

¹ **Projected warming will exceed the long-term
2 thermal limits of rice cultivation**

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⁵ Rice is a staple food for a significant portion of the global population, particularly
⁶ in Asia, where over one billion people rely on it for daily subsistence. Understanding
⁷ rice's historical thermal limits is imperative for predicting how it will respond
⁸ to future shifts in global climate. Here, we integrate diverse records of contempor-
⁹ ary rice cultivation extent, archaeological data spanning rice's long-term history
¹⁰ since its earliest cultivation, and temperature projections for the past, present, and
¹¹ future to assess how warm temperatures have influenced and may continue to in-
¹² fluence rice's geographical distribution, productivity, and the adaptive strategies
¹³ employed by human societies to sustain this important crop. Our findings indicate
¹⁴ a consistent pattern over the past 10,000 years: domesticated Asian rice varieties
¹⁵ have seldom thrived in regions where the mean annual temperature exceeds 28°C
¹⁶ or warm-season maximum temperature exceeds 33°C. By the end of this century,
¹⁷ climate projections estimate that the land area exceeding this thermal threshold
¹⁸ in Asia's major rice-producing nations could expand by ten to thirty times. Our
¹⁹ findings have significant implications for global food security, as regions heavily
²⁰ reliant on rice cultivation may encounter unprecedented challenges in staple crop
²¹ production under projected warming.

²² **Introduction**

²³ Members of the grass family (*Poaceae*), which include staples like rice, maize, wheat, and barley,
²⁴ provide a majority of the global human caloric intake. However, these crops face a looming
²⁵ threat: the rate of anticipated climate change eclipses that of historical niche adaptations in
²⁶ grasses. By 2070, temperatures are projected to rise at a rate 5,000 times faster than what most
²⁷ varieties of *Poaceae* have experienced throughout their evolution (1). Historically, *Poaceae*
²⁸ experienced temperature shifts ranging from 1-8°C per million years, yet future projections
²⁹ anticipate changes as swift as 0.02°C annually (1). Among these vital crops, domesticated
³⁰ Asian rice (*Oryza sativa*) serves as a primary food source for over half the global population.
³¹ More than 90% of the world's rice is grown in Asia, and one fifth of the world's population—
³² more than 1 billion people—depend on rice cultivation for their livelihood.

³³ *Oryza sativa* has a deep history of cultivation and domestication beginning at least 7,000 years
³⁴ ago. Over the course of its domestication and subsequent spread, Asian rice has made several
³⁵ adaptations to changes in climate and has expanded well beyond its original range of cultivation.
³⁶ Yet despite this expansion, rice exhibits a high degree of niche conservatism compared to its
³⁷ wild progenitor (2). Although human selection—and, in recent decades, scientific breeding—
³⁸ can accelerate the development of new traits far more rapidly than the thousands of years
³⁹ wild plant species often require to adapt to new climatic conditions, these advances have
⁴⁰ not successfully expanded rice's thermal tolerance. Notably, as global temperatures rise, rice
⁴¹ farming has shifted from warmer areas to cooler ones rather than adapting to increased heat
⁴² (3). Apparent increases in rice's harvested area over recent decades largely reflect advances
⁴³ in farming technology rather than an expansion of its climatic tolerance. For example, rice
⁴⁴ cultivation in the People's Republic of China has gradually extended northward from Central
⁴⁵ China into cooler regions, a shift that, combined with intensified irrigation in the country's
⁴⁶ hottest zones, has modestly increased rice yields and masked the adverse effects of rising
⁴⁷ temperatures (3, 4).

⁴⁸ While some areas may benefit from warming temperatures (5), this trend is not universal.
⁴⁹ In many regions, smallholder farmers rely on rice cultivation as their main source of income.
⁵⁰ Indeed, mismatches between rice-harvested areas and overall environmental suitability suggest
⁵¹ that subsistence farming in low-income regions has already stretched rice cultivation to its
⁵² climatic boundaries (6). To put this into perspective, projections indicate that 15-40% of
⁵³ India's current rainfed rice cultivation zones will experience a reduction in climatic suitability
⁵⁴ by 2050 (7). Since 1974, 88% of rice-harvested areas show significant shifts in yield due to
⁵⁵ climatic factors, with climate change reducing consumable food calories from rice by 0.4%
⁵⁶ compared to historical climate conditions (8).

⁵⁷ However, these findings are constrained by the current distributions of rice cultivation and
⁵⁸ prevailing temperature. Few regions of the world today experience the elevated temperatures
⁵⁹ projected in many future climate-change scenarios. This makes it challenging to distinguish
⁶⁰ between inherent thermal limits for rice growth and the practical geographic constraints set by
⁶¹ recent temperature distributions (9, 10). Global temperatures have already exceeded known

62 temperatures over the past 2,000 years and we are living in the warmest centuries of at least
63 the past 100,000 years (11). Contemporary studies of the thermal niche of rice have provided
64 crucial insights into specific regions and production systems, but those with a global scope
65 have often been reliant on limited datasets that may not capture the full diversity of rice dis-
66 tributions. Challenges include the potential underrepresentation of temperate rice varieties in
67 China, uneven sampling of rainfed or upland varieties, and the geographic scope of the studies,
68 which do not always encompass broad thermal ranges (4, 7, 9). Archaeological studies have
69 been instrumental in documenting the timing and geographic trajectory of rice's domestication
70 and spread across Asia (12–16). Recent integration of archaeological rice records with spatial
71 paleoclimate reconstructions has revealed that climate change played a major role in the early
72 diversification and spread of rice (17, 18), but the implications for rice's future adaptability
73 have yet to be fully explored.

74 Here, we integrate multiple lines of evidence from the extensive history of rice cultivation
75 to characterize the thermal range of rice and gauge its potential adaptability to impending
76 climate changes. By integrating diverse records of the current extent of rice cultivation with
77 archaeological data on the distribution of rice since its earliest cultivation and domestication,
78 we aim to establish *O. sativa*'s thermal limits—the temperature conditions under which rice
79 has been consistently cultivated throughout its domestication history. We estimate long-term
80 thermal limits associated with rice cultivation by comparing contemporary estimates of rice
81 extent with well-dated archaeological rice occurrences, and complement this with genetic anal-
82 yses of adaptation potential in rice subspecies. We focus specifically on Asian rice (*O. sativa*)
83 rather than African rice (*O. glaberrima*), as Asian rice comprises the vast majority of global
84 production and consumption and has the extensive archaeological record necessary for long-
85 term analysis. We use these results to assess the impact of projected climate changes by the
86 end of this century. Together, our analyses confirm that imminent changes in climate con-
87 ditions may force large regions of today's primary rice producers to confront mean annual,
88 seasonal, and monthly peak temperatures unprecedented in the history of rice cultivation and
89 domestication.

90 Results

91 We assess thermal limits on rice growth by comparing contemporary rice extents estimated
92 from satellite imagery, agricultural censuses, and herbarium collections to indicators of annual
93 and seasonal temperature (Figure 1). Our analysis combines present-day rice extent data
94 from diverse sources: satellite-based assessments of paddy rice extent in Asia (19), hybrid
95 satellite/census evaluations of global paddy rice cropping areas around the year 2000 (20),
96 and global point occurrences derived from herbarium records and germplasm accessions (22).
97 These datasets span a range of spatial scales, time periods, production systems (e.g. irrigated
98 vs. rainfed), and data collection methods with complementary biases, allowing us to test the
99 robustness of these thermal limits across methodologically independent data sources. We

100 supplement this empirical work with reviews of rice's response to warm temperatures from
 101 prior field and lab-based agronomic studies.

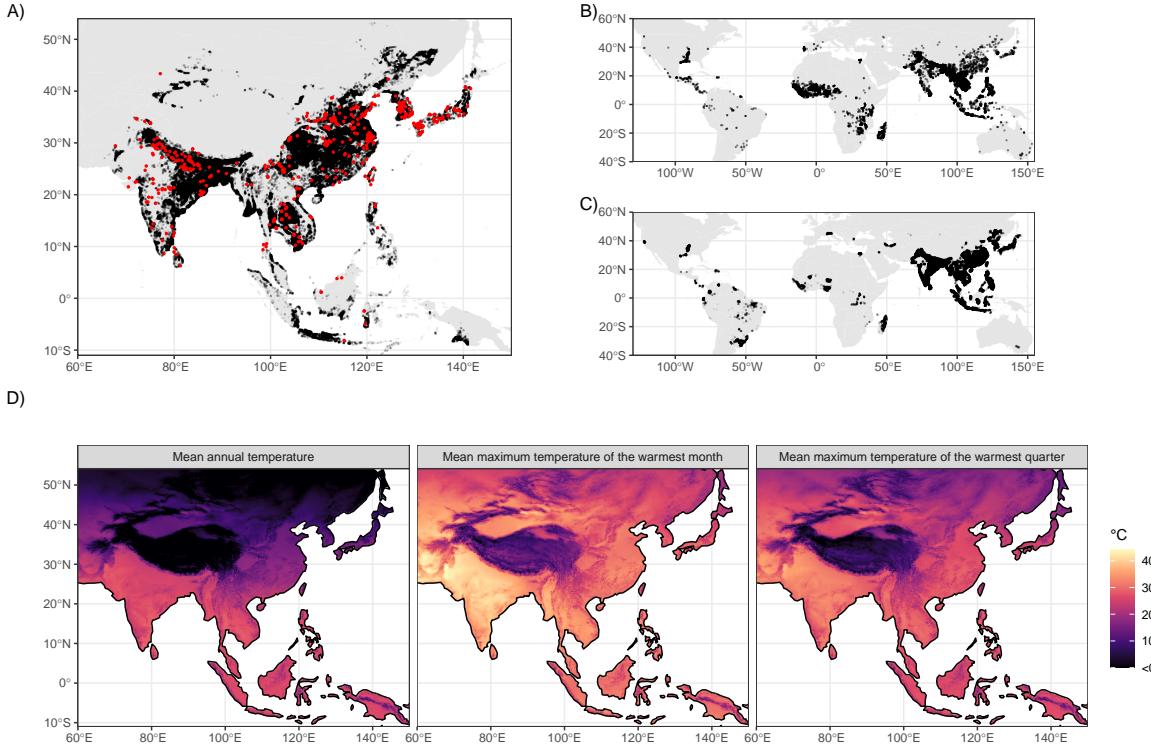


Figure 1: Observed rice extent data and thermal predictors. A) Map of lowland rice extent in Asia from the International Rice Research Institute based on estimates from MODIS satellite imagery (19) (black) overlain by archaeological sites with evidence for rice cultivation (red). B) Point based rice occurrences from global herbarium records and genetic accessions. C) Satellite-based estimates of rice cropped area in the year 2000 from (20). D) Maps of mean annual temperature, mean maximum daily temperature of the warmest month, and mean maximum daily temperature of the warmest quarter from CHELSA V2.1 averages for 1981-2010 (23–25).

102 We define the “thermal limits” of rice cultivation as the 95% central range of three tempera-
 103 ture indicators at all sampled rice occurrence locations in a given dataset—the temperature
 104 thresholds beyond which the likelihood of rice cultivation significantly decreases due to a com-
 105 bination of physiological, cultural, and economic factors. This empirical approach emphasizes
 106 the long-term feasibility of crop cultivation rather than short-term variations in yield or har-
 107 vested area. By focusing on these broader climatic measures, we can integrate a wider array

108 of data sources from the past and present to reveal the upper temperature thresholds of rice
109 cultivation over time.

110 Our approach offers a parsimonious tool for estimating future crop suitability (26, 27) that
111 complements process-based crop models. While such models can extrapolate yield responses to
112 climate change, they are sensitive to assumptions about meteorological inputs, agronomic and
113 physiological parameters, and cultural practices like planting dates and varietal preferences
114 over the long term (28–32). Translating these localized projections to global scales introduces
115 additional challenges, as does calibrating and validating their outputs using limited and incon-
116 sistent yield data from the recent or more distant past. Ultimately, a better understanding of
117 baseline thermal limits and their uncertainty through time and space can contribute to the de-
118velopment of future process-based models, many of which incorporate temperature thresholds
119 for pivotal crop development phases.

120 We focus primarily on temperature rather than precipitation or soil moisture, as water avail-
121ability can be more readily controlled through human interventions such as irrigation and
122 paddy field construction. These adaptations have allowed rice cultivation to expand beyond
123 its original aquatic and semi-aquatic environments. In contrast, adapting to new thermal
124 conditions is more challenging and often requires changes in planting dates or crop varieties,
125 which have their own limitations, particularly in higher latitudes where daylight variations
126 restrict growing seasons.

127 **Contemporary rice extents are constrained by high temperatures**

128 Contemporary rice extents fall within a relatively restricted thermal range. We use mean
129 annual temperature (MAT), mean maximum daily temperature of the warmest quarter
130 (TWARM), and mean maximum daily temperature of the warmest month (TMAX) to
131 estimate upper boundary temperatures for contemporary rice occurrences. The vast majority
132 of contemporary rice is grown in regions with MAT below 28.2°C, TWARM of 32.7°C, and
133 TMAX of 40.4°C (Figure [2](#)). Although we primarily report results from the satellite-based
134 estimates of lowland rice extent over Asia produced by the International Rice Research
135 Institute ([19](#)) due to its favorable balance of spatial resolution and extent, results from other
136 rice extent datasets with variable spatial extent, resolution, and time span are consistent
137 with these findings (Supplementary Table [S1](#)). There is much more variability across data
138 sources in lower temperature thresholds—reflecting the greater adaptability of rice to colder
139 temperatures through breeding, management, and growing season—than upper temperature
140 thresholds.

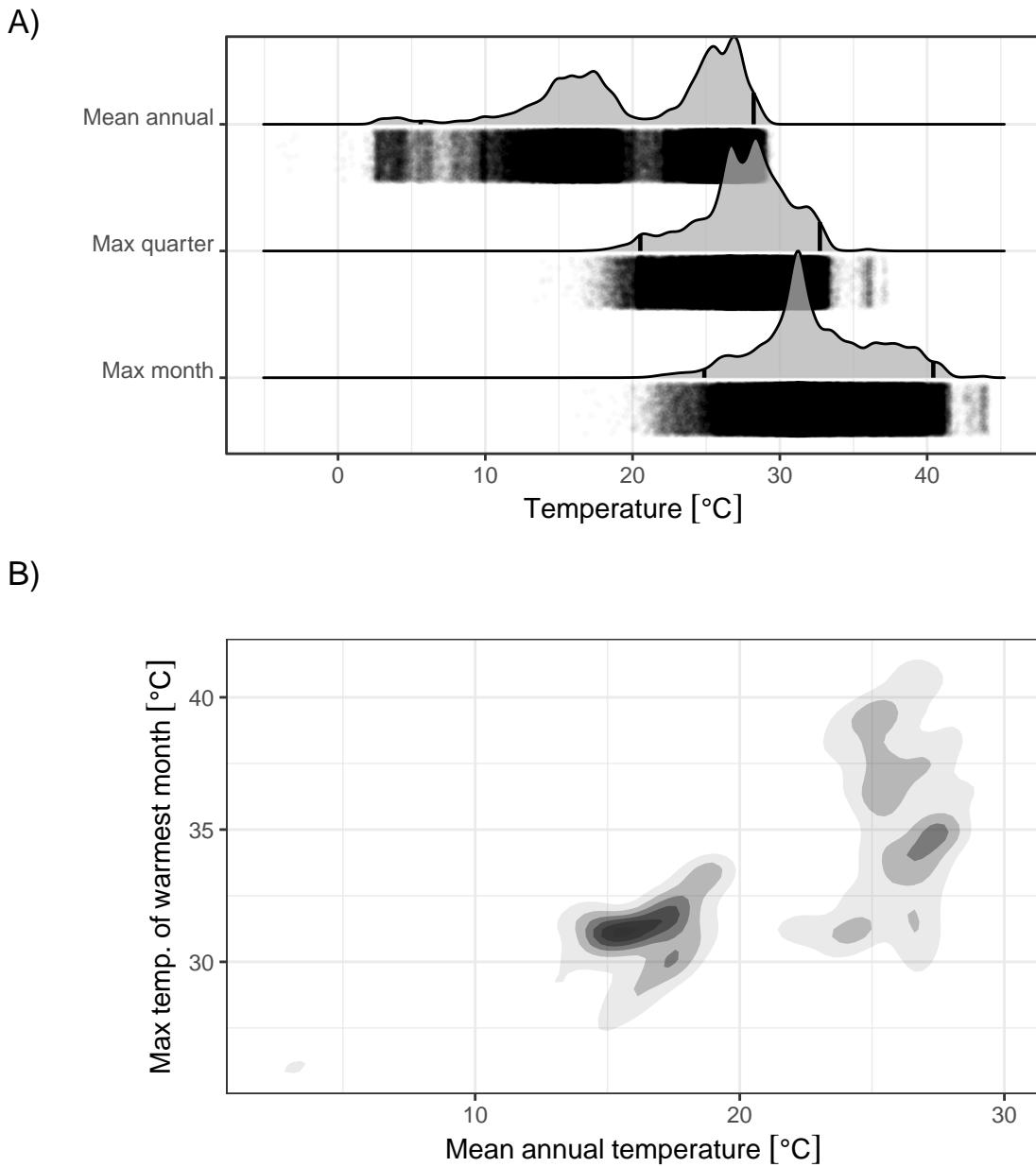


Figure 2: Kernel density estimates of temperature distributions over rice growing landscapes in Asia. A) One-dimensional kernel density estimates of mean annual temperature and mean maximum daily temperature of the warmest month in grid cells with lowland rice crops, based on data from the International Rice Research Institute (fig. 1). Vertical black lines indicate the 95% central range of the temperature values, and transparent black points indicate the raw occurrence data used in the calculation of the kernel density estimates. B) Two dimensional kernel density estimates for the same variables as in A.

141 These empirical thresholds are consistent with physiological parameters inferred from field-
142 scale agronomic studies and expert knowledge, which estimate that the optimum temperature
143 range for reproductive yield in rice is 23°C-26°C, biomass and pollen viability declines when
144 maximum temperatures exceed 33°C, and crop viability reaches zero at approximately 40°C
145 when photosynthesis begins to shut down in C3 plants like rice (33). In other words, rice
146 today is rarely grown in regions where the mean annual temperature exceeds its optimum
147 temperature for reproduction, warm-season maximum temperatures exceed its optimum for
148 pollen viability, and summer heat extremes will reliably stop photosynthesis.

149 These broad climate indices, while not capturing all nuances of local growing conditions, serve
150 as useful heuristics for identifying regions prone to thermal stress. This approach provides a
151 complementary perspective to typical empirical crop models, which often use fixed monthly
152 or seasonal predictors tied to the timing of the growing season. These predictors depend on
153 planting dates, which are themselves cultural adaptations to past and present climate. As
154 planting times and growing seasons shift with climate change, statistical analyses based solely
155 on “growing season” temperatures may become less reliable for long-term historical comparison.
156 Our approach provides a stable benchmark for integrating archaeological and contemporary
157 data across different time periods and cultivation practices, helping identify where adaptations
158 in growing seasons, crop types, genetics, or irrigation practices may become necessary.

159 **High-temperature constraints are consistent across 9,000 years of rice cultivation**

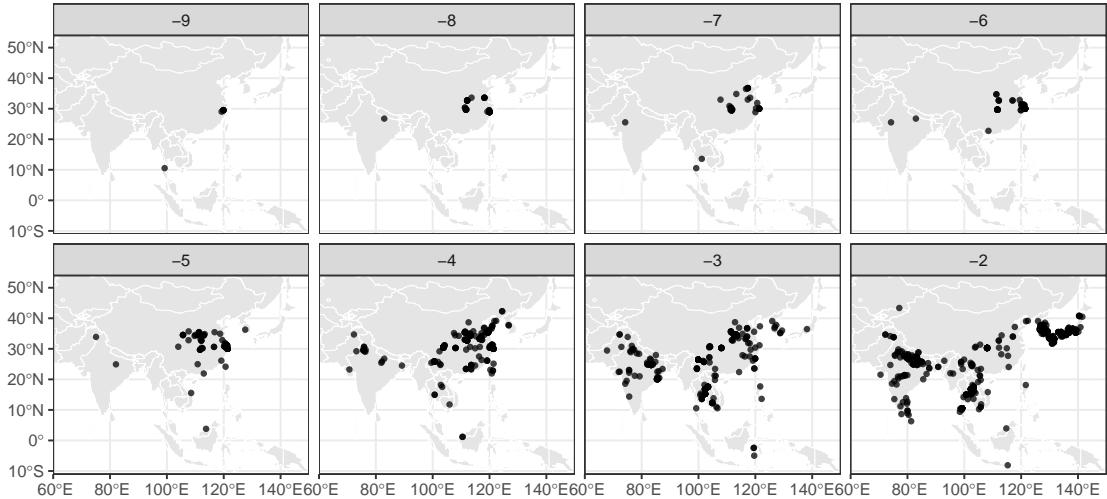
160 Although upper temperature limits on rice growth estimated from contemporary crop oc-
161 currences are consistent with previous agronomic studies, it is not yet clear how well these
162 thresholds will predict crop responses to future temperature changes. For example, there are
163 few places today that experience mean annual temperatures beyond 28°C (Supplementary Fig-
164 ure S1), and contemporary correlations between mean annual temperatures and monthly or
165 seasonal extremes may not hold in a changing climate. The archaeological record of rice culti-
166 vation in Asia, including direct dates of botanical remains and contextual dating of concurrent
167 archaeological sites, provides a unique opportunity to assess the robustness of these tempera-
168 ture limits over the long term. During the mid Holocene ca 8000-4000 calibrated years BP (cal.
169 BP), warm-season temperatures were generally warmer than present, reflecting increased sum-
170 mertime insolation in the Northern Hemisphere due to shifts in Earth’s orbit and consequent
171 feedbacks in the global climate system (34). Although not an exact analogue for projected
172 future warming caused by greenhouse gas emissions, this period provides a baseline for rice’s
173 response to shifting climates during the critical period of its domestication and dispersal.

174 *O. sativa* has been domesticated a number of times in prehistory. Archaeological data shows
175 that wild forms of rice were distributed as far north as northern China in the early Holocene
176 (ca 9000 cal. BP) and gathered by foraging populations (35). Tropical varieties of *O. sativa*
177 *japonica* were first cultivated in the middle and lower Yangtze and Yellow River valleys in
178 China by at least 7000 cal. BP (36–38) (Figure 3 A), where they began to exhibit traits
179 of domestication (e.g. the development of a non-shattering rachis) by roughly 5000 cal. BP

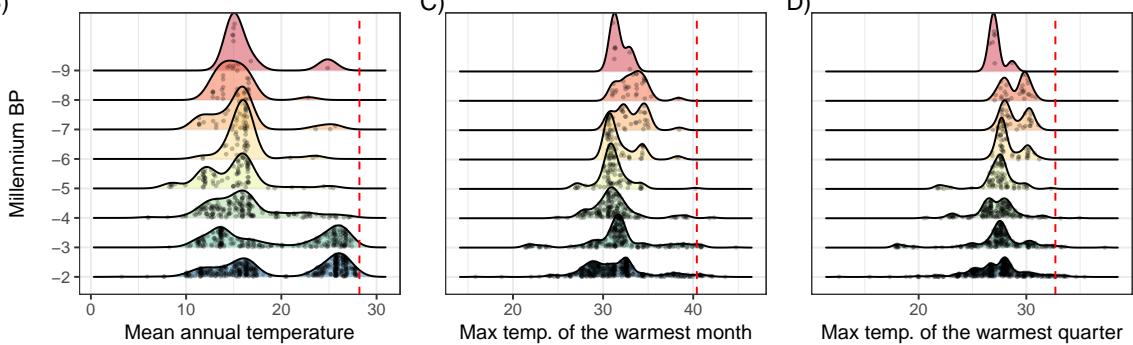
¹⁸⁰ (^{12, 39}). *Oryza sativa indica* rices on the other hand were likely domesticated in South Asia
¹⁸¹ sometime around 4000 cal. BP (^{40, 41}), after which it spread throughout southeast Asia and
¹⁸² China (Figure 3 A). There is substantially less archaeobotanical data, however, that speaks
¹⁸³ to the cultivation and subsequent domestication of this subspecies (⁴¹). This period of initial
¹⁸⁴ cultivation and domestication corresponds to the warmer mid-Holocene thermal maximum.

¹⁸⁵ Between roughly 5000-4000 BP, rice spread both north- and eastward in China (^{42, 43}) and
¹⁸⁶ westward onto the Chengdu Plain (⁴⁴) and highlands of Southwest China (^{45, 46}) (Figure 3
¹⁸⁷ A). Genetic and paleoclimate modeling have suggested that regional cooling around 4200 BP
¹⁸⁸ played an important role in this spread resulting in strong pressure for tropical *O. japonica* to
¹⁸⁹ develop temperate adaptations (¹⁸). Estimated divergence time for tropical and temperate *O.*
¹⁹⁰ *japonica* is indeed estimated at around 4100 BP (¹⁸). Following the development of temperate
¹⁹¹ *O. japonica* varieties, rice spread to both Korea (^{47, 48}) and Japan (¹⁴) (Figure 3 A). At the
¹⁹² same time, it appears that the area that tropical varieties of *O. japonica* were able to occupy
¹⁹³ shifted southwards to southern China (^{49, 50}) and southeast Asia (^{51–53}) (Figure 3 A), largely
¹⁹⁴ representing the dispersal of existing tropical varieties rather than novel adaptations to new
¹⁹⁵ thermal extremes. Indeed between 4000-3000 BP, rice farming spread into Thailand (⁵³), Laos,
¹⁹⁶ Bhutan, and then via maritime routes to Taiwan, the Philippines, Malaysia, and Indonesia
¹⁹⁷ (¹⁸) (Figure 3 A). A clear split in the distribution of rice with regards to temperature is evident
¹⁹⁸ following 4000 BP and we see a clear split into two populations: temperate varieties which
¹⁹⁹ occupy a mean annual temperature niche between roughly 8-18°C and tropical varieties which
²⁰⁰ occupy a niche between 22-27°C (Figure 3 B).

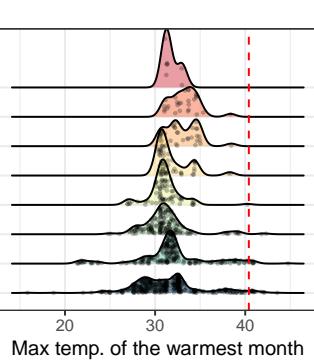
A)



B)



C)



D)

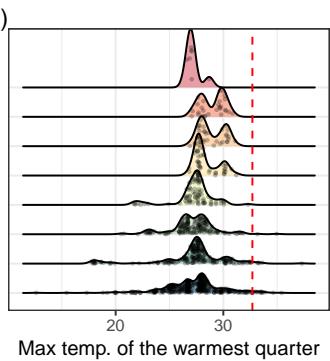


Figure 3: Archaeological remains of rice and corresponding temperature distributions throughout the Holocene. A.) Archaeological records of rice distribution over time. See Materials and Methods for archaeological data sources. Time units are thousands of years before present (1950 CE). B.) Kernel density estimates of the thermal distribution by millennium, with raw data points indicated in black and contemporary rice thermal limits in red. Rice occurrence data were derived from sources listed in the Materials and Methods. Temperature data are derived from CHELSA-TraCE21k V1.0 (Karger et al. 2023).

201 These repeated instances of rice's diversification and shifting ranges throughout its history
 202 primarily reflect genetic and cultural adaptations to cooler temperatures and shorter growing
 203 seasons. In contrast, movements into warmer regions generally involved range shifts by varieties

already suited to such conditions rather than novel adaptations. Across these shifts, rice's upper temperature limits have remained consistent. Out of 803 archaeological sites with rice remains, none have experienced MAT of greater than 28.2°C during the Holocene (Figure 3 B), in spite of warmer summer temperatures overall. Only a handful of sites experienced a TMAX of greater than 40.4°C (Figure 3 C), primarily in arid regions of northern India and Pakistan where archaeological dating is less certain and long-distance trade rather than local cultivation is more plausible. Regardless, the archaeological record of rice cultivation is consistent with the thermal limits estimated from contemporary data, and these results are robust to uncertainty in the dating of these archaeological remains and spatial biases in archaeological site preservation and recovery Supplementary Figure S2, as well as across different climate reconstructions with varying degrees of mid-Holocene warmth (Supplementary Figures S3 - S4).

Currently cultivated rice areas are projected to exceed these thermal limits over the next century

Although rice has spread to warmer environments since its domestication, the magnitude of this change over the past 9,000 years is small relative to anticipated changes by the end of this century. Multiple climate-model projections and future socioeconomic and emissions scenarios show large shifts in annual and warm-season temperatures in regions where rice is currently cultivated intensively, particularly in South, Southeast and Island Southeast Asia (Figure 4). Mean annual temperature will exceed 28°C for a substantial area of current occurrences in the years 2070-2100. Large parts of South, Southeast, and Island SE Asia will experience temperature conditions for which there is no analogue in the history of the cultivation and domestication of rice over at least the past 9,000 years (Figure 5, Supplementary Figure S5, Supplementary Tables 2-4). Although the extent of these projected shifts vary among climate models and emissions scenarios, the overall direction of this change is consistent (Supplementary Figures 6-8).

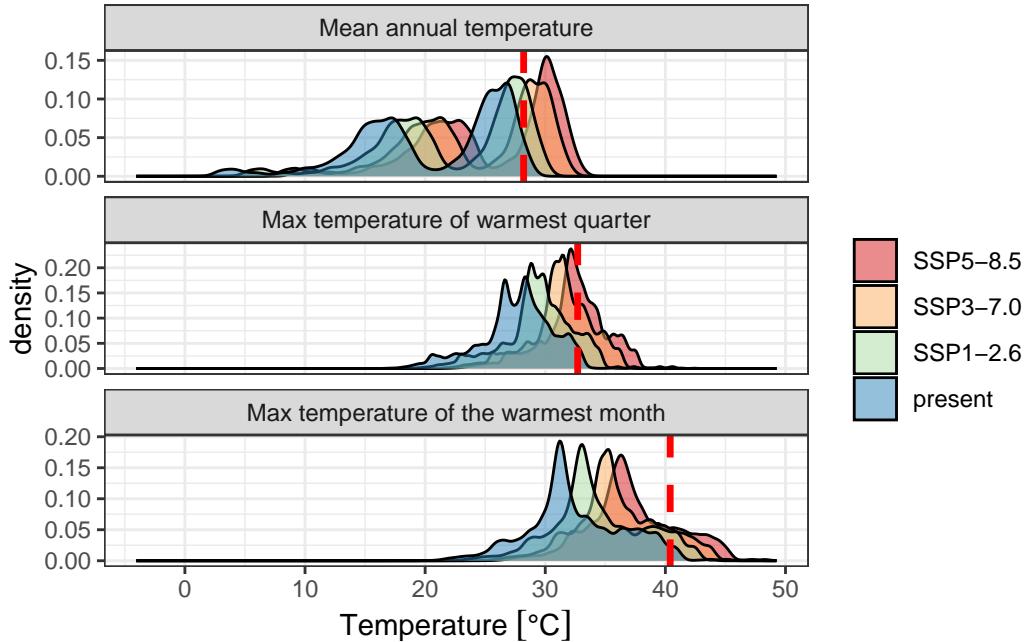


Figure 4: Predicted changes in biologically relevant temperature indicators over currently cultivated rice areas in Asia, relative to contemporary thermal thresholds (red dashed line). Shared socioeconomic pathways (SSPs) are scenarios of projected socioeconomic global changes used to derive greenhouse gas emission scenarios. SSP1 is a best case scenario where global cooperation and social and technological innovation are able to reduce greenhouse gas emissions. SSP3 is a middle-range scenario characterized by high population growth and global competition that hinders social and technological innovation. SSP5 is a worst-case scenario characterized by rapid economic growth and carbon emissions. All temperature estimates are derived from CMIP6 climate model ensemble mean estimates for the years 2071-2100, selected based on the ISIMIP3b protocol and downscaled by the CHELSA-V2.1 algorithm.

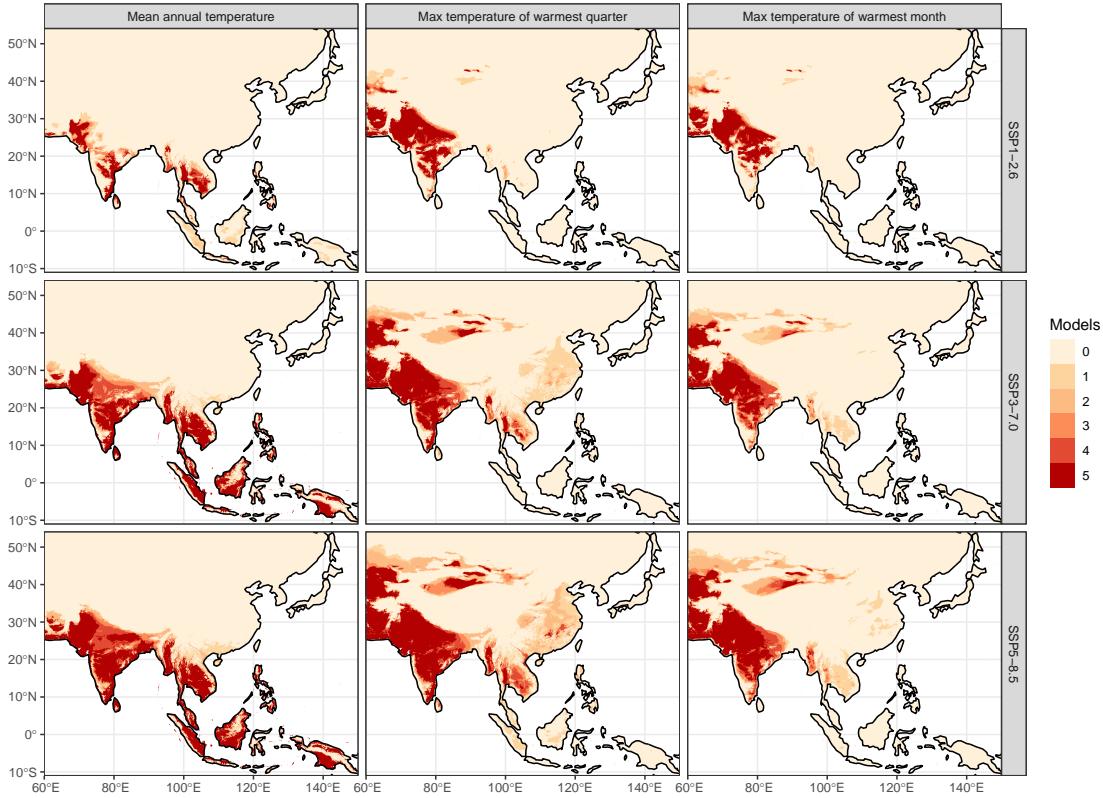


Figure 5: Land areas projected to exceed each temperature threshold by 2071-2100 from CMIP6 simulations, based on the ISIMIP3b protocol and downscaled by CHELSA-V2.1. Color intensity corresponds to the count of climate model ensemble members surpassing the given threshold at each grid cell.

While our spatial analyses reveal clear thermal boundaries in rice distributions, understanding the potential genetic capacity for adaptation provides added context to projected climate shifts. A genetic offset analysis assessing the potential maladaptation of *O. sativa* subspecies to future climate scenarios, correlating contemporary genetic variation with annual and seasonal temperature, indicates both subspecies are at a significantly higher risk of maladaptation under projected temperature regimes of the coming century (Figure 6). Genetic offset analysis estimates how climatically mismatched rice populations may become under future warming by calculating the multidimensional distance between current allele frequencies and those predicted to be adaptive under projected climate conditions. The analysis produces unitless distance values where larger numbers indicate populations whose current genetic makeup is more divergent from what would be optimal for future climates, suggesting higher vulnerability to climate-driven fitness declines. These distance metrics synthesize information across multiple climate-responsive genetic variants to forecast which populations face the greatest

adaptive challenges under temperature increases. When projecting to future climates across Asia, optimal growing locations for rice landraces (traditional crop varieties maintained by farmers and adapted to local conditions) of both subspecies show a greater skew away from the equator in the likeliest emissions scenarios (Supplemental Figure S9). For both *japonica* and *indica*, the degree of maladaptation increases with worsening emissions scenarios, but is generally greater than at any point experienced throughout the Holocene.

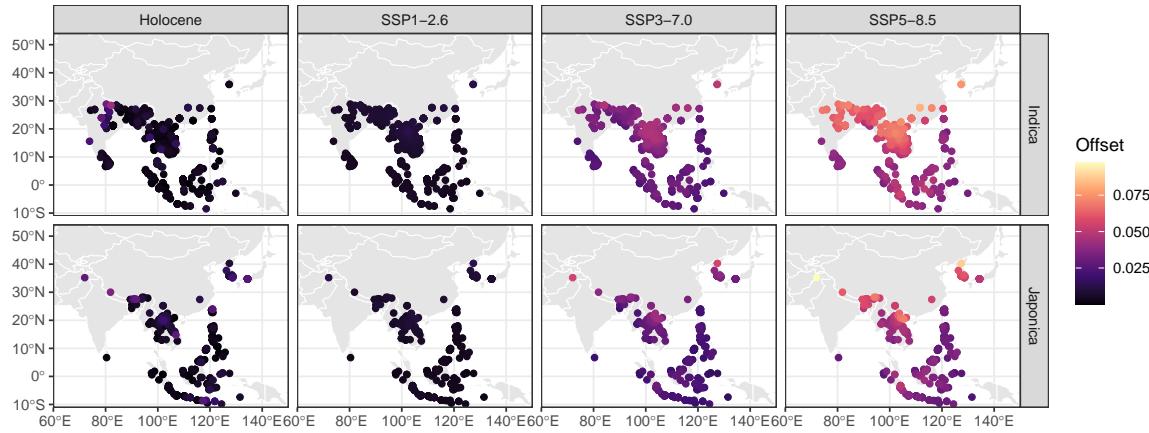


Figure 6: Estimated genetic offsets of sampled rice landraces for past and future scenarios relative to current baseline. Each point represents a distinct population sampled for genetic analysis. Higher genetic offsets indicate a greater degree of maladaptation to the particular temperature regime. The “past” scenario reflects the highest modeled temperature at each location over the past 12,000 years. The future scenarios are averaged across all climate models in the ensemble.

Discussion

There is a clear upper limit of mean annual temperature over 28°C and warm-season maximum temperature over 33°C for rice that has rarely been crossed since its domestication. Forward looking climate projections show that areas that currently house some of the highest densities of rice cultivation on Earth will surpass this limit by the end of this century (Figure 5). Today, 675 million people live in Southeast Asia and 1.9 billion people live in South Asia. By the end of this century, it is estimated that at least this number of people will live in the region that will surpass these thresholds. Today, mean annual temperatures greater than 28°C are distributed across only a very small area of the planet which includes only a small portion

257 of the gulf desert and the Sahara (54). Beyond the impact of this heat on rice cultivation,
258 this study raises serious concerns about the viability of other temperature-sensitive crops in
259 regions which will be impacted. The predictions for these areas of the world are out of the
260 historic sample of distribution for rice and have no analogue in the present climate.

261 While some regions, including parts of northern China and southern Russia, may become cli-
262 matically suitable for rice cultivation and could even see yield gains as temperatures approach
263 current optima (5, e.g. 55, 56), such potential benefits will be highly localized. Even if ag-
264 gregate yields were to stabilize or increase in some growing regions, they would not offset
265 the immediate livelihood and food security risks faced in regions projected to exceed current
266 thermal limits. Shifting rice production north to regions currently too cold to grow rice will
267 be insufficient to buffer these projected impacts. Beyond the potential for unanticipated social
268 and environmental impacts (57), this response would do little for the billions of people who
269 live in these hotter regions whose lives and livelihoods are directly threatened. This response
270 would also ignore that rice cultivation requires extensive niche construction through the con-
271 struction of paddies and that abiotic factors such as sufficient water for irrigation and soils
272 which can accommodate paddy rice. Indeed, many areas where rice is currently cultivated are
273 already at the limit of these secondary agronomic adaptations (6). Ethnographic work has
274 shown that in Southeast Asia and China rice paddy soils have been formed over thousands of
275 years of continuous farming which has increased their fertility (58). Such long-term processes
276 of niche construction cannot be easily replaced.

277 Although we do not directly assess yields, regions projected to warm beyond rice's historical
278 thermal limits are likely to experience sustained productivity declines without further adap-
279 tation, while some cooler areas could benefit as temperatures approach present-day optima.
280 Both outcomes underscore the importance of adaptation strategies to sustain production under
281 shifting climatic conditions. Shifts in planting dates to winter may provide solutions in some
282 regions, but higher temperatures are still a concern as rice is also sensitive to warmer nighttime
283 temperatures in the early growing period (59). While breeding for traits that improve resis-
284 tance to heat stress, such as early flowering (33), offers some promise, large-scale socio-cultural
285 adaptations to new crop varieties—and, in some cases, shifts in dietary preferences or staple
286 composition (60)—imply significant downstream impacts on regional cultures and economies
287 that can be difficult to anticipate and mitigate ahead of time. Additionally, tropical varieties of
288 *O. japonica* will likely need to shift northwards to higher latitudes, yet these varieties are highly
289 sensitive to day length, and the development of non-photosensitive temperate *O. japonica* may
290 have taken thousands of years. More recent efforts, however, such as the Green Revolution in
291 Asia, achieved rapid advances—including the development of non-photosensitive varieties that
292 enabled the expansion of rice cultivation into new latitudes (61). A major breeding objective
293 for the coming decades will thus not only be to develop non-photosensitive varieties of tropical
294 rice but also matching cultivation strategies (e.g. 62) and associated food system strategies
295 and cultural norms.

296 The stored germplasm of landraces will thus serve as important genetic resources to breed
297 climate-adaptive loci into high-yielding commercial rice varieties (63–65). Compared to mod-

298 ern cultivars, landraces contain higher genetic diversity (66, 67) and adaptations to a wider
299 range of climates (64). This genetic diversity can also be harnessed using traditional varietal
300 mixtures and diversified planting systems (68), where growing complementary crop varieties
301 with different heat tolerances together can buffer against temperature extremes. Maladaptation
302 of rice landraces under future climates may thus be amplified in modern cultivars and
303 cropping systems (69). Although there is uncertainty in genomic offset estimates due to model
304 averaging across climate scenarios and statistical uncertainty in genotype-environment associa-
305 tions, they remain powerful predictors of maladaptation in projected climates (70). A warming
306 climate also threatens wild relatives of rice and the genetic resources they contain, which are
307 currently largely limited to South and Southeast Asia and cannot disperse as quickly without
308 human intervention (1).

309 Our focus here on annual and seasonal temperature indicators allows for the integration of a
310 broader array of data and provides a more flexible analysis that is less sensitive to uncertainty
311 in cultivar type, growing season, and local management practices. However, future work could
312 explore this variability further by developing new thermal indicators more sensitive to the
313 unique requirements of various cultivars, growing seasons, and agro-ecological contexts. Tem-
314 perature is not the only climate variable that influences rice growth. Others like soil moisture
315 and solar radiation are also critical to rice growth in ways that, likewise, depend on culti-
316 var type, growing season, and management practices. Extending this analysis to the global
317 and regional climatic drivers of local climate response of these multiple variables, such as the
318 influence of sea surface temperature variability and atmosphere-ocean teleconnections, could
319 provide further opportunities to incorporate long-term climate reconstructions and projections
320 of climate impacts on rice viability. A more precise estimation of the long-range correlations
321 among key climate indicators in space and time, based on long-term insights from the archaeo-
322 logical and paleoclimatological record, would be particularly useful for developing holistic
323 recommendations for future agronomic and genetic adaptations.

324 Our interdisciplinary approach highlights a pressing reality: the vast historical perspective
325 of rice cultivation combined with past and present climate data provide a sobering outlook
326 for food security during future climatic shifts. Staple food resources entrenched in centuries
327 or millennia of cultural and socio-economic development face unprecedented challenges in the
328 coming decades. The implications of these challenges extend beyond agriculture and resonate
329 through economic systems, trade and migration flows, and deep-rooted cultural practices. The
330 potential displacement of rice cultivation zones suggests not merely a change in global food
331 patterns but a profound disruption of human societies rooted in these agronomic traditions.
332 Before us lies an urgent necessity for international research, collaboration, and adaptive policy-
333 making to strengthen the resilience of this crop that sustains billions.

³³⁴ **Materials and Methods**

³³⁵ **Climate Data**

³³⁶ We used high-resolution gridded climate data from version 2.1 of the CHELSA product
³³⁷ (71). CHELSA incorporates bias-corrected outputs from the ERA5 reanalysis (72) with
³³⁸ high-resolution terrain data using mechanistic relationships between local climate and terrain.
³³⁹ Compared to other global gridded climate products, CHELSA offers superior performance in
³⁴⁰ mountainous regions, and its reliance on high-quality reanalysis data instead of raw weather
³⁴¹ station data ensures greater accuracy and internal consistency among climate variables.

³⁴² For present-day observed climate, we used the CHELSA V2.1 product spanning the period
³⁴³ 1981-2010 at a 1km resolution. We further aggregated the native 1km data to 5km and 10km
³⁴⁴ grids to assess the sensitivity of our results to the scale of the analysis, given the variable spatial
³⁴⁵ support of the contemporary rice extent data. In all cases we used standard temperature
³⁴⁶ indicators used in ecological niche modeling studies (71), derived from monthly climatologies
³⁴⁷ of minimum and maximum temperature, which collectively represent annual means, monthly
³⁴⁸ extremes, and seasonality. Future climate model ensembles were derived from phase six of
³⁴⁹ the Coupled Model Intercomparison Project (CMIP6) (73), using the subset of bias-corrected
³⁵⁰ models and scenarios used in phase 3b of the Inter-Sectoral Impact Model Intercomparison
³⁵¹ Project (ISIMIP) (74), bilinearly interpolated to the CHELSA V2.1 basemap using the delta
³⁵² change approach (25).

³⁵³ Past climate data were primarily derived from the CHELSA-TraCE21k product, a downscaled
³⁵⁴ version of TraCE-21k simulation of the CCSM3 climate model spanning the last 21,000 years,
³⁵⁵ at 100-year intervals (76). This product uses the older CHELSA V1.2 algorithm, along with
³⁵⁶ a trend-preserving bias correction and topographic correction for shifting ice sheets across the
³⁵⁷ deglacial period. While TraCE-21k has known limitations (77–80), particularly in representing
³⁵⁸ mid-Holocene warmth, it was chosen for its unique combination of high spatial resolution and
³⁵⁹ seasonal temporal resolution necessary for assessing rice cultivation conditions. To validate
³⁶⁰ these findings, we compared our results with other low-resolution mean annual temperature
³⁶¹ reconstructions that show varying levels of mid-Holocene warmth (81, 82). Despite differences
³⁶² in overall temperature trends, the key patterns in rice cultivation temperature distributions
³⁶³ remained consistent between reconstructions (fig. S3).

³⁶⁴ **Contemporary Rice Distribution Data**

³⁶⁵ We collected rice occurrence data from a variety of sources combining information from satellite
³⁶⁶ imagery, administrative statistics, and herbarium collections to assess the sensitivity of our
³⁶⁷ results to various modes of data collection, sampling, spatiotemporal scale, and other potential
³⁶⁸ sources of bias. These three distinct data types sample different aspects of rice distribution
³⁶⁹ with complementary biases. Satellite estimates provide continuous spatial coverage but can

misclassify certain land cover types; census data offer detailed regional production information but suffer from administrative reporting issues and boundary effects; herbarium records provide precise, ground-truthed identifications across diverse production systems but show spatial bias in field accessibility and collection priorities. When these data types with different sampling approaches converge on similar thermal limits despite their distinct limitations, this suggests the patterns are less likely to be methodological artifacts. The specific datasets were:

- Satellite-based estimates of lowland rice extent in Asia from the International Rice Research Institute (19). This dataset employs high-resolution (500m) presence-absence markers from MODIS observations (2000-2012) and offers relatively uniform sampling across both temperate and tropical regions. It provides a more objective approach than spatially biased occurrence records. However, its coverage is limited to East and South-east Asia and it may poorly distinguish intercropped wheat and rice in Northeast China and natural wetlands and paddy rice cultivation in Indonesia. To minimize such sampling issues, we aggregated the 500m data into 5km grid cells, dropping occurrences with less than 20% coverage to minimize false positives from low-pixel observations. Subsequent analyses of these data proved robust to the exact resolution and coverage threshold used.
- Estimates of paddy rice harvested areas around the year 2000 (20). This dataset, integrates satellite-based estimates of cropland with sub-national statistics for rice harvested areas. It utilizes geospatial cropland maps to downscale harvest area and yield census data and offers global coverage at approximately 10km resolution. Countries that lack detailed administrative data at the subnational level, such as Laos and Kazakhstan, can exhibit overly smoothed areas. The use of harvested area as a metric can be misleading in regions with multiple annual harvests, leading to double or triple counting, but this is mitigated when converted to binary occurrence data.
- Geolocated, point-based occurrence records for rice and its wild progenitor synthesized from previous studies (2, 18, 21, 22), originally sourced from GBIF, the Rice Haplotype Map project, and other datasets based on herbarium specimens or germplasm samples from international genebank databases. Given their direct identification, these occurrence records generally offer greater reliability than area-averaged crop occurrences derived from satellites and sub-national statistics. Nonetheless, they are susceptible to spatial sampling bias. For instance, regions like China are underrepresented in GBIF in terms of sampling effort compared to neighboring countries with similar geographical extent, and herbarium collections may more accurately sample upland rice varieties at the expense of larger paddy fields. After creating the full combined datasets, geolocations were checked for anomalous entries then thinned to a uniform grid to minimize irregular spatial sampling.

We extracted the contemporary CHELSA climate data at each set of occurrence points for each data type to calculate temperature distributions and quantiles. We explored various combinations of grid/point resolution for the climate and occurrence datasets from 1-10km, but found this did not impact the upper temperature threshold estimates.

410 Archaeological Rice Distribution Data

411 We used past rice occurrence data sourced from archaeological sites in Asia, as synthesized in
412 (83) and (13) and primarily derived from version 2 (15) and 3 (Dorian Fuller 2023, personal
413 communication) of the Rice Archaeological Database. We also included observations from
414 (14) to increase data coverage in Japan. These records are typically of botanical remains,
415 believed to represent *O. sativa japonica* from these archaeological sites, with less intensive
416 sampling of *indica* varieties from northern India. However, based on their chronology, some
417 occurrences might instead reflect cultivation of wild-type *O. rufipogon* or *O. nivara*. After
418 data harmonization—which involved eliminating potential outliers, correcting misclassifica-
419 tions, and removing duplicated site data (see supplemental analysis code repository for the
420 reproducible workflow)—we were left with 1,595 dates from 803 archaeological sites. These
421 datasets comprise a mixture of direct radiocarbon dates on rice remains, alongside dates for
422 archaeological phases associated with rice remains that were not directly dated. For these
423 indirectly dated samples, we used median dates and minimum/maximum date ranges for the
424 archaeological strata or contexts in which the rice remains were found. We employed the
425 Intcal20 calibration curve for recalibrating all radiocarbon dates, barring a single site in the
426 southern hemisphere where we utilized SHcal20. We then extracted temperature variables from
427 the CHELSA-TraCE21k v1.0 dataset at each sampled location in time and space. To account
428 for chronological uncertainty, we generated 5,000 bootstrap replicates, sampling from the ra-
429 diocarbon dates' posterior density distribution and a uniform density for the dates based on
430 archaeological phases. Finally, we constructed unique kernel density estimates of the tempera-
431 ture distributions at each rice occurrence point for every bootstrap replicate and temperature
432 variable.

433 Genetic Offset Analysis

434 To assess the adaptive capacity of rice varieties beyond simple distributional limits, we per-
435 formed a genetic offset analysis to evaluate the potential maladaptation of *Oryza sativa* sub-
436 species *indica* and *japonica* under projected climate change scenarios. Genetic offset metrics
437 provide a complementary perspective to geographical threshold analyses by identifying where
438 genetic adaptation may or may not keep pace with changing thermal conditions. Landraces
439 are representative of the extant genetic diversity of crop species, and frequently exhibit local
440 adaptations from sustained cultivation in specific geographic localities. We leveraged previ-
441 ously published genomic datasets of geotagged rice landraces belonging to the subspecies *O.*
442 *sativa* ssp. *Indica* (18) and *O. sativa* ssp. *Japonica* (84), containing genome-wide biallelic sin-
443 gle nucleotide polymorphisms (SNPs) filtered for quality and imputed for missing genotypes.
444 The workflow entailed a gene-environment association analysis focusing on the first principal
445 component of the three temperature variables (MAT, TWARM, TMAX), which explained
446 over 84% of the environmental variance across the locations of both rice subspecies. Using the
447 first principal component addresses multicollinearity among the temperature variables while

448 retaining most environmental variation. The gene-environment association analysis was per-
449 formed using the `lfmm2` function from the R package LEA (v3.12.2)—on the two subspecies
450 separately—to identify variants associated with variation in temperature (85). To correct for
451 population structure in the GEA, we provided the number of ancestral populations, K, as the
452 number of latent factors in our latent factor mixed models (85). We selected the number of
453 ancestral populations based on the number of principal components of the genotype matrix
454 that explain a large proportion of the variance, the cross-entropy—a measure of model fit—of
455 different values of K, and information from prior studies (18, 84). Variants identified in the
456 GEA were clumped within 100 kilobases of each other, selecting the variant with the lowest
457 p-value as the candidate SNP from each linkage group. The genetic offset, indicative of mal-
458 adaptability to predicted climates (70), was calculated using these loci. These offset values
459 indicate the Euclidean distance between current genomic composition and the composition
460 theoretically required for adaptation to projected climate conditions. We averaged model pre-
461 dictions across multiple climate models (UKESM, MRI, IPSL, etc.) in the ensemble for each
462 Shared Socioeconomic Pathway (SSP).

463 We used the `genetic.offset` function of the R package LEA (85) to calculate genomic offset
464 statistics for rice landraces of *O. sativa* ssp. *Indica* and *O. sativa* ssp. *Japonica* while consider-
465 ing the temperature-associated variants as putative adaptive variants under the SSP1, SSP3,
466 and SSP5 projected pathways that are used to derive greenhouse gas emission scenarios. We
467 also calculated genomic offset statistics under the maximum estimated temperature at each
468 location in the past 12,000 years.

469 To make predictions about where the climate is likely to be optimal for rice-growing in the
470 future, we sampled 10,000 grids from across Asia and calculated genomic offset scores for each
471 individual in the environment of each grid, for the three SSP scenarios. We interpret the
472 grid with the lowest offset score as a possible future optimal location for each rice individual.
473 As a measure of the extent of movement that would be required for adaptation, we subtract
474 the absolute value of the current latitude of each rice individual from the absolute value of
475 the centroid latitude of the optimal grid; positive values of this absolute latitudinal distance
476 indicate movement away from the equator.

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567 Software: NG, OA. Formal Analysis: NG, OA. Validation: NG, JDG. Data Curation: NG,
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572 via reproducible .qmd notebooks available [here](#). All data required to reproduce the main
573 analysis and figures are included with the linked code repository or available from public
574 sources referenced therein.

575 **Supplementary Materials**

576 Supplementary Materials for **Projected warming will exceed the long-term thermal**
577 **limits of rice cultivation**

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580 **This PDF file includes:**

581 • Figures S1 to S9

582 • Tables S1 to S4

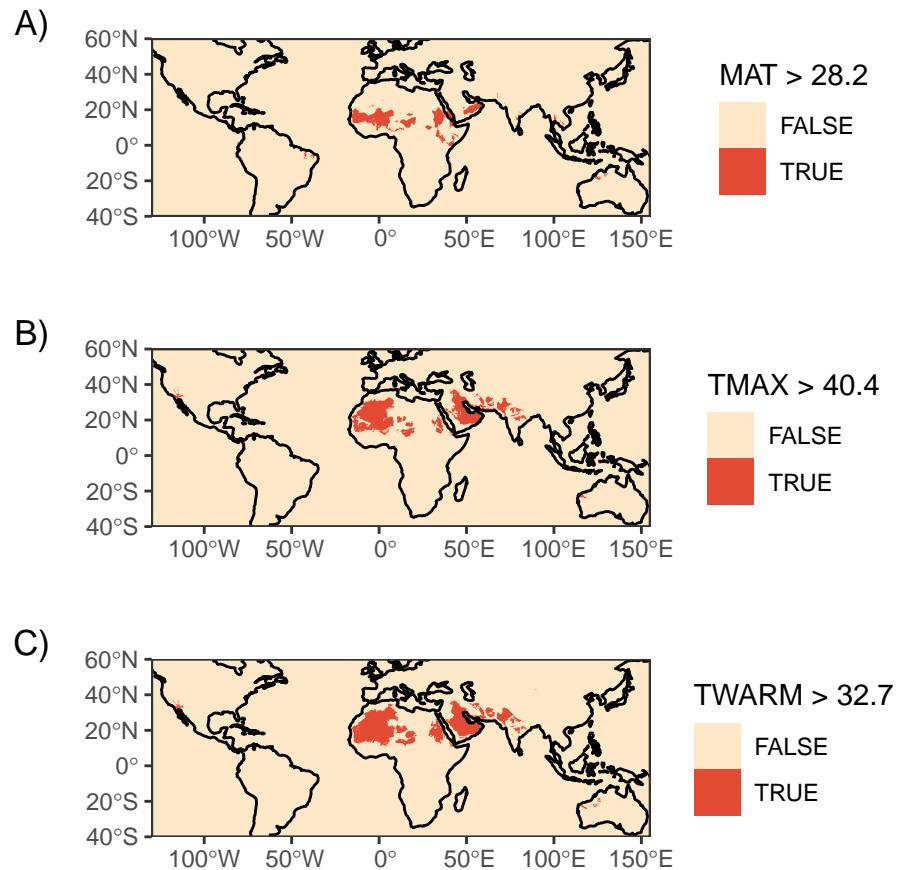


Figure S1: Present day geographic distribution of temperature thresholds in CHELSA V2.1 data. A) Mean annual temperature greater than 28.2°C. B) Mean maximum temperature of the warmest month greater than 40.4°C. C) Mean maximum temperature of the warmest quarter greater than 32.7°C.

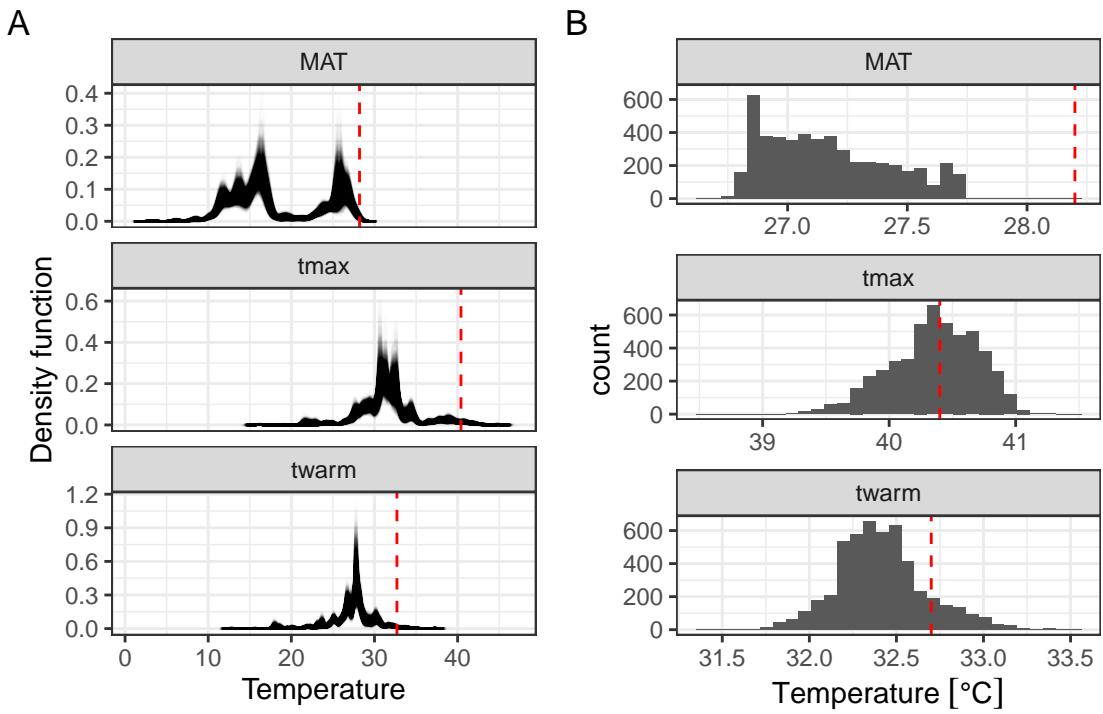


Figure S2: A) Bootstrapped kernel density estimates of rice's thermal extent throughout the Holocene. Bootstrap resampling accounts for uncertainty in radiocarbon and phase-based dating of archaeological rice finds. Contemporary temperature thresholds indicated in red. B) Estimated 97.5% quantiles from the bootstrapped dataset. Contemporary quantiles indicated in red.

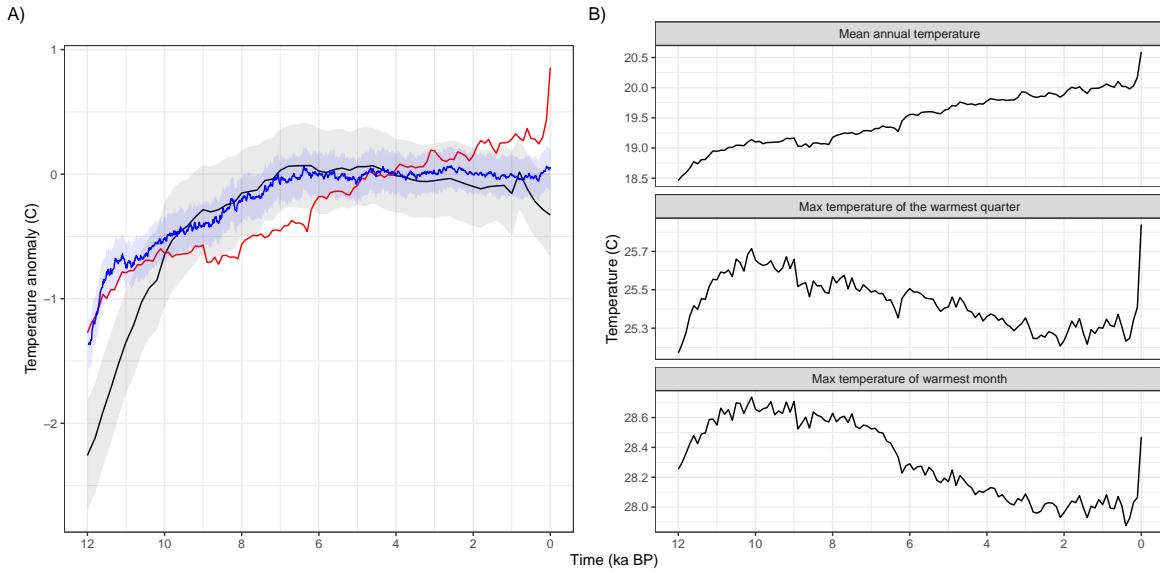


Figure S3: Comparison of Holocene temperature trends over Asia from transient climate models and reconstructions. A) Holocene trends in mean annual temperature, relative to the 3-5ka mean, from Osman et al. 2021 (black, one standard deviation uncertainty in grey), Erb et al. 2022 (blue), and CHELSA-TraCE21k (red). B) Comparison of annual, seasonal, and monthly temperature trends over Asia from CHELSA-TraCE21k.

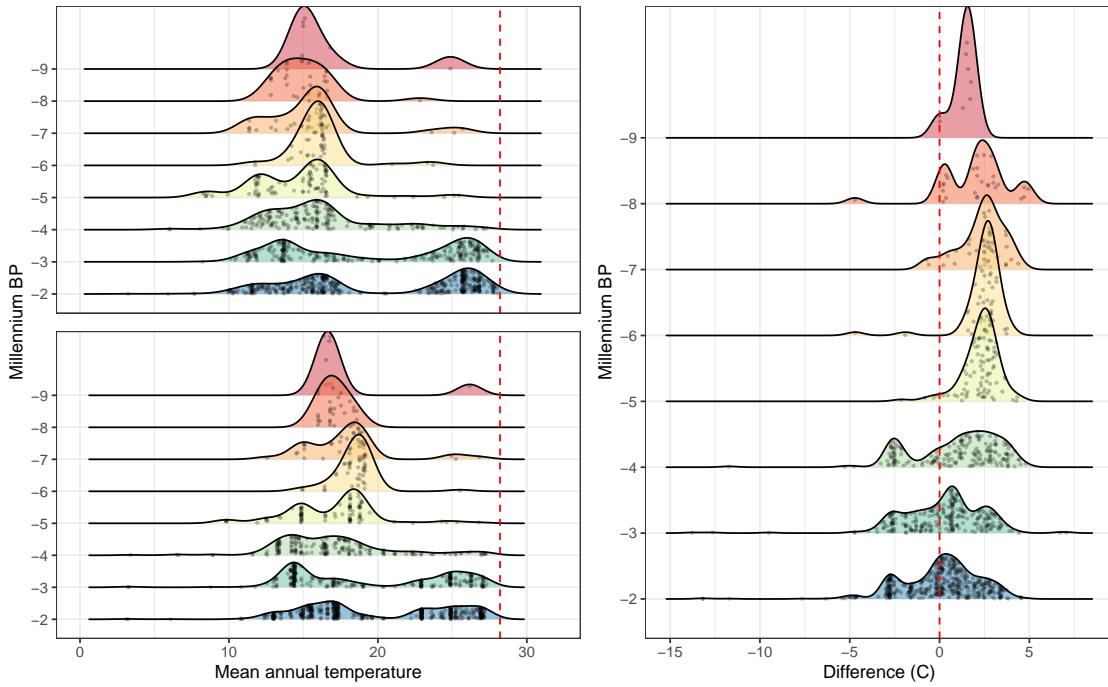


Figure S4: Kernel density estimates of the thermal distribution by millennium across two different temperature datasets, with raw data points indicated in black and contemporary rice thermal limits in red. A) Temperature data are derived from CHELSA-TraCE21k V1.0 (Karger et al. 2023) (same as Figure 3b in main text). B) Temperature data derived from the Last Glacial Maximum Reanalysis (LGMR) dataset (Osman et al. 2022). C) Difference in kernel density estimates of mean annual temperature (MAT) between the CHELSA-TraCE21k and LGMR datasets.

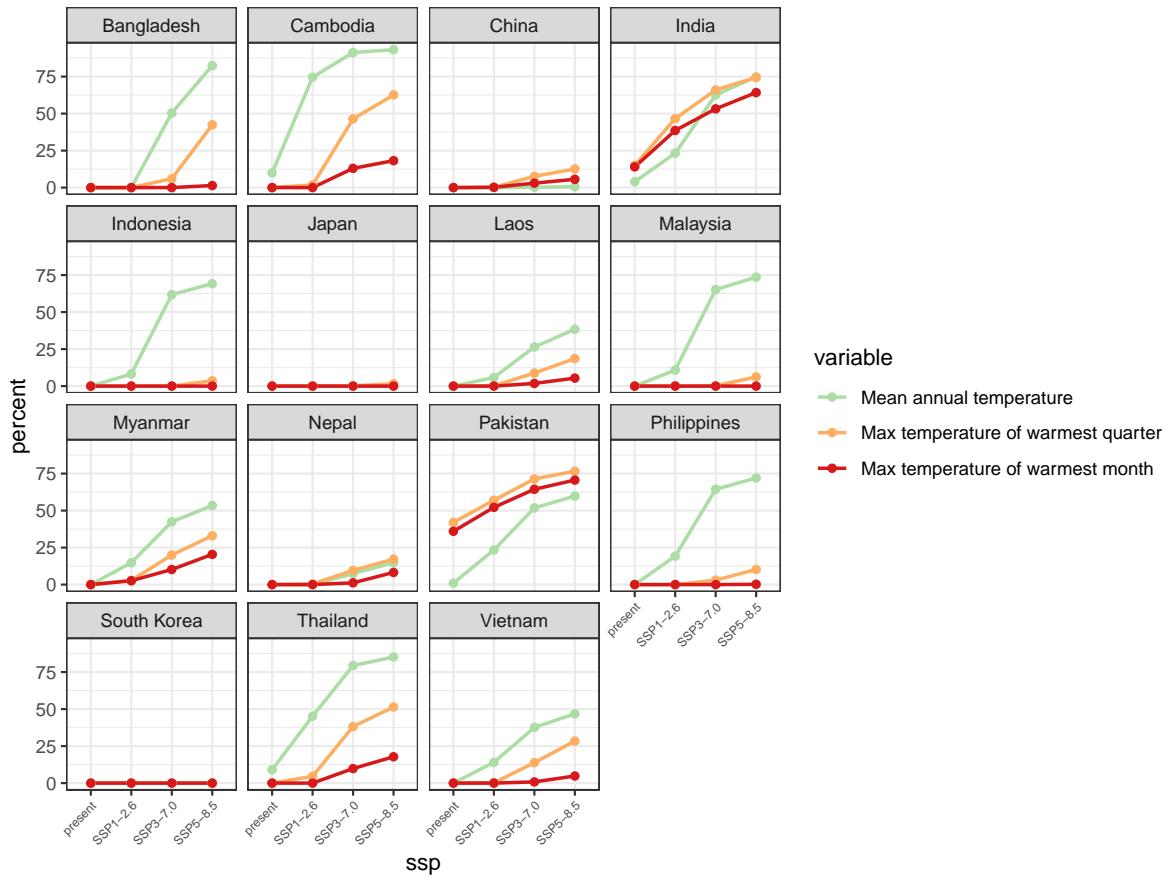


Figure S5: Projected increases in land area surpassing key temperature thresholds in each of the top 15 rice-producing countries in east Asia.

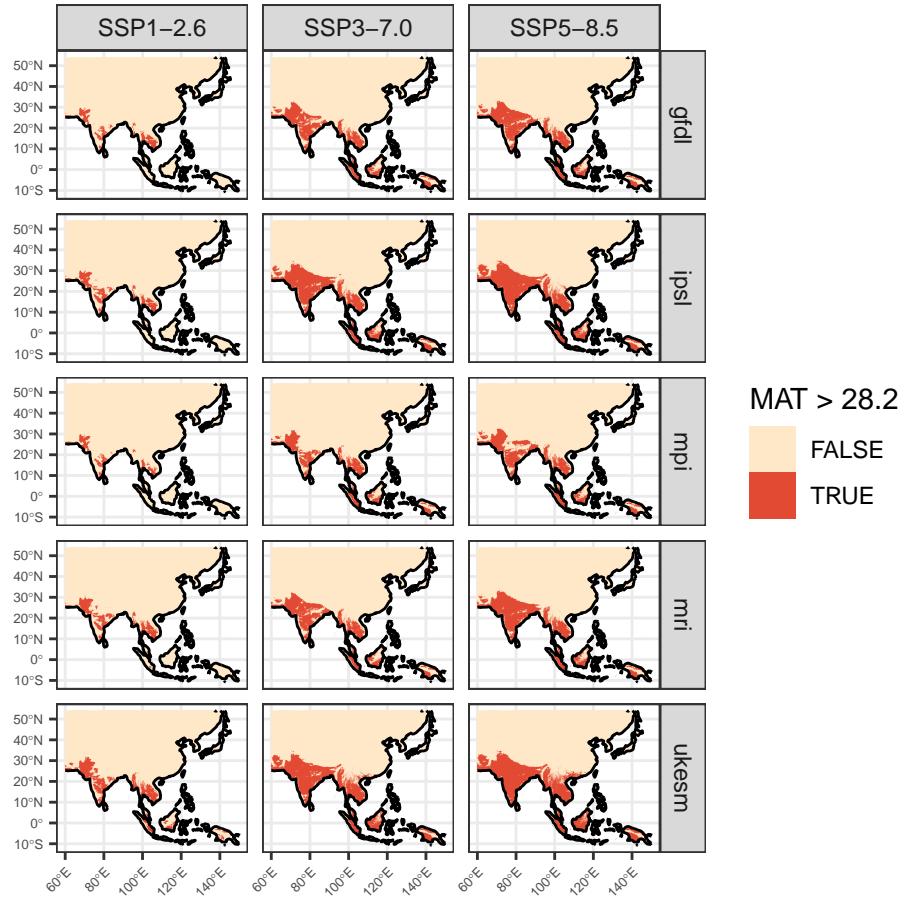


Figure S6: Predicted changes in mean annual temperature over currently cultivated rice areas in Asia for multiple CMIP6 ensemble members.

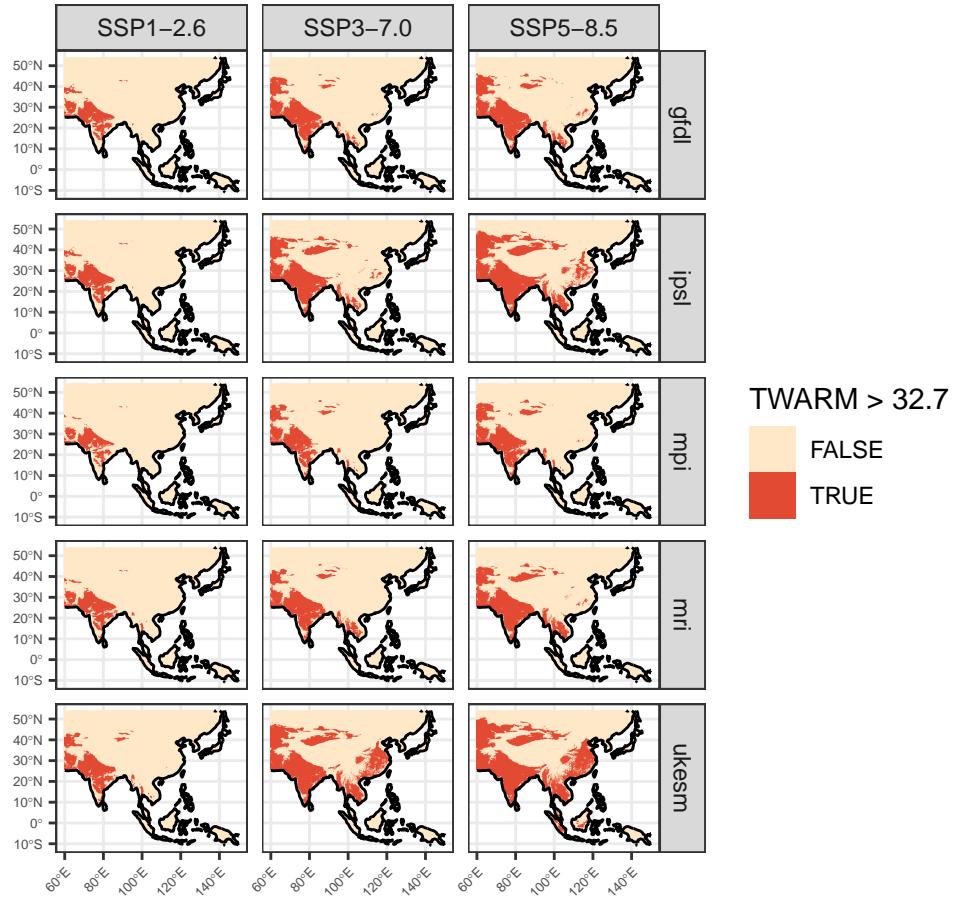


Figure S7: Predicted changes in mean maximum temperature of the warmest quarter over currently cultivated rice areas in Asia for multiple CMIP6 ensemble members.

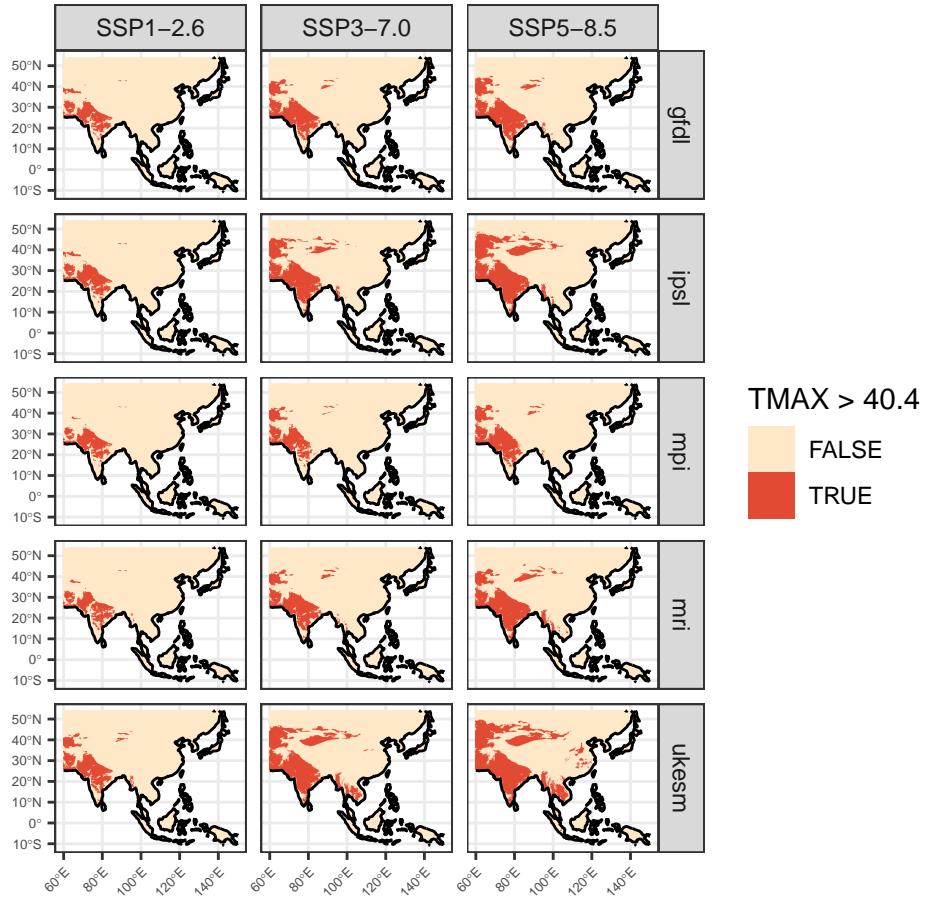


Figure S8: Predicted changes in mean maximum temperature of the warmest month over currently cultivated rice areas in Asia for multiple CMIP6 ensemble members.

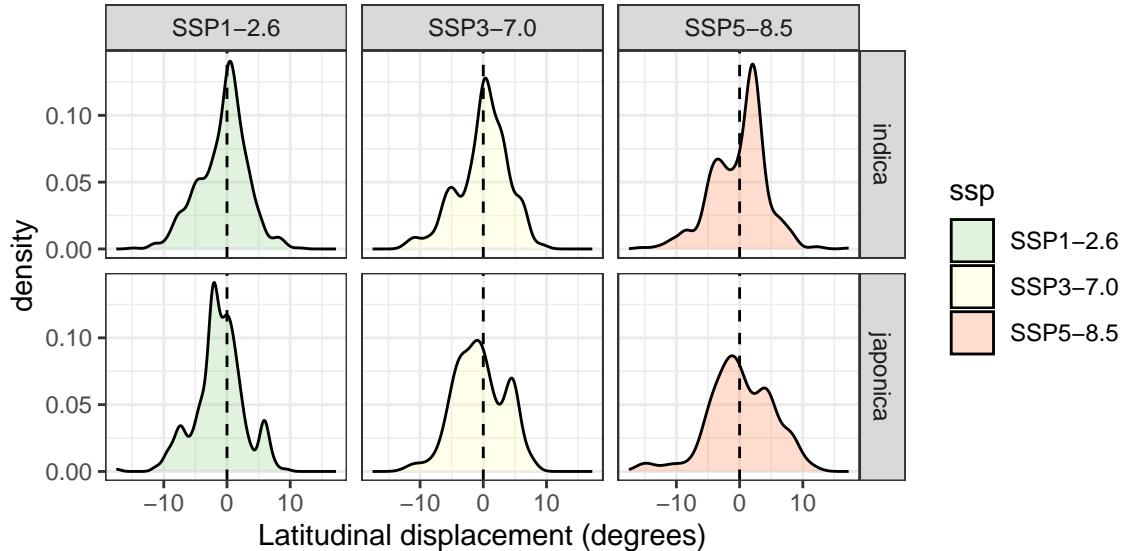


Figure S9: Estimated displacement of the optimal growing location of rice landraces away from the equator, based on genetic offset analysis across three future temperature scenarios. The x-axis indicates the difference between the absolute projected latitude in the future scenario and the absolute latitude today, with positive values indicating a shift in the optimal growing location of a given population away from the equator.

Table S1: Present-day rice extent quantiles (in °C) across three datasets of varying resolution and spatiotemporal support, compared to those calculated from archaeological sites in Asia throughout the Holocene.

Quantile	MAT				TMAX				TWARM			
	IRRI	Mon.	GBIF	Arch.	IRRI	Mon.	GBIF	Arch.	IRRI	Mon.	GBIF	Arch.
1.0 [%]	3.6	4.6	3.1	8.5	23.2	22.5	17.2	22.0	19.5	18.7	13.2	18.1
2.5 [%]	5.6	9.1	9.1	10.3	24.9	24.8	21.2	24.2	20.5	20.8	16.8	20.0
5.0 [%]	10.2	12.6	13.6	11.4	26.0	26.3	24.0	26.9	21.5	22.1	20.1	22.8
10.0 [%]	13.1	15.4	16.9	11.8	27.6	27.7	26.5	28.0	23.4	23.7	22.4	24.6
90.0 [%]	27.2	27.3	27.8	26.5	38.4	39.1	37.8	36.5	31.5	31.9	30.7	30.3
95.0 [%]	27.8	27.8	28.3	26.8	39.5	40.2	39.6	38.9	32.2	32.7	32.2	31.4
97.5 [%]	28.2	28.2	28.6	27.1	40.4	40.9	40.5	40.4	32.7	33.4	33.0	32.4
99.0 [%]	28.6	28.6	28.9	27.7	41.0	41.7	41.4	41.0	33.1	34.6	34.4	33.4

Table S2: Projected increases in percent land area surpassing MAT thresholds in each of the top 15 rice-producing countries in east Asia.

Country	Present	SSP1-2.6	SSP3-7.0	SSP5-8.5
Bangladesh	0	0	50	82
Cambodia	10	75	91	93
China	0	0	0	1
India	4	23	63	75
Indonesia	0	8	62	69
Japan	0	0	0	0
Laos	0	6	26	38
Malaysia	0	11	65	74
Myanmar	0	15	42	53
Nepal	0	0	7	15
Pakistan	1	23	52	60
Philippines	0	19	64	72
South Korea	0	0	0	0
Thailand	9	45	79	85
Vietnam	0	14	38	47

Table S3: Projected increases in percent land area surpassing TWARM thresholds in each of the top 15 rice-producing countries in east Asia.

Country	Present	SSP1-2.6	SSP3-7.0	SSP5-8.5
Bangladesh	0	0	6	42
Cambodia	0	2	46	63
China	0	0	8	13
India	15	47	66	74
Indonesia	0	0	0	4
Japan	0	0	0	2
Laos	0	0	9	19
Malaysia	0	0	0	6
Myanmar	0	3	20	33
Nepal	0	0	10	17
Pakistan	42	57	71	77
Philippines	0	0	3	10
South Korea	0	0	0	0
Thailand	0	5	38	51
Vietnam	0	0	14	28

Table S4: Projected increases in percent land area surpassing TMAX thresholds in each of the top 15 rice-producing countries in east Asia.

Country	Present	SSP1-2.6	SSP3-7.0	SSP5-8.5
Bangladesh	0	0	0	1
Cambodia	0	0	13	18
China	0	0	3	6
India	14	39	53	64
Indonesia	0	0	0	0
Japan	0	0	0	0
Laos	0	0	2	5
Malaysia	0	0	0	0
Myanmar	0	3	10	20
Nepal	0	0	1	8
Pakistan	36	52	64	71
Philippines	0	0	0	0
South Korea	0	0	0	0
Thailand	0	0	10	18
Vietnam	0	0	1	5