AGRICULTURE

# Biocultural vulnerability of traditional crops in the Indian Trans-Himalaya

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**Traditional agricultural landscapes are vital reservoirs of biocultural heritage and agrobiodiversity, yet traditional farming systems and their unique crop landraces face increasing marginalization and genetic erosion. Using northwest Himalaya as a case study, we examine the ecological resilience and genetic diversity of an understudied traditional crop, black pea (scientific name unclear), alongside barley (*Hordeum vulgare*), and compare them to the introduced cash crop, green pea (*Pisum sativum L.*). Participatory field experiments with local farmers revealed that traditional crops outperform introduced varieties in survival and reproduction traits across sites. To our knowledge, we generate the first whole-genome sequencing data for black peas. Clustering and nutritional analyses highlight black pea's genetic richness and dietary potential. Our findings underscore the importance of integrating traditional ecological knowledge with ecological science to sustain agrobiodiversity, enhance climate resilience, and promote sustainable food systems. We provide insights for global agrifood innovations and socioecological stability in fragile mountain ecosystems.**

## INTRODUCTION

Traditional farming landscapes and mountain communities are important reservoirs for conservation of biodiversity, biocultural diversity, and agroecological resources (*1*–*5*). Traditional farming knowledge (in the form of, e.g., local crop landraces and seedbanks) results from complex cultural and environmental selection (*6*) and supports diverse ecosystem services (*7*, *8*). However, traditional practices have often been overlooked in conservation and modern agronomic research (*9*), even as researchers have noted declines in the diversity of landraces and crop genetic erosion (*10*). This is concerning because traditonal production systems (e.g., locally adapted crop varieties) may inform nutritional, cultural, and ecological stability, especially in adverse climates (*11*, *12*). Therefore, research on local production systems is important for supporting regional livelihoods, sustaining socioecological stability and preserving cultural knowledge (*9*, *13*, *14*).

The stability and productivity of food systems are increasingly vulnerable to increased variation in weather patterns and in the frequency of extreme events (such as episodes of drought) often due to climate change (*15*–*17*). The high-altitude Trans-Himalayan landscape presents excellent case studies to examine traditional food systems and the impacts of climate change on agricultural production in mountainous communities (*18*). In that region and more broadly over Asian montane rangelands, climate is changing even faster than the global average (*19*, *20*), threatening both the agroecological landscape and local economy. These rangelands provide exceptional biodiversity and cultural richness (*21*, *22*) and are also known as the Third Pole because they hold the next largest reserves of fresh water and glacial ice after the polar regions. The human communities in these cold desert ecosystems share habitat with diverse wildlife, including the iconic but vulnerable snow leopard *Panthera uncia*, and depend closely on ecosystem services (*23*).

Our research examines traditional agricultural systems and their vulnerability in the fragile ecosystems of northwest Himalaya, in the state of Himachal Pradesh, India in the Spiti district (Fig. 1). Agricultural production in Spiti was traditionally subsistence based (*24*). The main crops grown were barley (*Hordeum vulgare*; neh or jau in Tibetan) and a local variety of pea called black pea (sanmoh nako or dhoopchum in Tibetan). The scientific name for black pea remains unclear (as we discuss in the Results section), and, until recently (*25*, *26*), there were no scientific research articles on black peas. In 1983, an agroeconomic revolution in Spiti was spearheaded by a family that experimentally planted green pea or garden peas (*Pisum sativum L.*) (*24*). In the subsequent two decades, the predominantly subsistence-based production of the village communities has been increasingly replaced by the market-oriented production of cash crops (mainly green peas and apples), destabilizing the sustainability of the cropping system (*27*–*29*).

During our sociocultural work, we learnt that black pea and barley (Fig. 2) are an integral part of ethnodietary recipes and of a climate-resilient farming system, but their cultivation has markedly declined because of market forces and lack of information (*29*). The practice of polyvarietal cultivation of barley (kneu, soha, nenak, and eumo) is nearly extinct (*24*). Kneu is the only variety grown currently with small quantities of soha for religious ceremonies. Without adequate research, the understudied black peas are close to facing cultural extinction. Grown for around 3000 years in the Tibetan-Qinghai plateau (*30*–*34*), barley and black peas are likely well adapted to the region's geoclimatic conditions and irrigation regimes.

In this research, we use a multipronged approach to providing an ecological, genetic, and nutritional characterization of black pea, which, to our knowledge, has not been done before. Using Indian Trans-Himalaya as a case study, we compared several traits (such as germination and flowering) for traditional crops (we include black peas and barley) and cash crops of green peas. The key research questions are as follows: First, we examined whether traditional crops are better adapted to changing climatic conditions in terms of their

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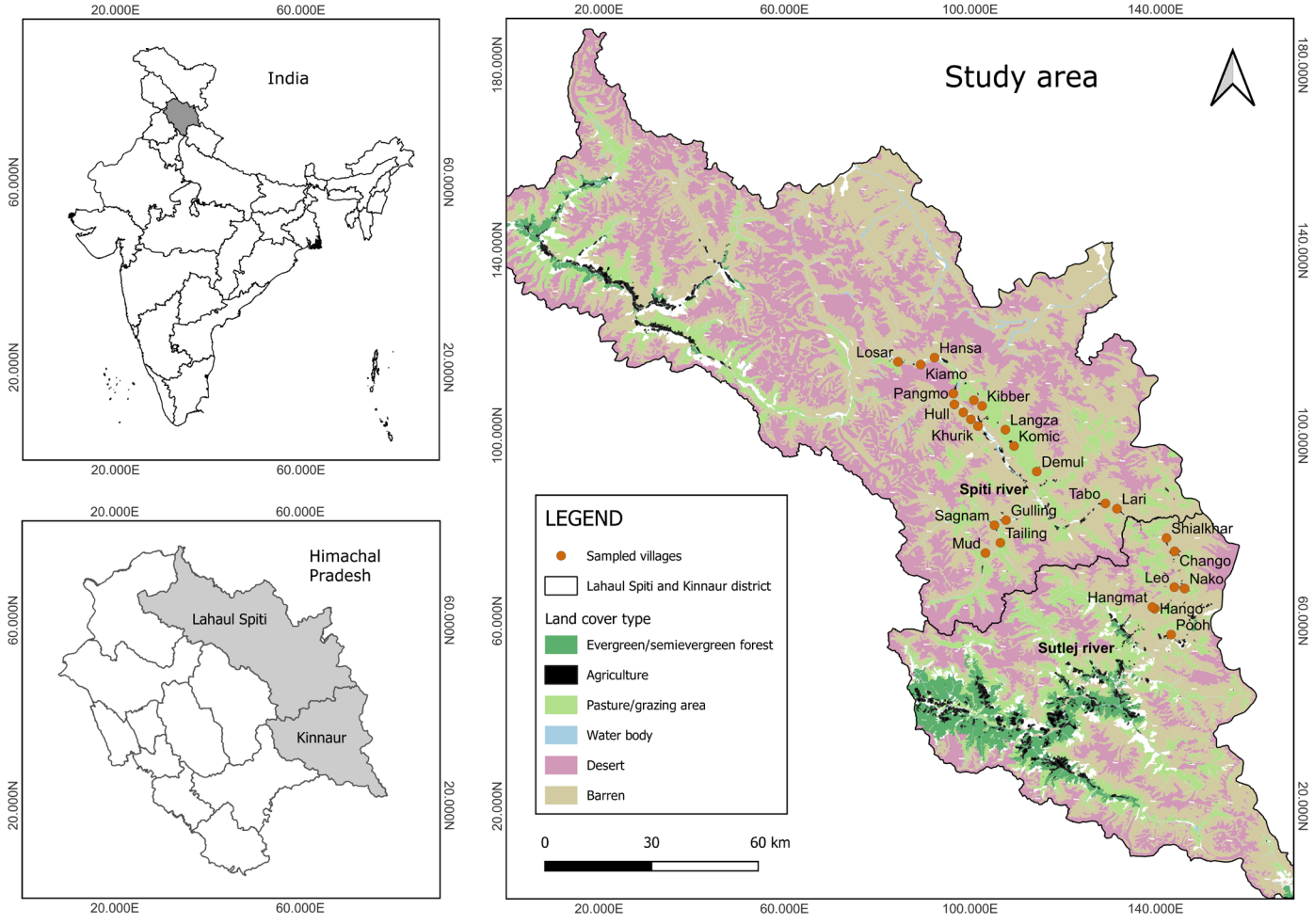


**Fig. 1. Study site.** Study sites within Spiti Valley and Kinnaur district where we interviewed local community members across 26 villages and helped codesign experimental plots at the three sites discussed in Materials and Methods. Different colors correspond to land use characterizations such as agriculture, grazing pastures, and barren among others. The orange circles correspond to the villages sampled. The bottom-left panel shows the extent of Spiti and Kinnaur district within the state of Himachal Pradesh, India.

survival and reproductive traits (such as stem height, number of pods, among others). Second, we examined whether black pea differs in genetic diversity from other peas in the *Pisus* genus. We expected genetic differences between black peas and green peas but did not have a prior on the magnitude and nature of those differences. Third, we examined the nutritional profile of back pea to address the lack of existing data on this crop.

We performed field experiments (March to September 2023) to compare the three different crops (black pea, barley, and green pea) for reproductive and photosynthetic traits under variable water treatments across three elevation gradients (see Materials and Methods). We codesigned the experiments with local farmers who advised on sowing density, soil depth, and bed preparation to ensure optimal growth conditions. To examine the second research question, we generated, to our knowledge, the first whole-genome sequencing (shotgun sequencing using the Illumina platform) for black pea using leaf sample (see Materials and Methods). We then performed a chromosome-wide clustering analysis and principal components analysis (PCA) to compare our black pea sample with pea accessions published in (*35*). For the third question, we collaborated with the Central Food Technological Research Institute (CFTRI) in India to provide a standardized nutritional profile for black peas.

Our study establishes ecological, genetic, and nutritional baseline data for black peas, addressing the existing knowledge gap on this crop. Previous studies (*28*, *25*, *36*) have noted trends in cropping patterns, but there has not been a comprehensive assessment of traditional food systems in the region, especially black peas, with respect to its ecology and genetic diversity, as well as their impacts on local communities that depend on them. In the next sections, we describe the study system, research methods, results, and recommendations. We close with a discussion on integrating local knowledge and modern science to examine lesser-known and underused crops to foster food systems that are environmentally sustainable and adaptable to changing climatic conditions.

## RESULTS

### Survival and reproductive traits from field experiments

We focused on three key aspects: ecology, genetics, and nutrition for traditional crops and cash crops. We hypothesized that traditional

**Fig. 2. Images of black pea crop and agricultural system.** The top panels show black pea flowers (left) and barley field (right). The bottom two panels show green pea fields as part of agricultural production system. Image credit: H.J., Princeton University.

crops are more resilient than cash crops as measured by traits such as stem height, number of pods, among others. We expected genetic differences between black peas and green peas but did not have a prior on the magnitude and nature of those differences. Nutritionally, we expected that black peas have a distinct and high nutritional profile compared to green peas because cash crops are consistently selected for particular nutritional values and sold in markets for this trait (*37*, *38*).

We first want to note that the results are averaged across water treatments because of high rainfall in the summer of 2023. The drought treatments received rainfall, and we therefore treated different treatments as replicates. Our first result from the field experiment shows that both black peas and barley have higher survival probability (or establishment rate since few seeds are eaten by birds, livestock, and ungulates) in comparison with green peas across all sites. The results are consistent across three different ecological settings as shown in Fig. 3A. The site Kiamo (at 4000 m) has highest average establishment rate for black peas with 0.51 overall. The high establishment rates for black peas (evidenced by the higher mean value) underscore a possible genetic or phenotypic advantage over green peas. These findings suggest that black peas may have attributes that confer greater survival advantages under the diverse conditions represented by the study sites.

Except one site (Tashigang) at 4500-m elevation, barley establishment rates are lower than green peas across all sites. Please note that there are no error bars for barley because some of our barley plots were destroyed and we were only able to preserve one plot per site. We also added another experimental site Thinam at 4600 m without replicates to note seed survival in high elevation. Farmers noted that they had been experimenting growing crops at even higher elevation (4600 m) due to better availability of snow melt and access to water. We find low success at this elevation across all crops at Thinam as shown in last panel of Fig. 3A.

Next, we evaluate nonreproductive traits such as average stem height and average number of leaves (correspond to higher photosynthetic activity). As shown in fig. S1 and S2, black peas outperform green peas consistently across all sites. The average stem height for black peas is 38.12, 24.3, and 25 cm compared to 18.2, 12.48, and 10.7 cm, across Kiamo, Kibber, and Tashigang, respectively. We do not consider barley in these plots because barley is a grass species from Poaceae family.

Important covariates for farmers include the reproductive traits such as proportion of flowering plants and pea pods. Figure 4A describes the distribution of survival-weighted proportion of flowering plants. Through the cropping season, we noted the proportion of flowering plants and weighted it by survival. We find that black peas have higher proportion of flowering plants for black peas on average (0.62) than green peas (0.27) at Kiamo site (4000 m) during peak flowering time. Black peas (0.5) have higher flowering proportion than green peas (0.31) at Kibber site (4200 m). However, at the highest elevation Tashigang (4500 m), green peas (0.3) outperform black peas (0.2), although both perform worse than at the two other sites. Similarly, the average number of pods per individual plant is also higher for black peas than green peas as shown in Fig. 4B.

Last, we evaluate the growth rate for all crops by taking stem height as a predictor in an ordinary least squares (OLS) regression and find that black peas, barley, and green peas have growth rates of 0.83, 0.6, and 0.38, as shown in Fig. 3B. OLS ignores site variance, assuming a single growth rate across all sites. Therefore, we also performed a linear mixed model (LMM) with site as a random effect, allowing for variation in baseline growth across different sites in Fig. 3B. For black pea, the growth rate was 0.8951 (SE = 0.0687, $P < 0.01$) in LMM, compared to 0.8266 (SE = 0.0703, pvalue <0.01) in OLS. For green pea, the estimated growth rate using the LMM was 0.428 (SE = 0.038), whereas the OLS regression estimated a slightly lower growth rate of 0.383 (SE = 0.039), indicating that accounting for site-level variation in LMM resulted in a slightly higher estimate. For barley, the growth rate estimated by LMM was 0.604 (SE = 0.040), while OLS produced a similar estimate of 0.600 (SE = 0.041), suggesting that site-specific effects had minimal impact on growth rate estimation for this crop. Our results are consistent, although the site variation is notably high for black peas as

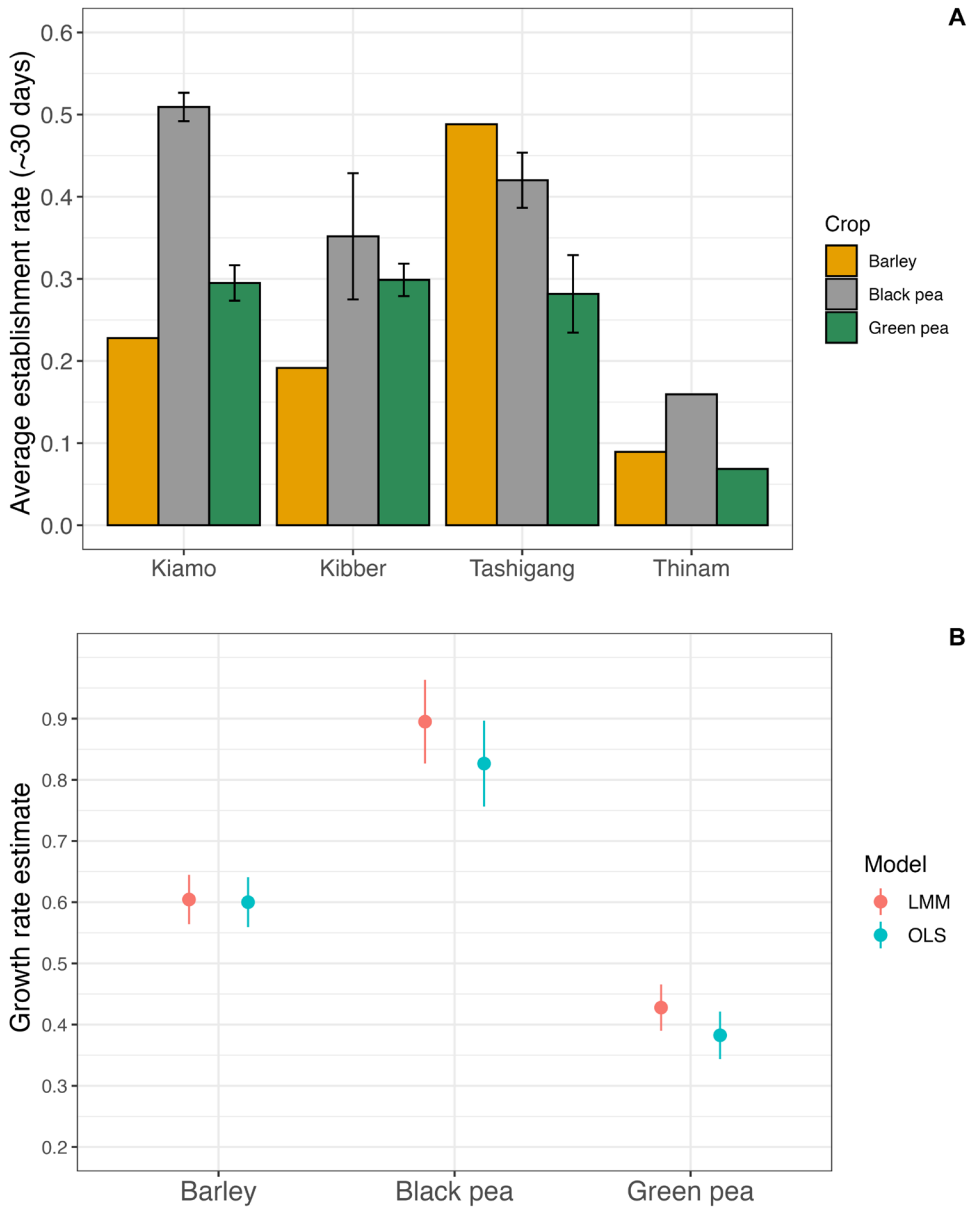


**Fig. 3. Establishment and growth rate of black peas, green peas, and barley.** (**A**) The *x* axis corresponds to four sites at different elevations: Kiamo (4000 m), Kibber (4200 m), Tashigang (4500 m), and Thinam (4600 m). The *y* axis corresponds to average establishment rates for the crops. Each color corresponds to different crops: barley, black pea, and green pea. The lack of error bars indicates that there was one replicate. (**B**) The *y* axis corresponds to the log growth rates from the regression analysis: ordinary least squares (OLS) and linear mixed model (LMM). The *x* axis corresponds to crops: barley, black pea, and green pea. The values are averaged over all sites and replicates.

discussed in table S1. We want to note that our dataset consists of observations from a single year (2023–2024 with a pilot in 2022). Therefore, we used simple statistical regression in the absence of repeated measurements across multiple years. Future studies over multiple years will provide a better estimate of growth rates and effects of site variation.

## Genetic diversity of black peas

Pea belongs to the most ancient set of cultivated plants and is known to be domesticated about 10,000 years ago in the Middle East and Mediterranean region (also known as Fertile Crescent) (*39*, *40*). Although the taxonomy of *Pisum* genus is complex and still under debate (*35*, *41*), there is consensus that the genus consists of two species: wild *Pisum fulvum* and *P. sativum* (*42*). *P. sativum* includes wild (subsp. *elatius*) and domesticated taxa (subsp. *sativum*).

We generated the first whole-genome sequencing data for the black pea and mapped it to the *P. sativum* reference genome. The average depth of coverage of our black pea data was 15× with a breadth of coverage across the reference genome of 86.6%. We combined these data with data for pea accessions in (*35*) and performed a chromosome-wide PCA analysis to infer the structure of *Pisum* collection. Since we were interested in our black pea subpopulation,

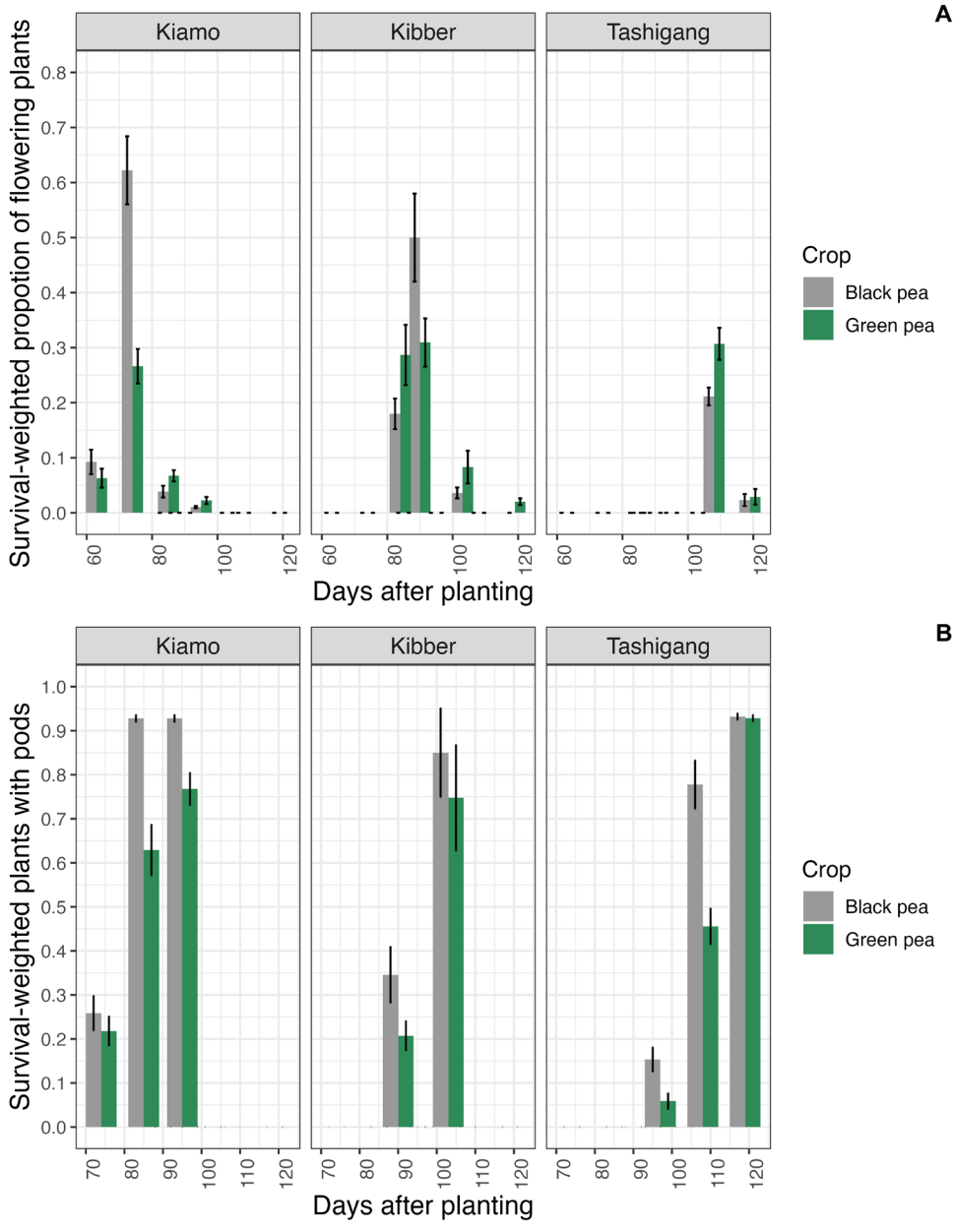


**Fig. 4. Flowering and number of pods for green and black peas.** (**A** and **B**) Each panel corresponds to three sites at different elevations: Kiamo (4000 m), Kibber (4200 m), and Tashigang (4500 m). The *x* axis corresponds to days after planting the seeds. The color corresponds to black peas and green peas. (A) The *y* axis corresponds to survival-weighted proportion of flowering plants. (B) The *y* axis corresponds to the survival weighted proportion of pods per plant.

we used samples from *P. sativum* and admixed accessions. In addition, we included *P. sativum* var. *arvense* (accession SRR19543725) and performed a PCA for each chromosome to compare the samples.

Our PCA results reveal the three principal components (PCs) explain ~50% of the observed genetic variation in the collection. We find that pea accessions were separated on the basis of the *P. sativum* subspecies consistent with previous studies (*35*, *43*). As shown in Fig. 5 (A and B), for chromosomes NC_066584 and NC_066585, our sample clusters neither with domesticated varieties nor the wild germplasms. In addition, the black pea sample (Kibber) clustered distinctly away from *P. sativum* subsp. *sativum* var. *arvense* sample. Although morphological study of black pea supports two recent studies (*25*, *26*) from Himalayan region that identify the local black pea to be *P. sativum* var. *arvense* or field pea, a winter legume belonging to the Fabaceae (Leguminosae) family, our genetic results question the claim.

Next, to validate the robustness of observed genetic variation from the PCA results, we performed clustering analysis on the covariance data. First, we implemented hierarchical and *k*-means clustering analysis of 18 different accessions for all chromosomes. Figure 5A illustrates the results for two chromosomes NC_066581 and NC_066583 for both methods. PC1 and PC2 accounted for about 25 and 16% of the observed genetic variance for each chromosome. Across both

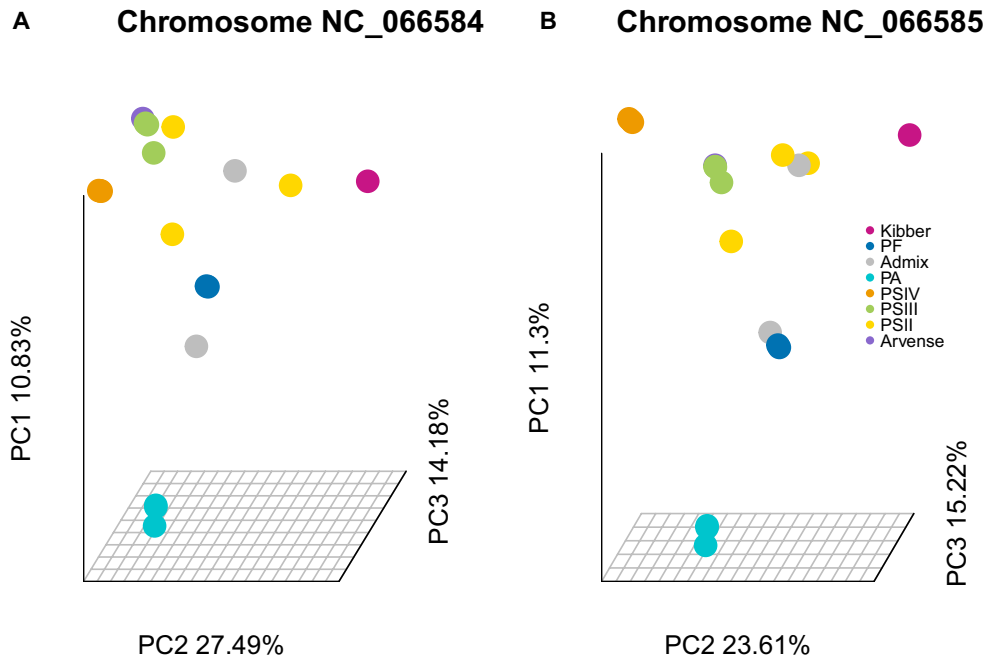


**Fig. 5. PCA for chromosomes.** (**A**) Results for chromosome NC_066584 and (**B**) results for chromosome NC_066585. The black pea sample (Kibber) is in pink color and is distinct from *arvense* (in purple color) and other domesticated samples such as *Pisum* II (PSII) and *Pisum* III (PSIII) (in green and yellow). PF and PA stand for *P. fulvum* and *P. sativum* var. *absynicum*, respectively.

chromosomes, five genetically distinct clusters are consistently observed. The black pea sample formed a closely related subcluster with a traditional Indian landrace, *P. sativum asiaticum* (PSII30), while maintaining phylogenetic separation from other accessions. The results suggest that the black pea shares a genetic affinity with Indian landraces while exhibiting divergence, potentially underscoring localized evolutionary or selective pressures. Consistent with (*35*), *P. fulvum*, *Pisum abyssinicum*, and cultivated *P. sativum* of *Pisum* formed separate single clusters as before. The results are also consistent for other chromosomes as shown in Fig. 5B. We present the results in two separate plots because, for chromosomes NC_066581 and NC_066583, the black pea sample (Kibber) clustered into a group of two, whereas for the remaining five chromosomes (NC_066580, NC_066579, NC_066584, NC_066585, and NC_066582), black pea grouped into a cluster of four, indicating possible chromosome-specific genetic structuring. In Fig. 5B, the subcluster of four includes PSII66 (*P. sativum asiaticum*), a traditional cultivar from Afghanistan; Admix2 (*P. sativum asiaticum*), a traditional cultivar from Tajikistan; and PS37 (*P. sativum*), a traditional landrace from China, Tibet.

We further implemented spectral clustering algorithm, which verified clustering patterns across all methods, reinforcing the reliability of observed population structure (as shown in figs. S10 to S16). We also present the plots for optimal clustering in figs. S3 to S9. Overall, by generating whole-genome sequencing data for black peas from the Trans-Himalayan region, we found substantial genetic diversity and demonstrated that black peas form a distinct genetic clusters, suggesting their importance as a genetic resource for future breeding programs. Our research emphasizes that high-altitude Himalayan mountains are a relevant secondary center of pea diversity, rich in primitive cultivated forms of field peas (*43*).

### Nutritional composition of black peas

Anecdotally, black peas are known for their diverse nutritional profile, but the nutrient content for black peas from the Trans-Himalayas has been unclear. We collaborated with CFTRI based in Mysuru, Karnataka, India to create a nutritional profile for black peas. We find that these legumes are rich in a variety of essential nutrients and offer a diverse combination of protein, fiber, vitamins, and minerals, making them not only culturally and ecologically important but also a valuable addition to a balanced diet. Table 1 provides a measure of nutrients and daily recommendation averages taken from National Institutes of Health (NIH) for an adult with a body weight of 70 kg. First, black peas are notably high in protein, with ~21.20% protein content/100 g. This makes them an excellent plant-based protein source, especially beneficial for individuals following vegetarian or vegan diets. Furthermore, black peas are a good source of dietary fiber (15.9%/100 g) in addition to crude fiber at 6.23%/100 g. Black peas also provide a range of essential vitamins such as vitamin C (13.1 mg/100 g), vitamin $B_1$ (0.61 mg/100 g), and vitamin $B_3$ (1.62 mg/100 g). They are a good source of minerals such as iron (9.11 mg/100 g), zinc (2.48 mg/100 g), calcium (108.09 mg/100 g), and magnesium (109.28 mg/100 g).

## DISCUSSION

Our multipronged approach provides a comprehensive baseline for traditional crops in high-altitude Trans-Himalaya, as these food systems are crucial to the stability of humans and their ecosystems (*44*–*46*). The results of our ecological study find potential for lesser-known, understudied, and underused traditional crops (black peas and barley) in terms of their survival and reproductive traits. We

**Table 1. Nutritional profile for black peas.** The table shows recommended daily intake (RDI) taken from National Institutes for Science (NIH) for an average adult with a body weight of 70 kg. The tests were performed at Central Food and Technological Research Institute, Mysuru, India. The percentage by weight corresponds to percentage of nutrient per 100 g.

| Nutrient | Value per 100 g | RDI (unit per 100 g) |
|---|---|---|
| Vitamin A | 109 µg | 900 µg |
| Vitamin E | 2.74 mg | 15 mg |
| Calcium | 108.09 mg | 1000 mg |
| Iron | 9.11 mg | 8 mg |
| Magnesium | 109.28 mg | 400 mg |
| Zinc | 2.48 mg | 11 mg |
| Fat | 1.03% | – |
| Dietary fiber | 15.9% | 25–35 |
| Crude fiber | 6.23% | – |
| Protein | 21.20% | 10–36% |
| Vitamin C | 13.1 mg | 75.6–100 mg |
| Vitamin $B_1$ | 0.61 mg | – |
| Vitamin $B_2$ | 0.09 mg | – |
| Vitamin $B_3$ | 1.62 mg | – |

find that black peas outperform green peas (cash crop) in terms of their establishment rates, survival-weighted proportion of flowering plants, and average stem height (Figs. 3A and 4A). The findings align with our sociocultural research during which local farmers underscored black peas are better adapted and more resilient (in terms of ease of growing and drought resistance) than green peas (*29*). We note that although we did not have sufficient replicates for barley, we included the crop in our study because barley holds profound cultural and religious importance in the Himalayan and Tibetan-Qinghai communities and is the primary crop for traditional farming. Ethnobotanical work has repeatedly underlined how the crop performs the function of a "cultural keystone species" (*47*).

To our knowledge, we generated the first whole-genome sequencing data for black peas from the Trans-Himalayan region to assess how genetically similar they are to other pea species. By generating first whole-genome sequencing data for black peas, we uncovered substantial genetic diversity and demonstrated that black peas form a distinct genetic clusters using three clustering algorithms along with PCA (Figs. 5 to 7). Our research suggests their importance as a genetic resource for future breeding programs. We expected genetic differences between black peas and green peas but did not have a priori knowledge on the magnitude and nature of those differences. Although earlier studies (*25*, *26*) identify black pea to be *P. sativum* subsp. *sativum* var. *arvense*, our findings show black peas to be distinct from *arvense*. Our research aligns with previous research (*43*) that emphasizes the high-altitude Himalayan mountains to be a relevant secondary centre of pea diversity, rich in primitive cultivated forms of field peas (*43*). As a future direction, linkage disequilibrium–based single-nucleotide polymorphism (SNP) pruning would be necessary for studies such as genome-wide association study (GWAS) to identify trait-associated loci, selection scans to detect regions under adaptive evolution, or demographic history inference using coalescent-based methods (*48*, *49*). We also find that black peas have high nutritional profile, offering high percentage of protein, dietary fiber, zinc, magnesium, among others. This makes them an excellent plant-based protein source, especially beneficial for individuals following vegetarian/vegan diets (*29*).

Many studies (*50*, *51*) have noted that wild pea diversity in peripheral regions is not adequately represented in the existing germplasm collections. Kosterin *et al.* (*50*) found two small populations of the wild pea *P. sativum* subsp. *elatius* in the Zagros Mts, Iran. They note that wild pea populations are rare and small in size and suffer from climate change and land exploitation (*50*). Another example is *P. sativum* subsp. *abyssinicum*, locally known as Dekoko peas, a unique subspecies endemic to Amhara and highland areas of Tigray, Ethiopia and to South Yemen (*51*, *52*). Dekoko peas are an important crop, widely mixed with the main cereal crops such as sorghum, barley, and teff. The crop qualifies for species status on the basis of its phenotype (early flowering and strongly serrate leaflets) and biological isolation (*53*). Although cultivation of Dekoko peas had markedly declined because of drought and political disruption, in the past 10 years, there has been a considerable renewal of interest, resulting in Dekoko germplasm collections, characterization studies aimed at crop improvement, and the extension of cultivation areas (*54*).

Looking beyond the *Pisum* genus, studies note that *Coffea stenophylla* can tolerate higher temperatures than the commercial species *Coffea arabica*, under threat from climate warming. Communities in Sierra Leone helped researchers at the Royal Botanic Gardens (Kew) to find coffee berries from *C. stenophylla* in the wild (*55*). In southwestern Ethiopia, the banana-like Enset (*Ensete ventricosum*) has starch-filled stems that are a main source of calories and nutrients, while the leaves are used for basket making, to feed cattle and to provide shade and build roofs. In addition, this species is remarkably tolerant of drought and short-term temperature variations (*9*). Furthermore, as a final example, we note that the United Nations (UN) recognized 2023 as the International Year of Millets (*56*), calling attention to their many nutritional and health benefits, their suitability for cultivation under adverse and changing climatic conditions, and their potential to contribute to the UN 2030 Agenda for Sustainable Development. Our research emphasizes greater recognition of and research

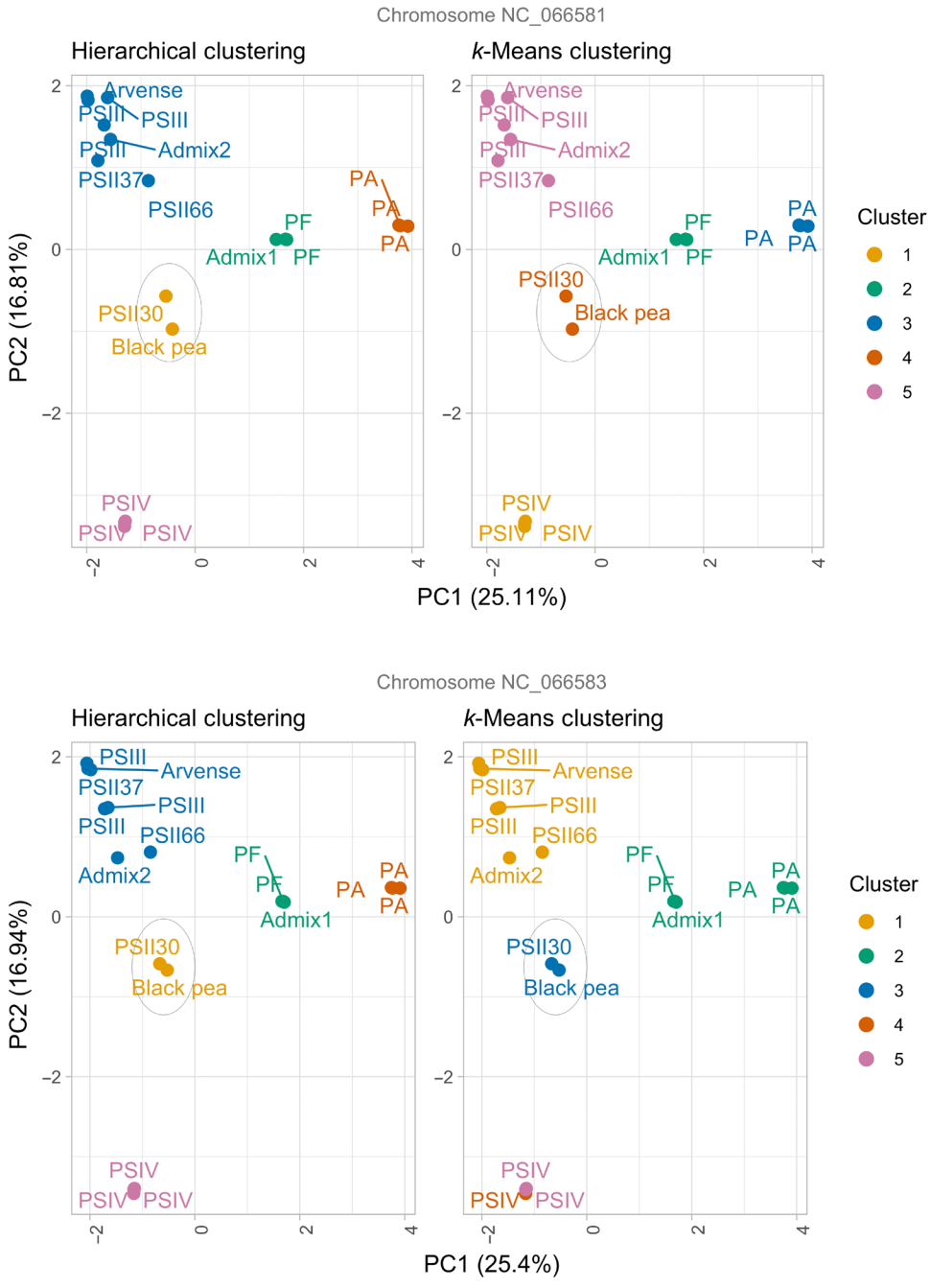


**Fig. 6. Hierarchical and *k*-means clustering results for two chromosomes.** Results for chromosomes NC_066581 (left) and NC_066583 (right). Each color corresponds to a cluster. The black pea sample clusters with *P. sativum asiaticum* (PSII30), a traditional Indian landrace for both methods (highlighted in the gray ellipse).

on lesser-known traditional crops in collaboration with communities who have long been using them and who can be the main beneficiaries.

Our findings have important policy implications. Given the genetic variation revealed in black peas, we see great potential for modern analytical approaches and crop wild relatives (CWRs) to harness this diversity for crop improvement (*57*, *58*). Approaches such as genomic prediction, machine learning, and multitrait gene editing offer innovative pathways to accelerate breeding efforts, enhancing the adaptability, yield, and nutritional quality of crops to meet future global food demands amidst increasing heat and drought stress (*59*). Recently, Verma *et al.* (*60*) emphasized utilization of CWRs to enhance resilience in the Indian mustard *Brassica juncea* (*L.*) *Czern.* and *Coss.* cultigen pool. We recommend research using introgression techniques to improve adaptive traits for green peas via hybridization with black peas. These approaches may also improve the ability to expand the cultivation of cash crops such as green peas into adverse environments of drought conditions and extreme environments (*61*).

GIAHS (Globally Important Agricultural Heritage Systems; identified by the Food and Agriculture Organization, UN) recognize and

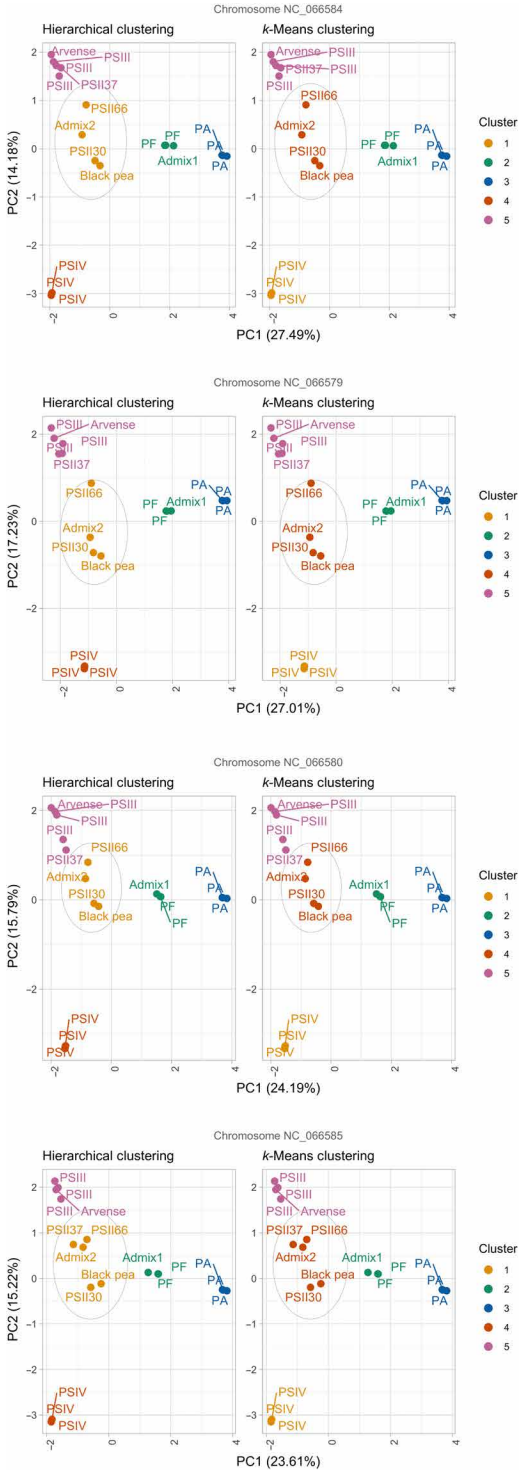


**Fig. 7. Hierarchical and *k*-means clustering results for chromosomes.** Results for chromosomes NC_066584, NC_066579, NC_066580, and NC_066585. Each color corresponds to a cluster. The black pea sample clusters with PSII30, Admix2, PSII66, and PSII37 for both methods (gray ellipse).

designate bioculturally important sites to safeguard agrobiodiversity, protect agricultural heritage, and recognize the knowledge and practices of local communities (*45*, *62*, *63*). These declarations have triggered the development of different tourism activities related to biocultural inheritance. There are several successful examples: The Indigenous "Bari System of Farming" practiced by the native people of North Eastern India (Assam) is recognized from the perspective of consumption, conservation, and biodiversity management (*64*). Another example is the campesino cooperatives in Mapuche-Pewenche territory (southern Andes) who practice community-based tourism incorporating Mapuche rural culture and agricultural practices that support local food systems/economy with a strong identity component (*65*).

On the basis of our results, we recommend the Trans-Himalayan agricultural systems for recognition within the GIAHS framework due to their exceptional biocultural importance, ecological fragility, and potential to serve as models of sustainable agrifood systems (*29*). The region's traditional farming practices have evolved over centuries in response to unique environmental pressures, resulting in agroecosystems that sustain both biodiversity and cultural heritage. Inclusion within the GIAHS framework could offer multiple benefits (*30*, *47*). First, it would safeguard local farming practices and associated traditional knowledge systems that are at risk of being lost because of the growing shift toward high-yield cash crops, thereby ensuring the continued cultivation of regionally meaningful landraces. Second, this could stimulate the creation of local and regional markets for traditional crops, such as black peas, which have demonstrated high nutritional value and resilience. Third, the GIAHS designation could promote sustainable tourism by drawing attention to the cultural and ecological uniqueness (such as snow leopards) of the region, creating considerable economic opportunities. Last, recognition would facilitate greater state-wide, national, and international collaboration, drawing resources for research, conservation, and sustainable development agroinitiatives. As the impacts of climate change intensify, safeguarding these bioculturally rich and ecologically sensitive systems becomes critical not only for local food security but also for global agrobiodiversity conservation efforts (*9*). In general, environmental and conservation outcomes could improve by recognizing and honoring the relationships between people and their landscapes and proposing actions based on local priorities (*66*–*68*).

Future research should address the limitations of our study, particularly the single-year dataset, by conducting long-term studies to assess demographic vulnerabilities under varying climatic conditions. These long-term data are needed to identify not only effects of climate change on the agroecosystem but also genetic variation in traditional crops. The long-term datasets may also shed light on other demographic patterns—which stage in life-cycle of crop is most vulnerable to water stress and plant pathogens? What makes traditional crops more resilient? A quantitative understanding of demographic trade-offs and effects of stochasticity on dispersal patterns will yield important insights for farmers and management interventions (*69*–*71*). Further research is needed to identify the level of genetic variation and what genes and loci may be associated with adaptive traits (*57*). This includes identification of desirable genes and traits from unadapted materials, such as CWRs, and their

transformation for creating resilient cultivars (*34*). In a recent study, Singh and Stetter (*72*) reconstruct the population history of amaranth and identify genomic loci under selection, suggesting that introduced crops can also act as reservoirs of genetic diversity. Last, we want to note that a complex systems perspective of agriculture can provide valuable insights into analysis of rapid and lasting land-use changes (*73*).

## MATERIALS AND METHODS

### Study site

In the state of Himachal Pradesh, about 26,000-km$^2$ area is potential snow leopard habitat (*21*). Within this habitat, we focused on Lahaul-Spiti district (Fig. 1). The area lies in the rain shadow of the main Greater Himalayan range, within the Trans-Himalaya region, bordering Tibetan plateau in the east. The landscape is typically above the treeline, between 3000- and 6000-m elevation range. Temperatures range from −30°C in peak winter to 30°C in peak summer. The landscape is mountainous cold desert and rocky, with steep slopes largely dominated by grasses and shrubs. Precipitation is received primarily in the form of snow in between November and March and starts to melt by April.

The major river system is the Spiti River that originates from Kunzum range and travels 150 km in Kinnaur district before its confluence at Khap with Satluj river (from Tibet). Spiti River flows in deep chasms and gorges for most of its length, with a catchment area of ~12,000 km$^2$ (*74*), most part being barren rocky land covered with thick moraines. The heavy snowfall in the winter months contributes to the Satluj's flow in spring. The Pin is the largest tributary of the Spiti River and Lingti, Parechu are other important tributaries. The townships and settlements are clustered close to the river systems or near a glacier from which they harvest water.

Spiti Valley has a low human population density (~1 person/km$^2$). Agriculture is the backbone of the economy, in addition to animal husbandry and tourism, and 80% of the population in Spiti and Kinnaur are predominantly agropastoralists (*75*). According to the 2011 census, the per capita annual income of the district is 2289.57 USD (192,292 INR).

Ecologically, there is a robust community of small and large carnivores (*22*), including the vulnerable snow leopard (*P. uncia*). The two main prey species of the snow leopard—blue sheep (*Pseudois nayaur*) and ibex (*Capra sibirica*)—mostly occur in high altitude pastures and in relatively rugged terrain (*76*). The livestock reared are sheep (*Ovis aries*), goat (*Capra hircus*), donkey (*Equus asinus*), yak (*Bos grunniens*), cattle (*Bos indicus*), dzomo (a yak-cattle hybrid), and horses (*Equus caballus*). The community has access to grazing pastures near the village over an area of ~70 to 100 km$^2$ with traditional grazing and collection rights in the pastures, where cultivation is not permitted. Relatively smaller-bodied livestock such as goats, sheep, donkeys, cows, and dzomo are taken grazing every day during the summer months, while larger-bodied livestock such as yak and horses are left to free-graze for most of the year except for a few weeks during extreme winter (*77*). All livestock are stall fed during the winter months. Fodder is collected from the pastures and crop fields and stored as winter forage.

We used a multidisciplinary approach to studying traditional production systems in the Indian Trans-Himalaya. We first used an ecological lens to perform field experiments comparing green pea, black pea, and barley on their growth performance. We then examined the genetic and nutritional diversity for black pea to assess how well these results align with farmers perceptions.

### Field experiment for survival and reproductive traits

The field study was conducted in March to September 2023 to evaluate the growth performance of three crop species: green peas, black peas, and barley under variable water treatments across altitudinal gradients. The experiment was carried at three sites characterized: low (4000 m), mid (4200 m), and high (4500 m) elevations. The experiment was laid out in a randomized block design with a factorial arrangement, incorporating three factors: crop species, water treatments, and elevation levels. Each treatment combination was replicated three times, and, thus, a total of 81 plots were monitored. The seeds were sown uniformly across all plots, and spacing was determined by interacting with farmers. The sowing density for green pea was lower than black pea seeds since black pea seeds are relatively smaller. The farmers also advised on sowing depth and bed preparation to ensure optimal growth conditions. The Institutional Review Board eprotocol number is 71749.

We set up plots for green, black pea, and barley (1.5 m by 1 m) along a climate gradient in three villages (at elevations of 4000, 4200, and 4500 m) with three water treatments. The water treatments represented varying levels of water availability: low, medium, and regular. The low water treatment simulated drought conditions, medium represented the less than standard recommended irrigation practice for the region, and regular simulated conditions of water used by farmers. The adjustment was made by altering the number of irrigation times rather than the quantity of water.

Throughout the cropping season, we monitored the plants for photosynthetic, nonreproductive, and reproductive traits such as germination rate, flowering time, height at maturity, leaf coloration (disease infestation), and flower/pod production. Data on growth parameters (plant height, leaf area, and biomass) were collected at regular intervals (every 7 to 10 days). Yield components were assessed at the time of harvest. Our dataset consists of observations from a single year (2023–2024 with a pilot in 2022), and so we used ordinary OLS to estimates growth rates with stem height as predictor variable for the crops. OLS ignores site variance, assuming a single growth rate across all sites. Therefore, we also performed an LMM with site as a random effect, allowing for variation in baseline growth across different sites. To compare site-level crop means, we analyzed the traits using analysis of variance (ANOVA) to determine the effects of the crop type, water treatment, elevation, and their interactions. All statistical analyzes were performed using the R software.

### Genetic diversity

For the genetic analysis, we first sampled fresh leaves and performed DNA extraction using DNeasy Plant Pro kit (catalog no. 69204). Illumina libraries were constructed using KAPA HyperPrep Kit, and whole-genome sequencing was performed at MedGenome Labs (based in Delhi, India) on an Illumina NovaSeq platform using a paired 150–base pair configuration. Illumina reads were mapped to the *P. sativum* reference genome (accession GCF_024323335.1) using BWA-MEM, and depth and breadth were calculated using SAMtools (*78*). We want to note that the whole-genome sequencing data generated for the black pea as part of this study have been deposited on National Center for Biotechnology Information (NCBI)–BioSample accession SAMN44380099.

We downloaded additional whole-genome sequencing data from the recent paper (*35*) for *P. sativum* II, *P. sativum* III, *P. sativum* IV,

and *P. sativum* var. *arvense* and also mapped these data to the reference genome using BWA-MEM. We list the whole-genome sequencing data for the PCA analyses in table S2. The resultant alignment files (.bam files) were then run through ANSGD with the following flags "-uniqueOnly 1 -remove_bads 1 -only_proper_pairs 1 -trim 0 -C 50 -baq 1 -minMapQ 20 -minQ 20 -doCounts 1 -GL 1 -doMajorMinor 1 -doMaf 1 -skipTriallelic 1 -SNP_pval 1e-3 -doGeno 32 -doPost 1" to generate posterior probability of genotypes. We then used the ngsCover function from ngsTools (*79*) to generate a covariance matrix for each of the seven chromosomes ($2n = 14$) and visualized the population structure using PCA.

Next, we used three clustering algorithms: hierarchical, spectral, and *k*-means clustering to delineate population structure among different *P. sativum* accessions. Hierarchical clustering builds a tree-like structure (dendrogram), allowing us to infer nested genetic relationships without a priori assumptions about cluster numbers (*80*). For *k*-means and spectral clustering, which require a predefined number of clusters, we determined the optimal clusters (*k*) using two methods: First, we implemented the elbow method, which minimizes within-cluster sum of squares, and then we implemented silhouette analysis, which maximizes intracluster cohesion and intercluster separation. These validation metrics were calculated across a range of *k* values (*2*–*10*) to avoid subjective bias. We performed spectral clustering because it uses graph-based similarity matrices and is better at capturing nonlinear, nonconvex genetic patterns that distance-based methods such as *k*-means might overlook (*80*). These methods were applied to PCs derived from covariance matrices. Our multimethod approach strengthened confidence in the inferred genetic subdivisions among accessions.

We note that our analysis does not rely on SNP array design or GWAS methodologies and does not require LD-based SNP pruning. The approach allows us to retain a representation of genomic variation without concerns of pseudo-replication from LD-linked SNPs, as covariance matrices inherently capture genome-wide patterns of variation rather than treating each SNP independently.

### Nutritional composition of black peas

The nutritional analysis for the black pea samples was done in collaboration with Council of Scientific and Industrial Research-CFTRI based in Mysuru, India. The aim was to create a nutritional profile for black peas that includes the percentage per 100 g of protein, carbohydrates, energy (in kilocalories), and micronutrients such as zinc, magnesium, and iron.

## Supplementary Materials

**This PDF file includes:**

Texts S1 to S3
Figs. S1 to S16
Tables S1 and S2

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# Biocultural vulnerability of traditional crops in the Indian Trans-Himalaya

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