, suggesting a surplus of medicinal plants, whereas blue indicates negative residuals, reflecting a
 160 deficiency. Botanical countries with significantly higher or lower medicinal plant diversity than expected ($p <$
 161 0.05) are marked with plus (+) and minus (-) signs, respectively. The map uses an Eckert IV projection.

162 We acknowledge that these regional patterns may partially reflect disparities in research
 163 and documentation efforts. Canonical medicine systems like Ayurveda (32) and Traditional
 164 Chinese Medicine (33), which reflect extensive accumulated traditional knowledge, may
 165 increase the number of recorded uses of medicinal plant species. In contrast, colonial
 166 influences and modernization may have contributed to the further erosion or non-
 167 recording of this knowledge (34), thus highlighting the need to better preserve and explore
 168 traditional ethnobotanical practices. For example, the decline of traditional knowledge, as
 169 seen in Ecuador relative to Peru (35), underscores the importance of cultural heritage in
 170 maintaining medicinal plant diversity. Finally, we recognize that differing phylogenetic
 171 histories and speciation rates may influence these patterns beyond cultural factors. Despite
 172 these caveats, our global findings may stem from variation in ethnobotanical knowledge
 173 and cultural practices (14, 15) that remain untested and should be investigated.

174 **Human arrival time and its association with medicinal plant diversity**

175 We also explored the relationship between medicinal plant diversity and potential climatic
 176 and anthropogenic predictors using a linear mixed-effect model. This model included seven
 177 fixed-effect predictors (fig. S4) and treated the phytogeographic region as a random effect
 178 to account for variations across regions. Beyond the known climatic predictors of plant
 179 diversity (20-23), we included human occupancy time (fig. S5) and language diversity (fig.
 180 S2), which is often used as a proxy for cultural diversity correlated with ethnobotanical
 181 knowledge (16, 17), to test our hypothesis that earlier human presence fosters the

182 development of traditional medicine systems, the cultivation of medicinal plants, and an
183 ultimate increase in overall regional medicinal plant diversity.

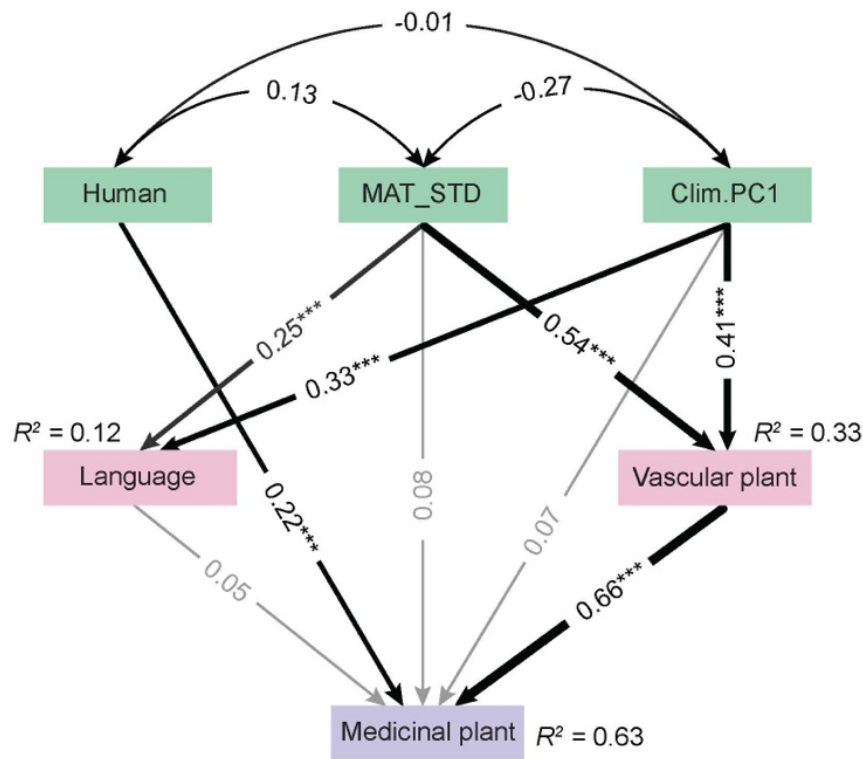
184 Our results confirmed the strong influence of vascular plant diversity on medicinal plant
185 diversity (fig. S4). Human occupancy time emerged as the second-most significant
186 predictor. These associations remained robust to uncertainties in estimating human
187 occupancy times (fig. S6), suggesting that the observed relationships are not artifacts of
188 estimation errors. This suggests that vascular plant diversity does have an influence on
189 medicinal plant diversity, but the length of human engagement within a particular
190 environment—perhaps via experimentation and traditional practices—is pivotal in
191 determining medicinal plant usage. These results raise the hypothesis that over time,
192 human societies within a region experiment with, and recognize the medicinal value of,
193 various plants, thereby enhancing diversity through shared knowledge and discoveries. As
194 most languages are unwritten, this botanical knowledge is largely orally transmitted,
195 reinforced by cultural learning and frequent interactions with plants (9, 11).

196 To test for these interactions among human ecological predictors, we used path (“causal”)
197 models at both global and regional scales. These models aligned with our mixed-effect
198 model results and identified direct and indirect effects (36). Both vascular plant diversity
199 (standardized path coefficient = 0.66; $P < 0.001$) and human occupancy time (standardized
200 path coefficient = 0.22; $P < 0.001$) significantly affect medicinal diversity globally and
201 regionally (figs. 4 and S7). Human occupancy time significantly explained the variation in
202 medicinal plant diversity (standardized path coefficient = 0.34; $P < 0.001$) even after
203 controlling for the effect of vascular plant diversity (fig. S8), highlighting the substantial
204 role of human occupancy time in shaping medicinal plant landscapes beyond commonly
205 explored factors.

206 **Limited impact of language diversity on medicinal plant diversity**

207 Although our mixed-effect model identified a significant global effect of language diversity
208 on medicinal plant diversity (fig. S4), the path model did not support a direct relationship
209 between these two variables at the same scale (fig. 4). This discrepancy highlights the
210 structural differences between these models. Linear models focus on direct interactions,
211 capturing the apparent significance of language diversity without accounting for complex
212 intermediaries. In contrast, path models explore intricate interdependencies, incorporating
213 indirect effects via mediating variables like climate (36). This suggests that language
214 diversity might indirectly influence medicinal plant diversity, mediated by environmental
215 factors significantly correlated with language and vascular plant diversity (see fig. 4).
216 Language diversity and biodiversity are linked (16, 17, 37) and mutually reinforcing due to
217 shared environmental influences and indigenous knowledge networks (38, 39).

218 Biodiversity-rich areas often foster diverse cultures with unique languages, as diverse
219 ecological resources support both biological and cultural diversity. These environmental
220 conditions may drive both biological and cultural evolution, allowing species and languages
221 to flourish. Our path model identifies this dependency, suggesting that there are likely
222 more complex dynamics between medicinal plant and language diversity.



$\chi^2 (3, N = 328) = 29.998, p = 0$
 *** $p < 0.001$

RMSEA = 0.166
 SRMR = 0.063
 CFI = 0.949

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Figure 4. Path model depicting influences on medicinal plant diversity. This model illustrates the relationships among climate, environmental heterogeneity, earliest human colonization, language diversity, and vascular plant diversity in explaining medicinal plant diversity. Standardized path coefficients are indicated along the paths. Variables include Human: Time of first modern human colonization; MAT_STD: Standard deviation of mean annual temperature; Clim.PC1: First principal component of 19 bioclimatic variables. Fit indices provided are RMSEA: Root mean square error of approximation, SRMR: Standardized root mean square residual, and CFI: Comparative fit index.

231 Conclusions

232 Our analysis identifies a likely pivotal role for human ecology in shaping global medicinal
 233 plant diversity. Although vascular plant diversity remains the primary correlate of
 234 medicinal plant diversity, our findings reveal that human occupancy time also significantly
 235 and directly influences medicinal plant diversity. This suggests that longer human
 236 occupancy fosters accumulated traditional knowledge, the use of local plants for medicine,
 237 and the emergence of local experts such as healers or shamans, resulting in increased
 238 medicinal plant diversity. Our results highlight the need for integrated approaches that
 239 consider both “natural” and anthropogenic factors in understanding plant distributions.
 240 Regions we identified as medicinal diversity coldspots, such as the Andes, New Guinea,
 241 Madagascar, the Cape Provinces, and Western Australia, certainly have unrecorded or
 242 unrecognized medicinal plant resources. Conversely, regions such as India, Nepal,

243 Myanmar, and China are hotspots of medicinal plant diversity and should be formally
244 recognized as biodiversity hotspots and prioritized for systematic preservation and in-
245 depth scientific research. Finally, although we did not find a direct impact of language
246 diversity on medicinal plant diversity, its indirect effects through shared environmental
247 factors suggest complex interdependencies worth further exploration. Preserving
248 ethnobotanical knowledge, especially in language hotspots (40), is crucial for maintaining
249 and enhancing medicinal plant diversity. These insights are vital for fostering sustainable
250 conservation strategies and leveraging the untapped potential of medicinal plants in
251 addressing future healthcare challenges (1).

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263 **Competing interests:** CCD and LG declares that they are supported by LVMH Research and
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266 **Data and materials availability:** The native distribution dataset of global vascular plant
267 species used in the current study has been deposited in Zenodo (41) except for the MPNS
268 dataset, which was obtained from Kew under CC-BY-NC license, with an additional
269 restriction against sharing with third parties. The gridded environmental data, language
270 data and human occupancy data, including the R codes used for data analysis and
271 visualization is hosted on GitHub (42).

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