

1 **Genomic history and ecology of the geographic spread of rice**

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27

## 28 **ABSTRACT**

29 Rice (*Oryza sativa*) is one of the world's most important food crops. We reconstruct  
30 the history of rice dispersal in Asia using whole-genome sequences of >1,400 landraces,  
31 coupled with geographic, environmental, archaeobotanical and paleoclimate data. We also  
32 identify extrinsic factors that impact genome diversity, with temperature a leading abiotic  
33 factor. Originating ~9,000 years ago in the Yangtze Valley, rice diversified into temperate  
34 and tropical japonica during a global cooling event ~4,200 years ago. Soon after, tropical rice  
35 reached Southeast Asia, where it rapidly diversified starting ~2,500 yBP. The history of  
36 indica rice dispersal appears more complicated, moving into China ~2,000 yBP.  
37 Reconstructing the dispersal history of rice and its climatic correlates may help identify  
38 genetic adaptation associated with the spread of a key domesticated species.

39

## 40 **One sentence summary**

41 We reconstructed the ancient dispersal of rice in Asia and identified extrinsic factors that  
42 impact its genomic diversity.

43

44 Rice (*Oryza sativa* L.) is a major staple crop, providing > 20% of calories for more  
45 than half of the human population. Domesticated rice encompasses genetically distinct  
46 populations grown in sympatry, including major subgroups japonica and indica (sometimes  
47 recognized as subspecies), as well as geographically more restricted *circum-aus*, and *circum-*  
48 *basmati* rices (1, 2). It is mainly cultivated in monsoon Asia, but rice is distributed across a  
49 wide latitudinal range, spanning tropical and temperate zones of Asia, likely requiring local  
50 water, temperature and photoperiod adaptation. Rice is grown in lowland ecosystems under  
51 paddy, deepwater, or seasonal flood conditions, as well as in upland rainfed areas (3).

52 Archaeological evidence (4–6) indicates that cultivation of japonica rice began ~9,000  
53 years before present (yBP) in the lower Yangtze Valley, while proto-indica rice cultivation  
54 started >5,000 yBP in the lower Ganges valley (7). Archaeological (8) and most population  
55 genetic analyses (9–11) suggest that important domestication alleles have a single origin in  
56 japonica rice in East Asia. The spread of japonica to South Asia ~4,000 years ago led to  
57 introgression of domestication alleles into proto-indica or local *O. nivara* populations and the  
58 emergence of indica rice (9–11). From the Yangtze and Ganges Valleys, respectively,  
59 japonica and indica dispersed across much of Asia over the last 5 millennia, providing  
60 sustenance for emerging Neolithic communities in East, Southeast and South Asia (12).

61 Archaeological data shows the general directionality of rice dispersal (7, 13); the  
62 details of dispersal routes, times, and the environmental forces that shaped dispersal patterns,  
63 however, remain unknown. Here, we undertake population genomic analyses to examine  
64 environmental factors associated with the geographic distribution of rice diversity, and  
65 reconstruct the ancient dispersal of rice in Asia. Together with archaeobotanical,  
66 paleoclimatic and historical data, genomic data allows a robust reconstruction of the dispersal  
67 history of *Oryza sativa*.

68

69 ***Structure of rice genomic diversity.*** We obtained whole genome re-sequencing data from  
70 rice landraces/traditional varieties across a wide geographical distribution in Asia. Our  
71 sample set includes 1,265 samples from the Rice 3K Genome Project (1) and additional 178  
72 landraces sequenced for this study (Supplementary Table 1); the panel consists of 833 indica,  
73 372 japonica, 165 *circum*-aus, 42 *circum*-basmati, and 31 unclassified samples. We identified  
74 ~9.78 million single nucleotide polymorphisms (SNPs) with 9.63x mean coverage (s.d. =  
75 5.03), which we used in subsequent analyses (Supplementary Fig. 1).

76 Analysis of molecular variance (AMOVA) indicated that subspecies affiliation  
77 explained >36% of the total variation [AMOVA, permutation  $P < 0.001$ ](14), congruent with  
78 results from multidimensional scaling (MDS) of genomic distances (Supplementary Fig. 2a).  
79 Only japonica and indica have wide geographic distributions (Fig. 1 a and b; Supplementary  
80 Fig. 3), and AMOVA of these two subspecies (n=1,205) revealed that genomic variance is  
81 explained by subspecies ( $r^2 = 0.32$ , permutation  $P < 0.001$ ), country of origin ( $r^2 = 0.11$ ,  $P <$   
82  $0.001$ ) and their interaction ( $r^2 = 0.06$ ,  $P < 0.001$ ). Landraces with mixed ancestry (n=154)  
83 were excluded using silhouette scores (Supplementary Fig. 2b); henceforth, we analysed  
84 these two subspecies independently.

85 We find support for isolation-by-distance (IBD) in japonica ( $r^2 = 0.294$ ,  $P < 0.001$ )  
86 and indica ( $r^2 = 0.265$ ,  $P < 0.001$ ) [Supplementary Fig. 4]. Geographic distance explains  
87 genetic distance much less in the Malay Archipelago (*i.e.* islands SE Asia) compared to  
88 mainland Asia, suggesting a stronger effect of local migration barriers on island IBD  
89 (Supplementary Fig. 5). Effective migration surfaces (15) identified geographic barriers for  
90 dispersal over the Hengduan Mountains which separate China from South/Southeast Asia,  
91 and the South China Sea which reduces movement between Borneo/Philippines and mainland  
92 Southeast Asia (Fig. 1c and d; Supplementary Fig. 6). For human-dispersed species such as  
93 crops, genetic distances may correlate better with travel resistance, meant to capture cost-

94 effective migration by humans. An isolation-by-resistance (IBR) model, using estimated  
95 human-associated land and marine travel times (16), is a better explanation than the IBD  
96 model for japonica landrace genetic distances based on Akaike Information Criterion (island  
97  $\Delta\text{AIC} = -34$ , mainland  $\Delta\text{AIC} = -17$ ), but not for indica (island  $\Delta\text{AIC} = +51$ , mainland  $\Delta\text{AIC} =$   
98  $+611$ )[Supplementary Fig. 5].

99

### 100 ***Factors associated with spatial genomic structure.***

101 We used redundancy analysis (RDA) to partition genomic variance (17) associated with 22  
102 different variables that include climatic and edaphic conditions, as well as interactions with  
103 humans and wild relatives (Supplementary Table 1). We assume that while environments in  
104 localities fluctuate over time, current genome diversity may be determined both by current  
105 environment as well as long-term evolutionary history. SNP variation is better explained by  
106 our predictors for japonica (adjusted  $r^2 = 0.363$ ; Fig. 1e) than indica (adjusted  $r^2 = 0.164$ ; Fig.  
107 1f). Associations between predictor sets and SNPs are substantially collinear with each other.  
108 For japonica and indica, travel time and geographic distance, respectively, explain most SNP  
109 variation (adjusted  $r^2 = 0.326$  and  $r^2 = 0.146$ ), followed by abiotic conditions, language  
110 groups, culinary properties (*i.e.*, cooked grain stickiness), and genetic composition of  
111 proximal wild rice populations (Figs. 1e and f; Supplementary Fig. 7). Among abiotic  
112 variables for japonica, temperature explains the greatest portion of SNP variation (adjusted  $r^2$   
113  $= 0.180$ ), followed by moisture ( $r^2 = 0.086$ ) and soil characteristics ( $r^2 = 0.081$ ). Similarly,  
114 temperature explains the most SNP variation in indica ( $r^2 = 0.064$ ), followed by soil  
115 characteristics ( $r^2 = 0.038$ ) and moisture ( $r^2 = 0.036$ ) (Supplementary Fig. 7), although these  
116 factors have weaker explanatory power in indica compared to japonica.

117 The first two RDA axes of environment-associated SNP variation (18) separated  
118 japonica landraces consistent with geography (Fig. 1g), recapitulating results using total SNP

119 variation (Supplementary Fig. 8a). Temperate japonica landraces from northern latitudes are  
120 most strongly identified by alleles associated with high coefficient of inter-annual variation in  
121 growing degree days, and low minimum temperatures early in the growing season (Fig. 1g;  
122 Supplementary Fig. 9a). Temperate landraces from upland rainfed ecosystems are further  
123 characterized by alleles associated with inter-annual variation in precipitation.

124 For indica, the first two axes also grouped individuals by their geographic origins  
125 (Fig. 1h; Supplementary Fig. 8b). Similar to japonica, indica Malay Archipelago genotypes  
126 are characterized by alleles associated with high precipitation prior to the growing season.  
127 Mainland Southeast Asian genotypes are characterized by alleles associated with warm  
128 minimum growing season temperatures and presence of nearby freshwater sources (Fig. 1h;  
129 Supplementary Fig. 9b). The latter contrasts with indica from China and most of India, where  
130 irrigation is common and there is less reliance on natural water sources (19)(Supplementary  
131 Table 1). Finally, genotypes in South India are identified by alleles associated with inter-  
132 annual variation in precipitation.

133

134 ***Discrete subpopulations within japonica and indica.*** We clustered landraces based on  
135 genomic distances by partitioning-around-medoids [PAM](20), identifying the number of  
136 discrete clusters (K) using silhouette scores (21) [see Methods]. This discretization procedure  
137 removed genetic gradients between subpopulations (Fig. 2a and 2d; Supplementary Figs. 10  
138 and 11). We compared PAM clusters to those from the ADMIXTURE algorithm (22).  
139 Silhouette filtering removed individuals with spurious subpopulation assignments  
140 (Supplementary Figs. 12 and 13). In general, the clustering fit using silhouette scores is  
141 greater for japonica than indica (Supplementary Fig. 14). We find consistently higher  $F_{ST}$   
142 values among japonica subpopulations (Supplementary Fig. 15), suggesting less migration  
143 compared to indica. Finally, subpopulations of both subspecies clearly correspond with

144 geography (Fig. 2b and 2e; Supplementary Figs. 10 and 11), suggesting that contemporary  
145 rice landraces retain genomic signals of past dispersal across Asia.

146

147 ***Relationships between japonica subpopulations.*** We modelled subpopulation relationships  
148 separately for japonica and indica using the admixture graph framework (23). We  
149 reconstructed relationships between japonica subpopulations at  $k = 2$  to 9 considering graphs  
150 with population f-statistic z-scores  $< 3$ . Throughout all  $k$  levels, we find two similar and  
151 consistent graph topologies (Fig. 2c; Supplementary Fig. 16), which we used to infer  
152 dispersal routes of japonica.

153 As expected (2), at  $k = 2$  we observe divergence between lowland temperate varieties  
154 in Northeast Asia (Korea, Japan, China and Taiwan) and tropical varieties from the Malay  
155 Archipelago (Malaysia, Philippines and Indonesia). At  $k = 3$ , we find a major lineage of  
156 tropical upland japonica in mainland Southeast Asia as sister group to Malay Archipelago  
157 landraces or from admixture with an ancestral temperate lineage (Supplementary Figs. 10 and  
158 16). At higher  $k$ , these mainland Southeast Asian upland landraces always incorporates  
159 admixture from an ancestral temperate japonica population (see below).

160 At  $k = 4$  we observe separation of primarily Indonesian from Philippine and Bornean  
161 landraces. Subsequently, at  $k = 5$ , upland temperate japonica in Northeast Asia emerges as an  
162 admixture between lowland temperate and upland tropical varieties. Further increase of  $k$   
163 allows separation of distinct Malay Archipelago subpopulations: a small subpopulation  
164 associated with the Philippines splits first, followed by a subpopulation in the Indonesian  
165 island of Java. Subsequent divisions among Malay Archipelago subpopulations are not fully  
166 resolved (Supplementary Fig. 16). Nevertheless, at  $k = 8$ , we identify a Bhutanese  
167 subpopulation closely related to upland Laotian landraces, and may represent a relict  
168 descendant population of the first early split in tropical japonica.

169

170 ***The rise of temperate japonica.*** Combining genomic, geographic, archaeological and  
171 paleoenvironmental data, we reconstructed routes and timing of the ancient dispersal of rice  
172 in Asia. Japonica represents the first domesticated *O. sativa* (9–11), and its tropical form was  
173 cultivated in eastern China between the Yangtze and the Huang He (Yellow) river valleys  
174 (13). This occurred during the Holocene Climate Optimum (HCO), a period of increased  
175 monsoon activity and warmer temperatures between ~9,000 and 4,000 yBP (24, 25); this  
176 coincides with the rise in frequency of non-shattering rice from ~20% just after 8,000 yBP to  
177 fixation at ~5,000 yBP (5, 6).

178         The first major population divergence in japonica separates temperate from tropical  
179 landraces (Supplementary Figs. 10 and 16). Using sequentially Markovian coalescent  
180 (SMC++), we estimated a cross-coalescence split time between temperate and tropical  
181 japonica at ~5,000 to 1,500 years ago, with 75% of estimates between ~4,100 to 2,500 years  
182 ago (Fig. 3a; Supplementary Fig. 17). Using dated archaeobotanical rice remains (13), we  
183 note that rice agriculture spread north- and eastward along the Huang He river (26) and  
184 westward into the Chengdu Plains and the Southwest China Highlands between ~5,000 to  
185 4,000 yBP (27–29)(Fig. 3b; Supplementary Fig. 18). During a minor climatic cooling event at  
186 ~5,000 yBP, rice appears maladapted in parts of eastern China (30). In the Shandong  
187 Peninsula, rice disappeared by 5,000 yBP and briefly re-emerged 4,500 yBP as a short-  
188 grained variety similar to contemporary temperate japonicas (31). A global temperature  
189 decrease that followed the HCO at ~4,200 years ago, the ‘4.2k event’ (24, 25), resulted in  
190 waning rice agriculture in East China and strong pressure for japonica to adapt to a temperate  
191 environment (31). Congruent with this, we observe that the highest density of estimated  
192 temperate japonica split times start at ~4,100 years ago (Fig. 3a; Supplementary Fig. 17).



193           Temperate adaptation created opportunity for northeastern dispersal of japonica in  
194 Asia. From our demographic analysis of temperate japonica we note a ~5-10-fold  $N_e$   
195 reduction between ~3,500 to 3,000 yBP (Fig. 3c; Supplementary Fig. 19), which we interpret  
196 as a founder bottleneck during expansion to its new temperate niche. Indeed, this is consistent  
197 with archaeological dates for the introduction of rice agriculture to Korea (32, 33) and Japan  
198 following decrease in rice remains in Eastern China (Supplementary Fig. 18).

199

200 ***The southward spread of japonica.*** Throughout the HCO, tropical japonica was cultivated in  
201 eastern China; its contemporary descendants however, are grown predominantly in Southeast  
202 Asia (1), and we indeed find that Southeast Asian subpopulations descend from the tropical  
203 lineage that diverged from temperate japonica. Demography reconstruction at  $k = 2-4$  shows  
204 that tropical japonica lineage experienced a ~50-100-fold population ( $N_e$ ) contraction  
205 between ~4,500 to 4,000 yBP, and partial  $N_e$  recovery starting ~2,500 yBP (Fig. 3d,  
206 Supplementary Fig. 19). The population contraction in tropical japonica is contemporaneous  
207 with the 4.2k event, raising the possibility that cooling explains the collapse of tropical rice  
208 cultivation in East Asia and its southern relocation. This coincides with the arrival of rice in  
209 the far south of China ~4,500 yBP and a shift to rainfed, upland cultivation (34).

210           Given the importance of temperature in shaping japonica genomic diversity across its  
211 geographic distribution (Fig. 1g), we used a thermal niche model (35) based on  
212 reconstruction of Holocene temperatures (36) to estimate the probability of tropical rice  
213 cultivation in different areas during the post-HCO period (Fig. 3e; Supplementary Fig. 20).  
214 Survival probabilities of tropical japonica between ~4,400 and 3,500 yBP dropped  
215 dramatically in eastern China and high-altitude South China (survival probability < 50%)  
216 compared to Southeast Asia [survival probability > 90%](Fig. 3e; Supplementary Video 1).

217 Indeed, after the cooling period we observe high densities of archaeological rice remains in  
218 Southeast Asia (Fig. 3b; Supplementary Fig. 18).

219 After the HCO, rice dispersed from China to Southeast Asia into Laos and Bhutan,  
220 and through maritime routes to the Philippines, Malaysia and Indonesia. In our admixture  
221 graph analysis, we find an early split in the tropical lineage that separates Bhutan and Laos  
222 upland rice from rice in the Malay Archipelago (Fig. 2c). From coalescence analyses we  
223 observe a ~50-100-fold population contraction in the remote upland (Bhutan) rice population  
224 between ~4,000 and 3,000 yBP (Fig. 4; Supplementary Fig. 19), which may arise from a  
225 bottleneck associated with population movements into these new areas. Emergence of upland  
226 rice in Laos and Bhutan coincides in time and space with widespread establishment of rainfed  
227 rice agriculture in mainland Southeast Asia, ~4,000 yBP (12, 37) and dispersal of metallurgy  
228 traditions from Bronze Age Yunnan, ~3,500 yBP southwards to Thailand by ~3,000 yBP (38,  
229 39). Subsequent agricultural intensification of rice production took place from ~2,500 to  
230 1,500 yBP and included evolution of irrigation systems in present-day Thailand (40).  
231 Consistent with these, ancient human DNA studies in Southeast Asia report two farmer-  
232 associated migration events from East Asia, one at least 4,000 years ago and a second before  
233 2,000 yBP (41, 42).

234 Our analysis also shows an ~5-10-fold  $N_e$  decrease in the Malay archipelago between  
235 ~3,000 and 2,500 yBP, and based on cross-coalescence analyses, divergence between  
236 mainland and Malay Archipelago rice occurred between ~3,000 to 1,500 years ago (75% of  
237 estimates in ~2,500 to 1,600 yBP) [Fig. 4; Supplementary Fig. 19]. Distinct island  
238 populations in the Malay Archipelago diverged at around a similar timeframe, in an interval  
239 from ~3,000 to 1,000 years ago (75% estimates fall between ~2,500 and 1,500 yBP). This  
240 period coincides with dispersal of Dong Son drums in the Malay Archipelago (~2,400 years  
241 ago) (38, 43), and suggests maritime dispersal of rice from a North Vietnam hub within the

242 Austronesian Trading Sphere, which stretched between Taiwan and the Malay Peninsula (44,  
243 45). Ancient DNA studies also suggest a wave of Austronesian human expansion into island  
244 Southeast Asia ~2,000 years ago (41), which agrees with our estimates of japonica movement  
245 into the area. Interestingly, upland temperate japonica in Japan appears to be an admixed  
246 population of local lowland temperate rice and upland tropical rice from the Malay  
247 Archipelago which may have moved northwards through Taiwan and perhaps the Ryukyu  
248 Islands ~1,200 yBP (46).

249

250 ***Relationships and dispersal of indica subpopulations.*** We reconstructed relationships  
251 between indica subpopulations with  $k = 2$  to 7. Divergence between Sino-Indian and  
252 Southeast Asian indica is present in all graph topologies beginning at  $k = 2$  (Supplementary  
253 Fig. 21). At  $k = 3$  we observe separation of mainland and island Southeast Asian  
254 subpopulations, while at  $k = 4$  we observe separation of Indian from Chinese landraces. With  
255  $k = 5$  and  $k = 7$  we note differentiation of mainland Southeast Asian landraces into  
256 subpopulations associated with Laos, Thailand and Cambodia (Fig. 2f). Interestingly, a  
257 subpopulation associated primarily with Cambodia, and another in Indonesia, share ancestry  
258 with the main Laos/Thailand Southeast Asian lineage as well as an early ancestral indica  
259 population. Increasing to  $k = 8$  also increases the number of admixture events in the model to  
260 four, which renders further exhaustive graph topology searches unfeasible.

261 Higher diversity of graph topologies in indica, likely due to weaker population  
262 structure and elevated gene flow (Supplementary Figs. 14 and 15), makes it difficult to  
263 reconstruct indica dispersal routes. Moreover, given the complexity in multiple reconstructed  
264 admixture graph topologies, we can only confidently date separation of Chinese and Indian  
265 indica, which is unaffected by admixture. Our analysis estimates this divergence at ~2,500  
266 and 1,100 yBP (75% of estimates between ~2,000 and 1,400 yBP)[Fig. 5; Supplementary Fig.

267 17]. Possible routes for indica dispersal from India to China could be the Silk Road or more  
268 direct passage to Southwest China across the Hengduan mountains. The timing agrees with  
269 written reports of the introduction of Buddhism from India to China at ~1,950 yBP (47), but  
270 is later than the earliest putative finds of indica rice in China (48). The close relationship  
271 between Indian and Chinese subpopulations is mirrored by higher proportions of irrigated  
272 varieties in both regions; in contrast, Southeast Asian varieties are more often rainfed (19).

273 Indica dispersal to Southeast Asia (e.g., Thailand and Cambodia) were either from  
274 India or China (Fig.5; Supplementary Fig. 22). From archaeobotanical studies, indica arrived  
275 in Central Thailand at ~1,800 years ago (40), at a time when Asian trade routes were well  
276 established (12). Late adoption of indica in Southeast Asia is hypothesized to be due to early  
277 availability of japonica in this region (12). There is no earlier archaeological evidence for  
278 indica cultivation in Southeast Asia, and hence it comes as a surprise that indica mainland  
279 subpopulations suffered dramatic population size reduction between ~5,000 and 3,500 yBP  
280 (Supplementary Fig. 23). It is even more puzzling that a bottleneck in indica subpopulation in  
281 Indonesia occurred between ~6,000 and 5,000 yBP, suggesting complex origins, perhaps  
282 partially from local wild ancestors or managed pre-domesticated varieties (Supplementary  
283 Fig. 22).

284

285 **Summary.** Rice domestication in the Yangtze Valley had an enormous impact on the peoples  
286 of East, Southeast and South Asia. In the first ~4,000 years of its history, Japonica rice  
287 cultivation was largely confined to China, and its dispersal and diversification did not occur  
288 until the global 4.2k cooling event. This abrupt climate change event, which was  
289 characterized by a global reduction in humidity and temperature, had widespread  
290 consequences: it is believed to have caused the breakdown of rice agriculture in East Asia  
291 (24, 31), turnover of cattle ancestry in the Near East (49), and the collapse of civilizations

292 from Mesopotamia (50) to China (51). We find from our genomic and paleoclimate  
293 modelling that the 4.2 k event coincides with the rise of temperate japonica and the dispersal  
294 of rice agriculture southwards into Southeast Asia. Moreover, indica began to be  
295 domesticated in South Asia at around this period, and spread later into China and Southeast  
296 Asia. Correlation between changing climate and rice distribution raises the possibility for a  
297 causal relationship, and indeed we find temperature is a key environmental factor patterning  
298 contemporary rice genomic diversity.

299         The ability to infer dispersal patterns of rice arises from the availability of extensive  
300 landrace populations, whole genome sequences and population genomic approaches, as well  
301 as environmental, archaeobotanical and paleoclimate data. Reconstructing the history of  
302 domesticated species provides insight into the evolutionary process, nature of human/plant  
303 co-evolutionary dynamics, and extrinsic landscape, environmental, and cultural factors that  
304 drive crop dispersal. Armed with knowledge of the pattern of rice dispersal and  
305 environmental features that influenced this migration, it may be possible to examine the  
306 evolutionary adaptations of rice as it spread to new environments, which could allow us to  
307 identify traits and genes to help future breeding efforts.

308

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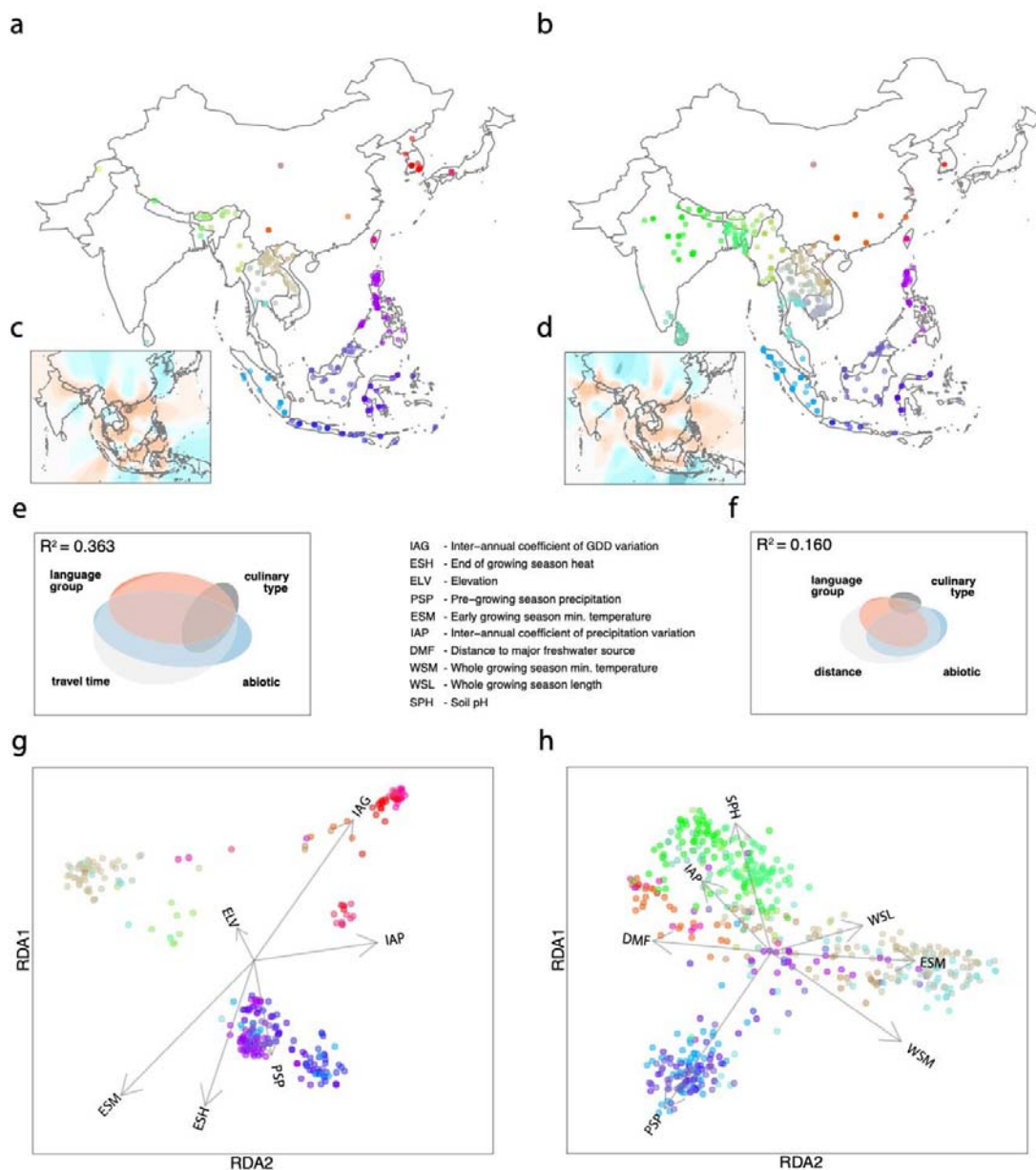


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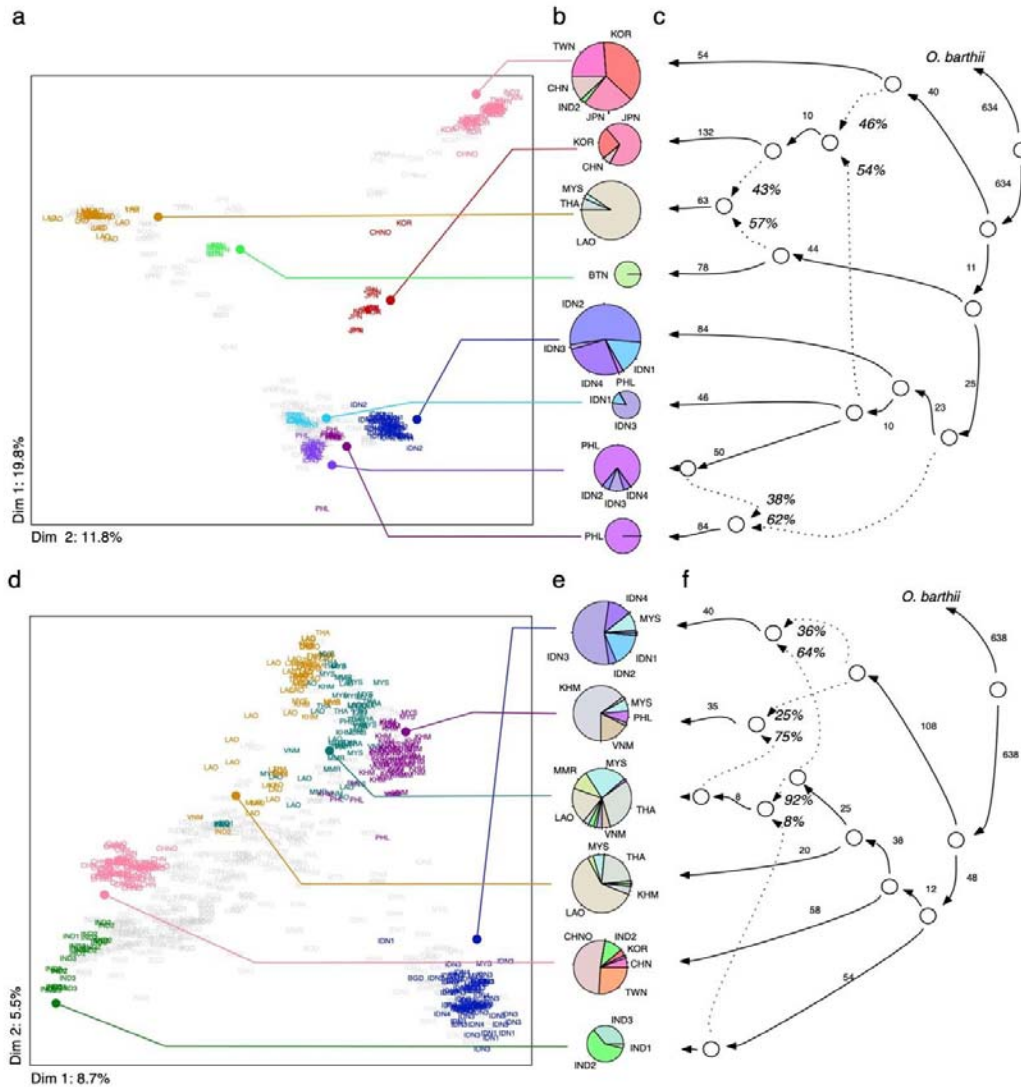
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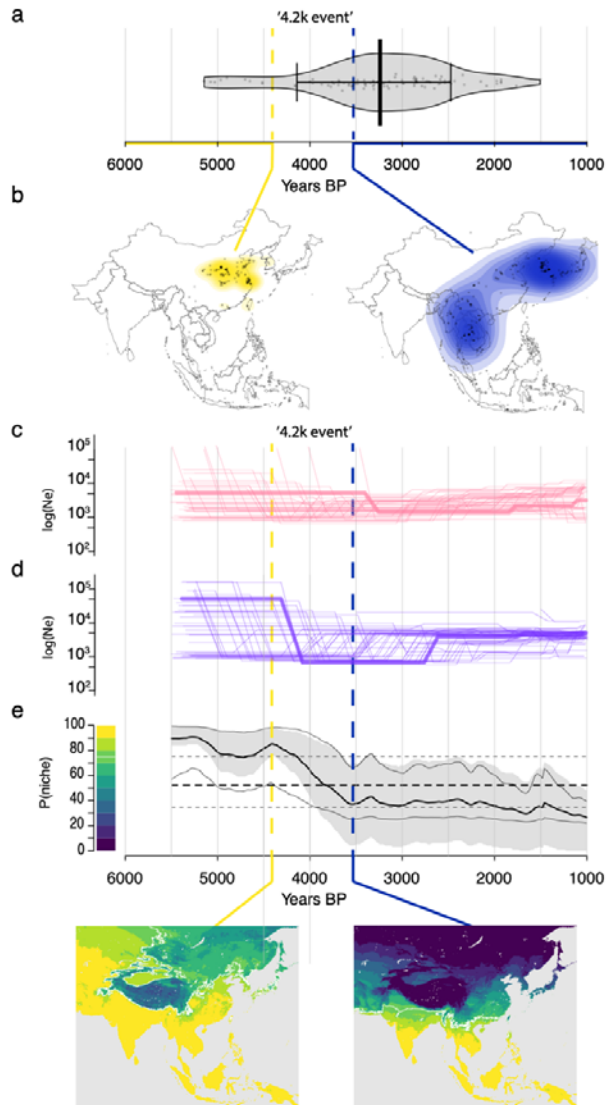
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487 assembled and processed the environmental data with input from JRL. JRL lead the spatial  
488 analyses with input from RMG. ESB and ERS carried out travel time analyses with input  
489 from JRL. JRL carried out RDA analyses. RMG carried out population structure, admixture  
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496 downloaded data are available in the supplementary materials. Code repositories are referred  
497 in the supplementary materials



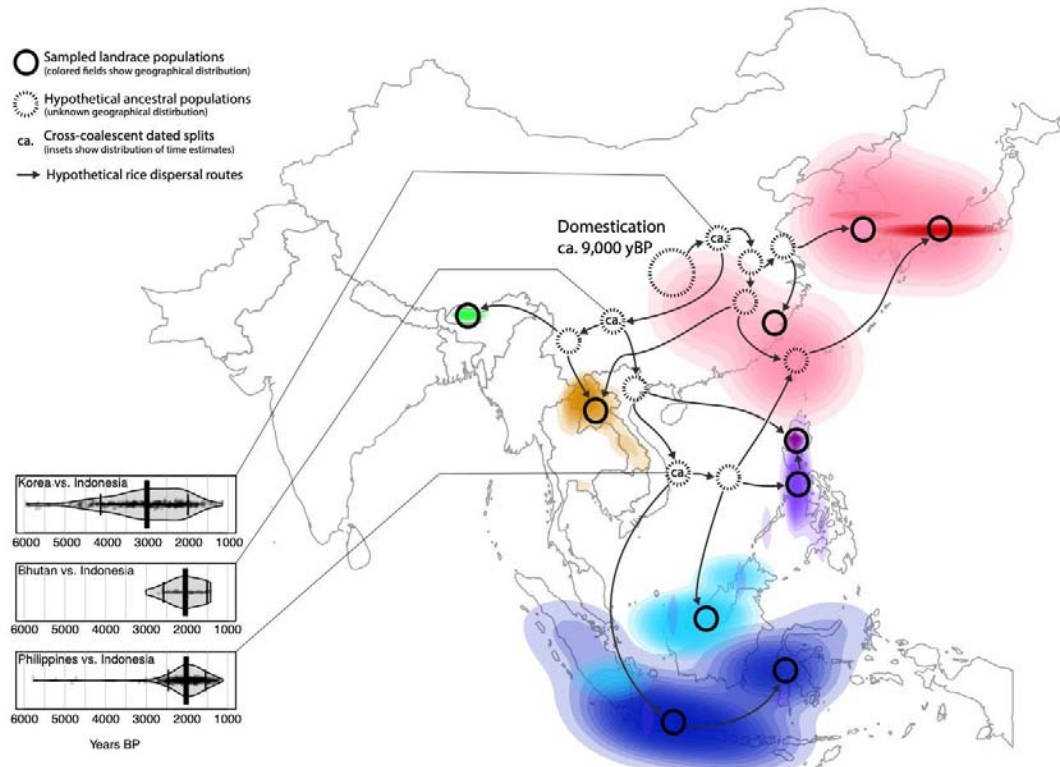
498  
 499 **Figure 1: Factors underlying geographic distribution of genomic diversity in japonica**  
 500 **and indica.** Maps of collection sites for (a) japonica and (b) indica landraces used in this  
 501 study. Colors represent regions of origin. (c) Japonica and (d) indica effective migration  
 502 surfaces representing migration barriers (orange) and channels (cyan). (e) Japonica and (f)  
 503 indica genomic diversity is best explained by a combination of four factors represented in  
 504 Euler plots: travel time (migration resistance) or geographic distance, abiotic variables  
 505 (temperature, moisture and soil characteristics), linguistic group, and culinary properties  
 506 (stickiness). Fields of squares represent total genomic variation, while elliptic shapes  
 507 represent genomic variation explained by particular factor. (g) Japonica and (h) indica  
 508 genotypes projected on the first two canonical axes of redundancy analysis. Arrows represent  
 509 environmental predictors (acronyms explained in the legend) that strongly correlate with a  
 510 maximal proportion of linear combinations of SNPs.



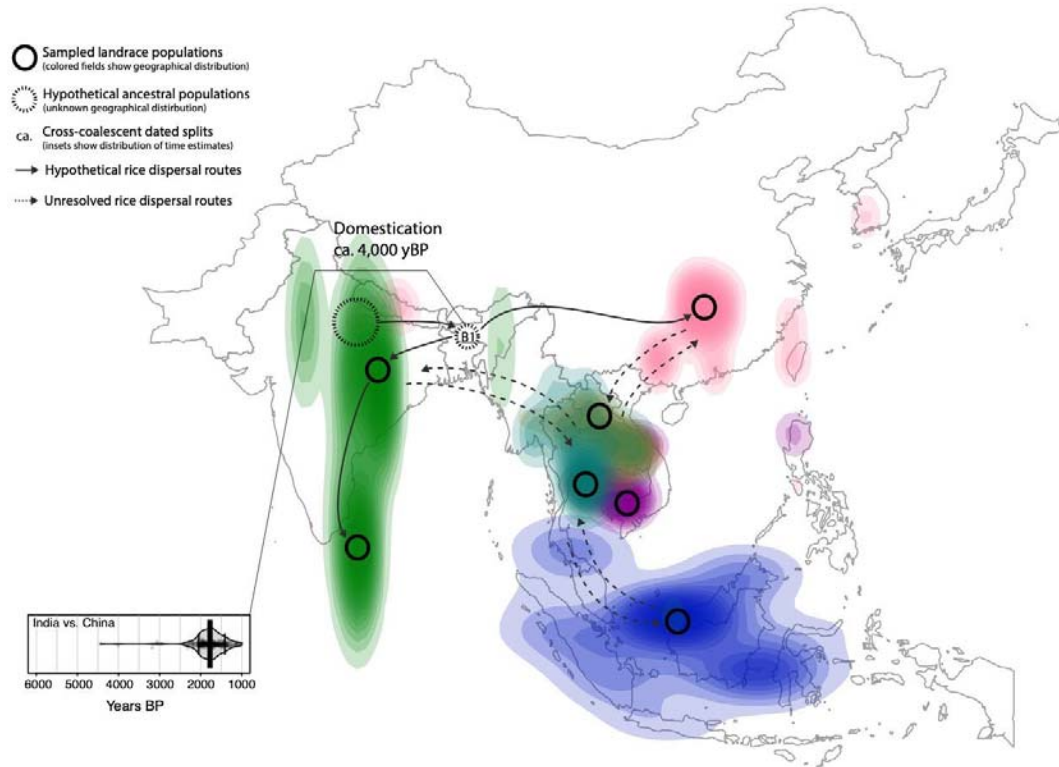
511  
 512 **Figure 2: Japonica and indica rice subpopulations.** (a) All japonica and (d) indica  
 513 landraces projected onto first two dimensions after multidimensional scaling of genomic  
 514 distances. (a) japonica genotypes were clustered using k-medoids ( $k = 9$  subpopulations) and  
 515 filtered using silhouette parameters, which resulted in  $K = 8$  discrete subpopulations (colored  
 516 labels). (d) indica genotypes were clustered using k-medoids ( $k = 7$  subpopulations) and  
 517 filtered resulting in  $K = 6$  discrete subpopulations (colored labels). Pie charts representing the  
 518 geographical composition of each discrete subpopulation of (b) japonica and (e) indica  
 519 subgroups. Chart diameter is proportional to the number of individuals in each subpopulation.  
 520 (c) Admixture graph for  $k = 9$ ,  $K = 8$  japonica subpopulations, rooted with *Oryza barthii* as  
 521 an outgroup. This graph represents topology consistent between models for all lower  $k$ 's. (f)  
 522 Best admixture graph for  $k = 7$ ,  $K = 6$  indica subpopulations, rooted with *O. barthii* as  
 523 an outgroup. Although this represents the best model, it is not consistent with other topologies at  
 524 lower  $k$ 's, likely due to complex history of indica. (c and f) Solid lines with arrowheads  
 525 represent uniform ancestries (attached numbers show scaled drift parameter  $f_2$ ), while dashed  
 526 lines represent mixed ancestries (% values indicate estimated proportion of ancestry).



527  
528 **Figure 3: Demographic, paleoenvironmental and archaeological context of temperate**  
529 **japonica rice emergence.** (a) The distribution of temperate-tropical split times estimated  
530 from cross-coalescence analysis carried out for 50 pairs of temperate and tropical individuals.  
531 (b) Maps indicating geographic locations and densities of archaeological sites with rice  
532 macro-remains. To the left: cumulative archaeobotanical evidence from 9,000-4,400 years  
533 BP, to the right: cumulative archaeobotanical evidence from 3,500-1,000 years BP. Effective  
534 population sizes over time in (c) tropical and (d) temperate japonica subpopulations. Thin  
535 lines represent demographic histories for 50 randomly sampled individuals, while bold lines  
536 represent joint models. (e) Probability of tropical rice being in the thermal niche (assuming  
537 requirement of 2900 growing degree days, at 10°C base) over time. The mean (thick black  
538 line) and the interquartile range, 25% to 75% (gray shaded area) of probability of being in the  
539 thermal niche. The thin black lines are the mean probabilities using the lower and upper  
540 confidence intervals of the temperature reconstruction. The two inset maps show the  
541 geographic distribution of niche probabilities; to the left: before climate cooling (4,400 years  
542 BP), to the right: after climate cooling (3,500 years BP).



543  
544 **Figure 4: Proposed dispersal map of japonica rice in Asia.** Map generated for japonica,  $K$   
545 = 8 discrete subpopulations. The geographic distributions of subpopulations were represented  
546 as colored, two-dimensional Kernel density fields. Bold circles represent leaves in the  
547 admixture graphs and are mapped close to the centers of subpopulation distributions. Dashed  
548 circles represent hypothetical ancestral subpopulations inferred from splits in best-matching  
549 admixture graphs; their precise geographic placement is uncertain. The distribution of split  
550 times between non-admixed subpopulations was created from cross-coalescence estimates  
551 summarized over all  $k$  levels and presented as violin plots. Arrows indicate hypothetical  
552 routes of dispersal.  
553



554  
555 **Figure 5: Proposed dispersal map of indica rice in Asia.** Map generated for indica,  $K = 6$   
556 discrete subpopulations. The geographic distributions of subpopulations were represented as  
557 colored, two-dimensional Kernel density fields. Bold circles represent leaves in the admixture  
558 graphs and are mapped close to the centers of subpopulation distributions. Dashed circle  
559 represents consistent split; its geographic position is uncertain. The distribution of split times  
560 between non-admixed subpopulations was created from cross-coalescence estimates  
561 summarized over all  $k$  levels and presented as violin plots. Solid arrows indicate hypothetical  
562 routes of dispersal, while dotted arrows indicate possible routes that remain unresolved from  
563 admixture graphs.  
564