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Genomic Selection and Polygenic Prediction for Climate-Resilient Livestock Production in the Tropics: Current Advances, Persistent Challenges, and Future Directions

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ABSTRACT

Climate change presents mounting and unprecedented challenges to livestock production across tropical regions, where smallholder farming communities depend on their animals for food security, livelihood, and cultural continuity. Progressive increases in ambient temperature, intensifying droughts, shifting disease ecologies, and erratic rainfall are steadily diminishing the productive potential of cattle, buffalo, goats, sheep, and poultry that have historically sustained rural populations across Sub-Saharan Africa, South Asia, and Southeast Asia. Conventional breeding strategies, relying on phenotypic selection and pedigree-based evaluation, lack the precision, speed, and resolution required to keep pace with the accelerating demands of climate-induced selection pressure. Genomic selection (GS), underpinned by high-density single nucleotide polymorphism (SNP) arrays and whole-genome sequencing, has transformed the breeding of temperate dairy and beef cattle over the past two decades; yet its application in tropical livestock systems remains nascent and unevenly distributed across regions and species. Polygenic prediction, the estimation of genomic estimated breeding values (GEBVs) and polygenic scores (PGS) from genome-wide marker data offers a scientifically rigorous and practically tractable framework for identifying animals with superior genetic merit for climate-adaptive traits. These include thermotolerance, water-use efficiency, feed conversion under heat stress, resilience to tick-borne and parasitic diseases, and reproductive performance under nutritional stress. This review synthesises current advances in genomic selection theory and practice as applied to tropical livestock, examines the biological underpinnings of key climate-adaptive traits and their genetic architectures, evaluates the performance of diverse genomic prediction models ranging from GBLUP to deep learning, discusses the integration of multi-omics data streams, and critically assesses the infrastructural, economic, and policy barriers that constrain large-scale adoption. Research priorities and translational pathways are identified through which genomic tools can be embedded within national livestock improvement programmes to deliver measurable gains in productivity, animal welfare, and sustainability across the tropics. It is argued that the future of tropical livestock breeding lies not in the wholesale transplantation of temperate genomic pipelines, but in building regionally anchored reference populations, leveraging indigenous breed diversity, and co-designing genomic tools with the farming communities they are ultimately intended to serve.

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INTRODUCTION

Livestock agriculture sustains the livelihoods of more than one billion people worldwide, the vast majority of whom inhabit tropical and subtropical regions where environmental conditions are challenging, input systems are constrained, and formal breeding infrastructure is limited or entirely absent. Cattle, buffalo, small ruminants, and poultry raised under these circumstances simultaneously fulfil multiple livelihood functions, supplying food, traction, savings, manure, and social capital that simple productivity metrics consistently fail to capture. Over centuries of natural and low-intensity human selection, these animals have developed remarkable resilience to heat, humidity, drought, endemic parasites, and nutritionally sparse forages. However, the pace and breadth of contemporary climate change now threaten to exceed the adaptive capacity of even the most resilient indigenous breeds, while growing demand for animal-source foods, driven by urbanisation and dietary transition, places new productivity pressures on systems simultaneously losing environmental predictability.

The Intergovernmental Panel on Climate Change (IPCC) projects mean global surface temperatures to rise between 1.5°C and 4.0°C above pre-industrial levels by 2100, with tropical land masses facing disproportionately severe warming, altered precipitation regimes, and increased frequency of extreme heat events (IPCC, 2021).[1] For livestock, the primary pathways of climate impact operate through three interconnected channels: direct thermal stress impairing thermoregulation, feed metabolism, fertility, and immune competence; indirect effects mediated through changes in forage availability, water supply, and disease ecology; and systemic disruption of smallholder production systems through extreme weather events, market volatility, and forced herd liquidation.[2,3] The economic and nutritional consequences are substantial. Heat stress alone is estimated to cost global livestock industries more than USD 40 billion annually, with the heaviest burden falling on tropical low- and middle-income countries where veterinary services, cooling infrastructure, and risk-management instruments are most limited.[4,5]

Conventional livestock improvement in the tropics has historically relied on two parallel strategies: exotic breed importation and crossbreeding leveraging the superior milk and meat productivity of temperate breeds such as Holstein Friesian, Brown Swiss, or Large White and within-breed selection of indigenous types based on phenotypic assessment and estimated breeding values (EBVs) derived from progeny testing or performance recording. Both approaches carry significant limitations in tropical contexts. Crossbreeding schemes persistently sacrifice adaptability for productivity, yielding animals that require expensive inputs, veterinary support, and supplementary nutrition, and that exhibit dramatically reduced fertility, disease resistance, and longevity under resource-constrained conditions.[6,7] Indigenous breed selection programmes, by contrast, have been undermined by inadequate recording systems, small effective population sizes, poorly organised breeding societies, and the chronic undervaluation of adaptive traits that are inherently difficult to measure phenotypically under field conditions.

The emergence of dense SNP genotyping arrays and whole-genome sequencing technologies during the first decade of this century opened a fundamentally new paradigm for animal improvement. Meuwissen et al.[8] demonstrated in a seminal paper that the simultaneous fitting of all SNP markers across the genome could produce accurate breeding value estimates even for traits lacking direct phenotypic measurement provided that a sufficiently large and well-phenotyped reference population had been genotyped. This concept, operationalised as genomic selection (GS), was rapidly adopted in temperate dairy cattle breeding, where large reference populations, automated performance recording, and commercial genotyping services created the conditions for transformative genetic gain. Annual genetic progress for milk yield, mastitis resistance, and fertility in North American and European Holstein populations accelerated two- to threefold following the adoption of genomic selection in the late 2000s.[9-11]

The application of these tools to tropical livestock systems has, however, proceeded far more cautiously. The challenges are multifactorial: reference populations for indigenous tropical breeds remain small and geographically fragmented; phenotypic recording infrastructure is underdeveloped; the genetic architectures of climate-adaptive traits are incompletely understood; and the economic rationale for investment in genomic infrastructure has proven difficult to establish in contexts where even basic veterinary services and animal identification systems remain under construction. Nevertheless, a growing body of research from institutions across Sub-Saharan Africa, South Asia, Latin America, and Southeast Asia is demonstrating that genomic selection is both technically feasible and economically promising for tropical breeds, and that the unique diversity of indigenous livestock germplasm represents an underexplored reservoir of alleles for thermotolerance, disease resistance, and drought resilience that temperate genomic resources cannot provide.[12-14]

This review provides a comprehensive and critical synthesis of current knowledge at the intersection of genomic selection, polygenic prediction, and climate-adaptive livestock breeding in the tropics. It is organised into eight substantive sections addressing such as climate change impacts and their biological pathways in tropical livestock; the genetic architecture of climate-adaptive traits; genomic selection theory, statistical models, and predictive performance; multi-omics integration; digital technologies and precision phenotyping; implementation challenges; policy, governance, and institutional dimensions; and future research priorities. The review draws on literature spanning animal genetics, quantitative genetics, genomics, climate science, and development economics, with the explicit aim of bridging methodological advances in high-resource settings and the practical imperatives of low-resource tropical livestock systems.

CLIMATE CHANGE AND TROPICAL LIVESTOCK: BIOLOGICAL IMPACT PATHWAYS

Thermal Stress Physiology in Livestock

Heat stress is the most extensively studied and economically consequential pathway through which climate change affects livestock performance in the tropics. The thermoneutral zone (TNZ), the range of ambient temperatures within which an animal can maintain core body temperature without additional metabolic expenditure varies by species and breed but generally spans 10-25°C for cattle and 15-30°C for goats and sheep. When ambient temperature and humidity combine to push the temperature-humidity index (THI) above critical thresholds (approximately THI > 72 for high-producing dairy cattle), animals enter a state of heat stress characterised by elevated core body temperature, increased respiratory rate, reduced dry matter intake, redistribution of blood flow away from visceral organs, and activation of heat shock protein cascades.[15,16]

The metabolic consequences of heat stress are wide-ranging and involve extensive crosstalk between neuroendocrine, immune, and reproductive systems. Secretion of cortisol and corticosterone increases, suppressing appetite and redirecting glucose to support thermoregulatory processes at the expense of productive functions. Insulin signalling is disrupted, impairing muscle anabolism and mammary glucose uptake. Follicular development and luteal function are compromised by elevated uterine temperature, resulting in reduced conception rates, early embryonic loss, and lengthened calving intervals that may persist for weeks or months after an acute heat event.[17,18] In dairy systems, milk yield reductions of 10-40% have been documented under sustained heat stress, with concurrent decreases in protein and fat composition that reduce milk value beyond the volumetric decline alone.[15]

Tropical indigenous breeds, including Zebu (*Bos indicus*) cattle, Murrah and Surti buffalo, Marwari and Garole sheep, Black Bengal and Osmanabadi goats, and Aseel and Kadaknath chickens exhibit substantially superior thermotolerance compared to their temperate counterparts, owing to a suite of morphological, physiological, and metabolic adaptations accumulated over millennia of selection in hot environments. These include a larger surface-area-to-mass ratio facilitated by longer limbs and ears, denser sweat gland distribution, slick coat phenotypes conferred by variants in the prolactin receptor (PRLR) and slick (SLICK) loci, greater cardiovascular efficiency under thermal load, higher constitutive and inducible expression of heat shock proteins (HSP70, HSP90), and superior renal concentrating ability that reduces obligatory water losses.[19-21] Identifying and leveraging the genetic variants underlying these adaptations represents one of the most promising avenues for climate-proofing tropical livestock through genomic approaches.

Feed and Water Resource Limitations Under Climate Change

Beyond direct thermal effects, climate change fundamentally alters the availability, quality, and predictability of the feed and water resources upon which tropical livestock depend. Rising temperatures and shifting precipitation patterns are projected to reduce the productivity of C3 pastures and legume forages while partially benefiting C4 grasses in certain zones, creating complex spatial and temporal heterogeneity in feed resource availability.[3] Droughts of increasing frequency and severity are reducing the carrying capacity of rangeland systems, accelerating soil degradation through overgrazing, and forcing smallholder farmers to sell animals at distress prices or suffer catastrophic herd losses.

The nutritional quality of available forages also deteriorates under elevated CO_2 and temperature conditions. Reductions in crude protein content of 6-10% and increases in cell wall components, notably neutral detergent fibre (NDF) and acid detergent fibre (ADF) have been documented across multiple forage species under warming scenarios.[22] For ruminants already operating at or near nutritional maintenance thresholds in marginal environments, these reductions in dietary protein and digestibility translate directly into declining body condition, impaired immune function, suppressed ovarian cyclicity, and heightened susceptibility to metabolic disease. Water availability poses an additional critical constraint: livestock in arid and semi-arid tropical systems require 20-60 litres of water per animal per day, and seasonal water scarcity already limits herd sizes, drives seasonal migrations, and fuels multi-species conflicts over water points. Breeding animals with superior water-use efficiency and drought resilience traits with significant but incompletely characterised genetic components represents a direct and high-impact pathway to climate adaptation.

Changing Disease Ecology and Parasite Burden

Climate change is fundamentally reshaping the geographic distribution, seasonality, and intensity of livestock diseases and parasites throughout the tropics. Rising temperatures are expanding the suitable habitat range of tick species including *Rhipicephalus microplus*, *Amblyomma variegatum*, and *Hyalomma spp.*, bringing tick-borne diseases such as East Coast Fever, heartwater, anaplasmosis, and babesiosis into previously unaffected highland areas and extending transmission seasons in endemic zones.[23] The geographic range of tsetse fly (*Glossina spp.*) and associated trypanosomiasis is also shifting with changing rainfall and vegetation patterns, threatening livestock populations in areas that have not historically required prophylactic management.

Gastrointestinal nematode (GIN) burdens are intensifying across many tropical regions as warmer and wetter conditions accelerate larval development on pasture, reduce hypobiosis, and extend transmission seasons. *Haemonchus contortus*, the causative agent of barber's pole worm disease in small ruminants, is of particular concern: it is already the leading cause of production losses and mortality in tropical sheep and goat systems, and climate projections suggest its burden will increase substantially across Sub-Saharan Africa and South Asia in coming decades.[24] Genetic resistance to nematode infection measured through faecal egg counts (FEC), packed cell volume (PCV), and FAMACHA scoring is moderately heritable ($h^2 = 0.15\text{-}0.35$) and has been successfully incorporated into selection indices in several temperate breeds; however, the genomic basis of resistance in tropical indigenous breeds is only beginning to be systematically characterised.

GENETIC ARCHITECTURE OF CLIMATE-ADAPTIVE TRAITS

Heritability and Genetic Parameters of Key Traits

The feasibility and expected rate of genetic progress under selection for any trait are governed fundamentally by its heritability (h^2), the proportion of phenotypic variance attributable to additive genetic effects and by the genetic and phenotypic correlations between target traits and broader trait complexes. For climate-adaptive traits, heritability estimates vary considerably across species, breeds, and production environments, and are generally lower than those for production traits such as milk yield or growth rate, reflecting greater contributions from environmental, maternal, and genotype-by-environment interaction components to phenotypic variance.[25]

Rectal temperature (RT) and respiration rate (RR), the most widely measured indicators of acute heat stress response, show moderate heritability estimates ranging from 0.15 to 0.40 across *Bos indicus* and *Bos taurus* × *indicus* crosses.[26,27] Body temperature measured through vaginal or rumen bolus sensors in more recent studies shows similar heritability, with the additional advantage of continuous recording that enables longitudinal modelling of temperature trajectories as more informative phenotypes than single-point measurements.[28] Tick burden, assessed as tick count scores or composite infestation indices, has reported heritability estimates of 0.12-0.38 in *Bos indicus* and crossbred cattle across Africa and Brazil, confirming the feasibility of selection for tick resistance.[29] Faecal egg count as an indicator of gastrointestinal nematode resistance in small ruminants carries heritability estimates of 0.15-0.40 across studies in Merino, Dorper, and tropical breeds.[30,31]

Production traits measured under heat stress, including milk yield at elevated THI, growth rate in hot-dry environments, and feed conversion ratio during heat challenge frequently display evidence of genotype-by-environment (G×E) interaction, meaning that the genetic ranking of animals for these traits shifts across thermal environments. The magnitude and pattern of G×E interactions for tropical livestock production traits have been examined through reaction norm models, wherein the breeding value of an animal is expressed as a linear or curvilinear function of an environmental gradient.[32] Detection of significant G×E interaction implies that optimal selection decisions differ by environment, and that sires evaluated under one climatic regime may not rank consistently when their progeny are raised under markedly different conditions, a critical consideration for genomic reference population design spanning multiple production environments.

Genome-Wide Association Studies for Climate-Adaptive Traits

Genome-wide association studies (GWAS) have been the primary analytical tool through which the genomic landscape of climate-adaptive traits in tropical livestock has begun to be mapped. GWAS identifies statistical associations between individual SNP markers distributed across the genome and phenotypic measurements or estimated breeding values for the target trait, enabling the localisation of quantitative trait loci (QTL) and the nomination of candidate genes for functional follow-up. The statistical architecture of GWAS results specifically the number, effect size distribution, and genomic locations of significant associations provides critical information about the underlying genetic architecture of the trait, which in turn informs the selection of an appropriate genomic prediction model.

For thermotolerance, GWAS conducted in *Bos indicus* and tropically adapted composite breeds have identified significant associations on chromosomes 5, 6, 14, 23, and 27, with several studies converging on genomic regions harbouring genes involved in heat shock protein expression (HSPA1A, HSPA1B, HSPB8), ion channel regulation (TRPM8, TRPA1), circadian rhythm (PER2, CLOCK), and hypothalamic-pituitary-adrenal axis function (CRHR1, POMC).[33-35] The slick coat mutation in the PRLR gene on chromosome 20 of Senepol and Romosinuano cattle represents one of the best-characterised major QTL for heat tolerance, with slick-coated animals demonstrating significantly lower rectal temperatures, higher sweating rates, and better-maintained fertility under thermal challenge.[20,21] The characterisation of this large-effect variant suggests that for some climate-adaptive traits, major-gene effects coexist with a polygenic background, a hybrid genetic architecture with direct implications for model selection in genomic prediction.

GWAS for tick resistance in African cattle populations has identified candidate regions on chromosomes 2, 3, 7, 10, 12, and 22, with genes involved in immune recognition (TLR4, CD14), complement activation (C3, CFB), and skin barrier integrity (FLG, DSP) among the most consistently implicated.[36,29] In small ruminants, GWAS for *Haemonchus contortus* resistance in tropical breeds has highlighted genomic regions on ovine chromosomes 1, 3, 6, and 20, with candidate genes encoding MHC class II molecules, natural killer cell receptors, and mucin proteins expressed in the abomasal mucosa.[37,38] The predominantly polygenic architecture of parasite resistance traits characterised by many markers of small effect rather than a few of large effect suggests that genomic selection models capturing the full genomic relationship matrix will outperform marker-assisted selection approaches targeting only the most significant QTL.

Indigenous Breed Diversity as a Genomic Resource

One of the most strategically important insights from population genomic studies of tropical livestock has been the extent and distinctiveness of genetic variation harboured by indigenous breeds, much of which is absent from or occurs at low frequency in commercial temperate populations. Comprehensive SNP diversity analyses using 50K to 777K arrays have documented substantially higher nucleotide diversity, longer linkage disequilibrium (LD) blocks, and distinct FST outlier signatures in indigenous Zebu, Sanga, and African taurine cattle compared to European taurine breeds, reflecting divergent evolutionary histories shaped by selection pressures including climate, disease ecology, and human management.[29,39]

Signatures of positive selection identified in tropical indigenous breeds through methods including the integrated haplotype score (iHS), cross-population extended haplotype homozygosity (XP-EHH), and pairwise FST analysis are systematically enriched for functional categories relevant to climate adaptation, encompassing heat stress response, immune function, metabolic regulation, and circadian rhythm. This observation provides genome-wide evidence that these breeds carry distinct adaptive alleles shaped by centuries of natural and human selection in tropical environments.[40-42] This diversity represents an irreplaceable resource: once lost to genetic erosion through indiscriminate crossbreeding or neglect, it cannot be recovered. This reality underscores the co-importance of genetic conservation and genomic characterisation in any sustainable tropical livestock improvement strategy.

The concept of admixture, the detection and quantification of historical gene flow between divergent populations has added further nuance to our understanding of climate adaptation in tropical livestock. Many tropical cattle breeds carry varying proportions of *Bos indicus* and *Bos taurus* ancestry that correlate with altitude, latitude, and historical disease challenge in their home environments.[39] Genomic regions introgressed from *Bos indicus* into historically taurine-dominated African cattle populations in tsetse-fly zones are disproportionately associated with immune gene clusters, consistent with selection maintaining indicus-derived immunity alleles even as overall body conformation retained taurine characteristics. Leveraging these admixture patterns in genomic selection models requires careful attention to population structure in reference population design and in statistical correction of GWAS results.

GENOMIC SELECTION: THEORY, MODELS, AND PERFORMANCE IN TROPICAL LIVESTOCK

Theoretical Foundations of Genomic Selection

The conceptual foundation of genomic selection rests on the recognition that when SNP markers are sufficiently dense relative to the LD structure of the genome, every QTL influencing a trait of interest will be in linkage disequilibrium with at least one marker, allowing the aggregate effect of all QTL to be captured in the genomic estimated breeding value (GEBV). Meuwissen et al.[8] proposed three statistical frameworks for estimating marker effects simultaneously: ridge regression BLUP (RR-BLUP), assuming equal variance for all marker effects; BayesA, allowing unequal marker effect variances drawn from a scaled inverse chi-squared distribution; and BayesB, which additionally allows a proportion π of markers to carry zero effect. These models differ in their implicit assumptions about QTL effect size distributions, with BLUP approaches reflecting an infinitesimal architecture and Bayesian approaches accommodating variable sparsity.

The single-step genomic BLUP (ssGBLUP) model, proposed independently by Aguilar et al.[43] and Christensen & Lund[44], resolved a major practical limitation of early genomic selection by combining the genomic relationship matrix (G) from genotyped animals with the pedigree-based numerator relationship matrix (A) from non-genotyped animals into a unified H matrix. This integration allows simultaneous, coherent analysis of phenotypic records from both genotyped and non-genotyped animals within a single mixed model, maximising the utility of all available phenotypic information for GEBV estimation. The ssGBLUP framework has become the dominant implementation platform for national genomic evaluation systems worldwide and is of particular relevance to tropical livestock contexts, where the proportion of genotyped animals relative to the total phenotyped population is typically very low.

The accuracy of genomic prediction, the correlation between GEBV and true breeding value (TBV) depends on several interacting factors that collectively define the practical ceiling of genetic gain achievable through genomic selection. These include the size and representativeness of the reference population; the heritability of the target trait; the extent and persistence of LD between markers and causal variants across the reference and selection candidate populations; the allele frequency spectrum of causative variants; the appropriateness of the statistical model for the trait's genetic architecture; and the quality and completeness of phenotypic data.[10,45,46] Each of these factors poses specific challenges in tropical livestock systems that differ materially from the temperate commercial contexts in which genomic selection was first developed and validated.

Genomic Prediction Models: From GBLUP to Deep Learning

Genomic BLUP (GBLUP), implemented through the genomic relationship matrix G constructed from SNP marker data following VanRaden[47], remains the most widely applied model in both commercial and research genomic evaluation systems, valued for its computational tractability, statistical robustness, and competitive predictive accuracy across a broad range of traits and species. In GBLUP, the GEBV for each animal is estimated as a weighted sum of phenotypic deviations from all animals in the reference population, with weights proportional to their genomic relationship to the candidate; a formulation that implicitly assumes an infinitesimal genetic architecture. GBLUP is particularly well-suited to highly polygenic traits characterised by many loci of small effect, which describes the majority of economically important livestock traits including production, growth, and fertility.

Bayesian variable selection methods, including BayesA, BayesB, BayesC, BayesCπ, and the Bayesian LASSO extend the GBLUP framework by allowing heterogeneous marker effect variances and, in some formulations, explicit sparsity. These methods can achieve superior prediction accuracy for traits with a genetic architecture characterised by a moderate number of QTL of larger effect, such as disease resistance traits or those for which major QTL have been empirically validated.[8,48] For tropical livestock applications, Bayesian approaches may offer advantages for traits like tick resistance or slick-coat thermotolerance where major-effect loci have been identified, but require larger reference populations to reliably estimate the π parameter and are substantially more computationally demanding than GBLUP.

Machine learning and deep learning approaches have entered the livestock genomic prediction arena in earnest over the past decade, motivated by their capacity to capture non-linear relationships, epistatic interactions, and higher-order genomic feature combinations that are invisible to linear models. Convolutional neural networks (CNNs) applied to genomic data treat ordered sequences of SNP markers as analogous to image data, using convolutional filters to detect locally co-varying marker patterns that may correspond to haplotype blocks or LD clusters.[49] Recurrent architectures, including long short-term memory networks (LSTM) and transformer-based models, leverage the sequential structure of chromosomal SNP data to model long-range dependencies between distant genomic regions.[50] While deep learning models have demonstrated competitive or superior accuracy in simulation studies and some real livestock datasets, their data requirements, interpretive opacity, and computational demands currently limit practical deployment in tropical livestock programmes operating with small reference populations and constrained computational infrastructure.

Reference Population Design for Tropical Breeds

The reference population; the set of animals with both phenotypic records and genotype data used to estimate SNP effects or construct the genomic relationship matrix is the cornerstone of any genomic selection programme. In temperate dairy cattle, reference populations numbering in the hundreds of thousands of bulls with reliably estimated daughter yield deviations have accumulated over decades of progeny testing, enabling genomic prediction accuracies of 0.70–0.90 for major production traits.[11,51] For tropical indigenous breeds, current reference populations typically number in the hundreds to low thousands, constraining prediction accuracy to 0.30-0.60 for most traits even under optimistic assumptions.[6,29]

Strategies for expanding reference population size in resource-constrained tropical contexts include multi-breed reference population merging, imputation-based approaches to cost-effective genotyping, and the formation of regional or international breed consortia. Multi-breed genomic evaluation pools phenotypic and genotypic data from multiple breeds into a common analysis, leveraging the greater statistical power of the combined dataset while accommodating breed differences in allele frequency and LD structure. Studies in African *Bos indicus* breeds have shown that multi-breed reference populations can improve GEBV accuracy by 10-30% compared to single-breed analyses, particularly for breeds with very small individual reference populations.[52,53]

Low-pass whole-genome sequencing followed by imputation to high density offers a cost-effective alternative to commercial SNP arrays for genotyping large numbers of animals in tropical settings. At 1-2× sequencing depth, modern imputation pipelines using breed-specific reference panels can recover 95-99% of common variant genotypes at error rates below 2-3%, delivering data quality comparable to 50K arrays at a substantially reduced per-sample cost.[54,55] The development of breed-specific imputation reference panels requires initial investment in deep sequencing of representative individuals but subsequently enables affordable expansion of genotyped reference and candidate populations. Several African genomics initiatives including the Pan-African Livestock Genomics and Improvement Network (PAGLN) and the Africa Dairy Genetics Gains (ADGG) programme have adopted low-pass sequencing strategies to cost-effectively expand genotyping coverage across East African dairy cattle populations.

MULTI-OMICS INTEGRATION FOR ENHANCED CLIMATE ADAPTATION BREEDING

Transcriptomics and Gene Expression Under Heat Stress

Transcriptomic profiling of livestock tissues under experimentally controlled or naturally occurring heat stress has provided detailed molecular maps of the cellular response to hyperthermia that complement and substantially extend genomic QTL mapping. RNA-sequencing (RNA-seq) studies in *Bos indicus* and *B. taurus × indicus* crossbred cattle subjected to heat stress have consistently identified upregulation of heat shock protein genes (HSPA1A, HSPA1B, HSPA4, HSPB1, HSPD1), molecular chaperones, antioxidant enzymes (SOD1, CAT, GPX1), and autophagy pathway components, alongside downregulation of genes involved in cell cycle progression, mRNA translation, and primary metabolism.[56-58]

Tissue-specific transcriptomic responses reveal biologically important heterogeneity in the molecular consequences of heat stress. Mammary gland transcriptomes of high-producing dairy cattle under heat stress show pronounced suppression of casein gene expression, lipogenic enzyme activity, and glucose transporter abundance that directly accounts for the observed reductions in milk volume and compositional quality.[18] Hypothalamic transcriptomes under heat stress show altered expression of neuropeptide Y, gonadotropin-releasing hormone (GnRH), and kisspeptin signalling components that mechanistically link hyperthermia to suppression of the hypothalamic-pituitary-gonadal axis and thus to the well-documented effects of heat stress on fertility. Leukocyte transcriptomes captured through blood sampling, a non-invasive approach applicable under field conditions show heat stress-responsive expression signatures that differ significantly between breeds of contrasting thermotolerance, offering a promising avenue for blood-based biomarker development in field-scale breeding programmes.

Epigenomics: DNA Methylation and Chromatin Regulation

Epigenetic modifications-heritable changes in gene expression that do not involve alterations to the underlying DNA sequence have emerged as a significant dimension of climate adaptation in livestock that existing genomic selection models do not capture. DNA methylation at CpG dinucleotides, the most extensively studied epigenetic mark in livestock, shows environmentally responsive dynamics that can persist through mitotic cell divisions and, in some documented instances, across generations, with implications for the transgenerational transmission of acquired adaptive states.[59,60]

Whole-genome bisulfite sequencing (WGBS) studies comparing *Bos indicus* and *Bos taurus* breeds have identified thousands of differentially methylated regions (DMRs) in blood, liver, and sperm, with enrichment of DMRs in promoter regions of genes involved in heat stress response, immune regulation, and metabolic adaptation.[61] Notably, DMRs detected in sperm at loci differentially expressed in offspring tissues raise the possibility that epigenetic marks acquired in response to thermal challenge in one generation can influence gene expression in the next, a mechanism for more rapid population-level adaptation than DNA sequence-based selection alone can account for. The incorporation of epigenomic variation into genomic prediction frameworks, through methylation quantitative trait loci (meQTL) analysis or epigenome-wide association studies (EWAS), is an active area of methodological development with potential to improve prediction accuracy for traits with significant epigenetic components.

Metabolomics and Proteomics in Stress Biology

Metabolomics-the systematic profiling of small-molecule metabolites in biological fluids or tissues provides a functional readout of the integrated biochemical response to environmental challenge that bridges genotype and phenotype at a resolution inaccessible to genomic or transcriptomic approaches alone. In livestock, plasma and serum metabolomics under heat stress have identified consistent alterations in amino acid catabolism, glucose metabolism, lipid oxidation, and antioxidant capacity that reflect the systemic metabolic reorganisation imposed by sustained hyperthermia.[62,63]

Quantitative proteomics of plasma, milk, or tissue samples from heat-stressed versus thermoneutral animals has identified differentially abundant proteins including acute phase response proteins (haptoglobin, serum amyloid A), complement components, heat shock proteins secreted into the extracellular environment, and metabolic enzymes reflecting altered substrate utilisation patterns.[64] These proteomic signatures represent potential blood-based biomarkers of heat stress severity and recovery that could support cost-effective field phenotyping in climate-adaptive breeding programmes. The integration of metabolomic and proteomic data with genomic information through genomic structural equation models or multi-omics factor analysis represents a frontier at which mechanistic understanding of adaptation can be translated into more biologically informed and accurate genomic prediction pipelines.

DIGITAL TECHNOLOGIES AND PRECISION PHENOTYPING FOR CLIMATE-ADAPTIVE TRAITS

Wearable Sensors and IoT-Based Data Collection

Precision phenotyping of climate-adaptive traits has historically been among the most significant bottlenecks in livestock genomic breeding programmes in the tropics. Traits such as rectal temperature, respiration rate, tick burden, and reproductive cyclicity require skilled labour, animal handling facilities, and frequent measurement to generate phenotypic records of sufficient volume and quality for use as reference population data in genomic evaluation. The proliferation of low-cost wearable sensors, Internet of Things (IoT) connectivity platforms, and automated data collection systems is beginning to transform this constraint, enabling continuous and high-resolution phenotypic data capture at scales previously unachievable under tropical field conditions.

Subcutaneous or rumen-bolus temperature loggers now enable continuous recording of core body temperature at 1 to 30-minute intervals over periods of months without disturbing the animal, generating phenotypic trajectories that are far more informative for characterising thermotolerance genotype than single-point rectal temperature measurements.[65] Ear-tag-mounted accelerometers combined with machine learning classifiers can quantify rumination time, feeding behaviour, oestrus activity, and locomotion patterns, from which heat stress load, body condition, and reproductive status can be inferred in real time.[66] Infrared thermography of eye, nasal, and skin surface temperature captured through handheld or remotely mounted cameras provides a non-invasive, high-throughput indicator of peripheral thermoregulatory status that correlates with core body temperature and can be deployed at scale in field settings.[67]

Deployment of these technologies in smallholder tropical livestock systems faces practical challenges of cost, power supply, connectivity, environmental robustness, and farmer digital literacy that have not been encountered in their original commercial dairy farm contexts. Solar-powered edge computing platforms, low-power wide-area network (LPWAN) connectivity through LoRa or NB-IoT protocols, and community-operated data hubs are among the technological architectures being explored for deploying precision livestock monitoring in resource-limited tropical settings. Data interoperability standards, farmer consent frameworks, and benefit-sharing arrangements within community-based data collection programmes are additional dimensions requiring sustained attention to ensure that digital phenotyping initiatives are both equitable and durable.

Remote Sensing and Environmental Data Integration

The integration of high-resolution satellite remote sensing data with livestock genomic and phenotypic datasets offers a powerful approach to characterising the environmental gradients across which genotype-by-environment interactions for climate-adaptive traits are expressed. Land surface temperature (LST) derived from MODIS or Landsat satellites, normalised difference vegetation index (NDVI) as a proxy for forage availability, precipitation estimates from CHIRPS or GPM products, and vapour pressure deficit data can be combined with farm location coordinates to assign nuanced environmental covariates to each phenotypic observation, enabling more precise reaction norm models of G×E interaction for adaptive traits.

Climate-informed genomic selection models that incorporate environmental covariates as interaction terms with marker effects have been demonstrated to improve prediction accuracy for traits exhibiting significant G×E interaction, compared to standard GBLUP models that treat the environment as a fixed effect or disregard it entirely.[68,69] The environmental-marker interaction (EMI) model extends the GBLUP framework to include a term capturing the genomic variance component attributable to environmental sensitivity, effectively decomposing the GEBV into a main-effect component (breeding value in an average environment) and an interaction component (deviation of breeding value as a function of environmental gradient). For climate-resilient livestock breeding, EMI-type models offer a principled framework for identifying animals with stable performance across a range of thermal environments, a plasticity-resilience distinction that is both biologically meaningful and operationally important for selection decisions.

IMPLEMENTATION CHALLENGES IN TROPICAL LIVESTOCK GENOMIC PROGRAMMES

Genotyping Infrastructure and Cost Constraints

The economics of genotyping remain a primary barrier to scaling genomic selection in tropical livestock systems, particularly in smallholder-dominated production contexts where farm sizes are small, livestock populations are dispersed across vast geographic areas, and formal breed societies are absent or underdeveloped. Commercial SNP genotyping arrays at 50K density, the standard platform for dairy genomic evaluation in temperate systems cost approximately USD 25-50 per sample for large commercial entities with established laboratory agreements, but effective costs in low- and middle-income country settings, when accounting for sample collection, DNA extraction, cold chain logistics to certified laboratories, and data management, frequently reach USD 80-150 per sample.[53]

For a reference population of 5,000 animals, a minimum threshold for achieving prediction accuracy above 0.60 for moderately heritable traits, total genotyping costs at these rates represent investments of USD 400,000-750,000, exceeding the annual budget of most national livestock improvement programmes in Sub-Saharan Africa or South

Asia without substantial external donor support. Customised low-density arrays (5K-10K markers) designed around markers with the highest information content for specific breed-by-trait combinations offer a cost-reduction pathway, with subsequent imputation to medium or high-density using breed-specific reference panels.[70] GeneSeek Genomic Profiler (GGP) products including the Indicus HD and Africa multi-breed arrays have been specifically designed for tropical cattle populations, providing cost-optimised genotyping with coverage of markers informative for traits of relevance in these breeds. Their deployment through African and South Asian CGIAR research programmes has materially accelerated reference population construction.

Phenotyping Systems and Data Quality

The reliability of genomic selection depends as fundamentally on the quality of phenotypic data in the reference population as on the density or accuracy of genotyping. In tropical livestock systems, the formal performance recording infrastructure, livestock identification systems, milk recording schemes, on-farm data collection networks, and centralised databases that underpins the phenotypic data streams used in temperate genomic evaluation is largely absent, underfunded, or confined to a small subset of commercial farms unrepresentative of predominant smallholder production systems.[6] The consequences for genomic prediction accuracy are severe: phenotypic records of low precision, inconsistently defined, incompletely documented, or confounded with unaccounted environmental effects inflate error variance, attenuate marker-trait associations, and reduce the correlation between GEBV and true breeding value.

Community-based breeding programmes (CBBPs) have emerged over the past two decades as an organisationally appropriate model for integrating genetic improvement with on-farm performance recording in smallholder tropical systems. CBBPs organise groups of farmers around a shared breeding objective, a common recording system, and collective use of genetically evaluated sires, with technical support from public-sector extension services or development organisations.[71,72] Incorporating the genomes of community-owned sires and a stratified sample of dams into a genomic reference population built on combined phenotypic records creates a sustainable, farmer-anchored platform for genomic improvement that does not require top-down genotyping of individual smallholder animals. The ADGG initiative in East Africa, the Sub-Saharan Africa Dairy Genomics project, and the SMARTER project for small ruminants provide operational models from which tropical programmes can draw practical lessons.

Computational and Bioinformatics Capacity

The computational requirements of modern genomic evaluation, fitting mixed models with relationship matrices derived from hundreds of thousands of markers across tens of thousands of animals, imputing low-density genotypes to high density, conducting GWAS with appropriate genomic control, and increasingly training deep learning models on genomic data are substantial and have historically demanded access to high-performance computing (HPC) clusters and specialised bioinformatics expertise that are not equitably distributed across the global research landscape. National agricultural research institutes in tropical low-income countries frequently lack the server infrastructure, licensed software, and trained personnel to independently run or validate genomic evaluation systems, creating dependencies on international partners or commercial service providers that undermine the long-term sustainability of national genomic programmes.

Cloud computing platforms, including Amazon Web Services, Google Cloud, and Microsoft Azure, as well as research-oriented platforms such as the CGIAR Genebank Platform and Africa Genomics Research Network (AGReNet) are progressively democratising access to high-performance genomic analysis through pay-per-use computational resources accessible from any internet connection. Open-source genomic analysis software including BLUPF90[73], GCTA[74], PLINK[75], BEAGLE[76], and the R package breedR provide validated computational tools for reference population management, GWAS, imputation, and genomic prediction that are freely available to all. Building practical capacity in their use through regional training programmes, graduate curriculum integration, and south-south collaboration networks is a critical prerequisite for sustainable genomic livestock improvement across the tropics.

POLICY, GOVERNANCE, AND INSTITUTIONAL DIMENSIONS

National Genomic Breeding Programme Frameworks

Institutionalising genomic selection within national livestock improvement programmes requires policy and governance frameworks that address the full value chain from breed registration and genetic resource conservation through to semen distribution, performance recording, and genomic evaluation. In most tropical countries, this chain involves multiple institutions such as ministries of agriculture, national livestock research institutes, breed societies, artificial insemination centres, and veterinary services whose mandates, incentive structures, and information systems are rarely well integrated.[6] The absence of a coordinating architecture that aligns these institutions around a common genomic improvement strategy remains one of the most persistent governance failures constraining genetic progress in tropical livestock.

Successful national genomic programme models from temperate contexts share several design features that are instructive for programme architects in tropical settings: a clear and agreed national breeding objective with economically derived weights assigned to relevant traits; a statutory or voluntary national performance recording scheme with minimum data quality standards; a national genomic reference population with defined and funded update protocols; transparent and publicly accessible genetic evaluation results; and a competitive marketplace for genotyped genetic material with formal guarantees of pedigree integrity. Adapting these design principles to tropical institutional contexts, where statutory authorities are weaker and the commercial livestock sector less developed requires country-specific institutional analysis and flexible programme architectures informed by stakeholder engagement.

Several countries have made meaningful progress in establishing genomic livestock improvement frameworks. Ethiopia has integrated genomic selection into its national dairy cattle improvement programme for Boran × Holstein crossbreds, with a reference population exceeding 3,000 genotyped cows and ongoing collaboration with ILRI and Wageningen University.[71] Kenya's national dairy genomics programme, developed through the ADGG project, has genotyped over 35,000 smallholder dairy cattle and constructed one of the largest tropical dairy reference populations in the world, enabling GEBVs for milk yield, fat and protein percentage, and udder health to be estimated with accuracies approaching those achieved in small temperate breed programmes.[77] India's national programme on bovine genomics, coordinated by the National Bureau of Animal Genetic Resources (NBAGR), has advanced the genomic characterisation of 35 registered indigenous cattle breeds, including GWAS for milk production, heat tolerance, and disease resistance in Sahiwal, Tharparkar, and Kankrej breeds.[19]

Genetic Resource Sovereignty and Data Governance

The collection, storage, and international exchange of genomic data from indigenous livestock breeds raises important questions of genetic resource sovereignty, intellectual property rights, and equitable benefit sharing, governed by an evolving international legal framework. The Convention on Biological Diversity (CBD, 1992), the Nagoya Protocol on Access and Benefit Sharing (2010), and the International Treaty on Plant Genetic Resources for Food and Agriculture (ITPGRFA, 2001) collectively establish the principle that countries hold sovereign rights over their genetic resources, and that prior informed consent and agreed benefit-sharing arrangements should govern their international exchange. The application of these principles to animal genetic resources is less clearly elaborated than for plant resources, but the Interlaken Declaration on Animal Genetic Resources (2007) and FAO's Global Plan of Action for Animal Genetic Resources provide normative frameworks that national programmes should align with.[78]

In practice, many tropical countries lack the regulatory and monitoring capacity to effectively implement access and benefit-sharing provisions for livestock genomic data. The internationalisation of genomic reference populations through CGIAR consortia and bilateral collaborations has at times proceeded without adequate attention to data sovereignty considerations. The development of data governance frameworks that protect the interests of source countries and farming communities including data-sharing agreements with defined benefit-sharing provisions, community data trusts for smallholder genomic data, and open-access publication of marker effect estimates is an area of active normative development that the livestock genomics community must engage with constructively and systematically.

Investment Cases and Funding Architecture

Building the business case for public and private investment in tropical livestock genomic programmes requires rigorous economic analysis that captures both the direct productivity gains achievable through accelerated genetic progress and the broader social, environmental, and food security co-benefits of climate-resilient breeding. Economic returns on investment for genomic selection in temperate dairy cattle are well documented, with producer benefit per dollar invested in genomic evaluation infrastructure estimated at USD 5-20, driven by the acceleration of annual genetic progress and reduction in generation interval achievable through genomic selection compared to conventional progeny testing. Comparable analyses for tropical livestock genomic programmes are fewer and more heterogeneous, but generally indicate positive returns over 10-20-year time horizons, with marginal cost-effectiveness improving as reference population size grows and genotyping costs continue to decline.

The funding landscape for tropical livestock genomics encompasses international development banks, bilateral development agencies, multilateral research programmes, philanthropic foundations, and domestic government appropriations. The fragmentation and project-based nature of much of this funding creates a persistent challenge for building the long-term institutional and human capacity that genomic programmes require. Longer funding cycles, co-financing requirements from national governments, and the embedding of genomic improvement within broader livestock system development programmes rather than as standalone research projects represent funding architecture reforms that would substantially improve the sustainability and impact of investments in tropical livestock genomics.

FUTURE RESEARCH PRIORITIES AND PROSPECTS

Expanding Reference Populations and International Consortia

The single most impactful action the tropical livestock genetics community could take to accelerate genomic breeding progress is the coordinated expansion of reference populations for key breeds and species through international consortia. The fragmentation of current tropical reference populations across national programmes, CGIAR centres, and university research groups each with modest numbers in the hundreds to low thousands means that individual programmes operate well below the statistical power thresholds needed for high-accuracy genomic prediction of complex adaptive traits. Pooling genotypic and phenotypic data from multiple countries and institutions under harmonised data standards and governance agreements would immediately multiply reference population size and geographic coverage, improve prediction accuracy and extend the applicability of GEBVs across diverse production environments.

The Pan-African Livestock Genomics Network (PAGLN), the SMARTER project for European and Mediterranean small ruminants, and the Asia Animal Genomics Network represent nascent models that have achieved early successes but remain limited in geographic and species scope. Extending these consortia to include West and Central African breeds, South and Southeast Asian cattle and buffalo populations, and indigenous small ruminants of Latin America would create reference populations, targeting 10,000-50,000 genotyped animals per breed group of the scale needed to push genomic prediction accuracies into the 0.60-0.80 range for climate-adaptive traits. Technical and governance architectures for such consortia must address data format harmonisation, phenotypic trait definitions, imputation reference panel sharing, and equitable benefit-sharing arrangements.

Novel Phenotyping Technologies and Functional Genomics

Progress in tropical livestock genomic breeding will require sustained innovation in phenotyping technologies that can cost-effectively generate high-quality data on climate-adaptive traits at population scale. Novel phenotyping platforms being explored include automated tick counting through computer vision and machine learning applied to standardised body zone photographs; real-time continuous rumen temperature monitoring through retrievable rumen boluses; drone-based infrared thermography for remote sensing of skin surface temperature in free-roaming rangeland cattle; and automated ultrasound body composition phenotyping to capture fat distribution and muscle mass traits relevant to drought resilience and carcass merit.

The integration of functional genomics resources for tropical livestock including annotated genome assemblies, tissue-specific transcriptome atlases, single-cell RNA-seq datasets, and ATAC-seq chromatin accessibility maps with genomic prediction frameworks represents a high-priority research avenue for improving the biological accuracy and cross-breed transferability of GEBVs. Functional annotation of SNP variants, through methods including GenoCanyon, FarmGTEx, and livestock-specific PolyPhen implementations, can assign prior probabilities of functional effect to markers, improving Bayesian genomic prediction by weighting markers in regulatory and coding regions more heavily than intronic or intergenic variants.[33,79] The construction of comprehensive functional annotation tracks for *Bos indicus*, buffalo, goat, and sheep reference genomes analogous to the ENCODE and GTEx resources available for human genomics would be an enduring public good that the tropical livestock genomics community could pursue collectively.

Gene Editing and the Future of Climate-Adaptive Livestock

The accelerating capability of precision genome editing technologies, particularly CRISPR-Cas9, to introduce specific genetic variants with defined phenotypic effects offers a complementary pathway to genomic selection for hastening climate adaptation in tropical livestock. The introgression of the PRLR slick coat mutation, a single nucleotide change conferring significantly superior thermotolerance from Senepol into high-producing dairy breeds through conventional backcrossing requires 5-7 generations spanning 15-20 years; targeted CRISPR editing could in principle introduce the identical variant into elite breeding animals of any breed within a single generation, bypassing the chromosomal drag and generational time penalty of conventional introgression.[20,80] Similarly, the precise introduction of genetic variants conferring resistance to East Coast Fever or trypanosomiasis into productive but susceptible breeds would represent high-value climate and disease adaptation targets for gene editing.

The regulatory landscape for gene-edited livestock remains heterogeneous and continues to evolve, with significant divergence in how different jurisdictions treat single-nucleotide edits that could theoretically arise through natural mutation versus transgenesis. For tropical countries, the development of clear, science-based national biosafety regulatory frameworks for gene-edited livestock, anchored in Cartagena Protocol on Biosafety principles while accommodating the distinct risk profile of precision editing relative to transgenesis is a governance priority that will determine whether this technology can contribute to climate-adaptive livestock improvement within a framework that safeguards public trust and food system integrity.

Integration with Climate Models and Breeding Programme Simulation

The design of genomic breeding programmes for climate-resilient livestock production requires forward-looking integration of projected climate scenarios with quantitative genetic models that simulate the trajectory of population-level adaptation under different selection strategies and demographic conditions. Stochastic simulation tools including AlphaSim, QMSim, and MoBPS can model the accumulation of genomic gain under defined selection intensities, generation intervals, and reference population expansion trajectories, enabling comparison of alternative programme designs before costly real-world implementation.[80-82] When these frameworks are parameterised with projected temperature and precipitation scenarios from CMIP6 climate models and G×E interaction estimates from current breed data, they can project the expected genetic gap between the breeding population's performance trajectory and the environmental requirement for sustained productivity identifying when additional adaptation is needed and the selection intensity required to achieve it.

The concept of a climate-informed genomic breeding objective, where economic weights assigned to climate-adaptive traits in the aggregate genotype are dynamically updated to reflect the changing relative economic value of thermotolerance, drought resilience, or disease resistance as climate projections evolve provides a principled framework for keeping breeding programmes prospectively aligned with future rather than present environmental realities. Operationalising such a dynamic breeding objective requires periodic updating of economic weight estimates using bio-economic modelling that incorporates projected changes in feed costs, disease prevalence, and thermal stress indices, linked to climate model outputs through interdisciplinary collaborations between animal breeders, agricultural economists, and climate scientists. Building this modelling capacity for key tropical livestock species represents a research investment with long time horizons but potentially transformative consequences for the resilience of tropical food systems under accelerating climate change.

CONCLUSIONS

Tropical livestock systems stand at a critical juncture where the compounding pressures of accelerating climate change, rising food demand, and biodiversity loss converge upon farming communities that have long been underserved by the institutions and technologies of modern animal science. Genomic selection and polygenic prediction offer scientifically validated and increasingly cost-effective tools for accelerating genetic improvement of livestock for climate-adaptive traits like thermotolerance, drought resilience, disease resistance, and feed efficiency under environmental stress at a pace and precision that conventional breeding methods cannot approach. The evidence synthesised in this review demonstrates that genomic prediction is technically feasible in tropical breed populations, that climate-adaptive traits carry sufficient heritability to respond meaningfully to selection, that indigenous tropical breeds harbour unique adaptive genetic diversity of inestimable value to future breeding, and that multi-omics, precision phenotyping, and digital data capture technologies are maturing in ways that will progressively reduce the bottlenecks constraining genomic programme scale across the tropics.

Yet translating this technical promise into measurable, equitable, and durable outcomes for smallholder farmers and their communities requires considerably more than genomic science alone. It demands sustained, long-term investment in national livestock improvement institutions, encompassing recording systems, artificial insemination networks, reference laboratories, and genomic evaluation services that most tropical countries have not yet built to the standard required. It requires governance innovations around data sovereignty, benefit sharing, community-based breeding programme design, and regulatory frameworks for gene editing that governments and the international community are only beginning to develop with appropriate seriousness. It requires funding architectures that support genuine institutional capacity building over long timescales rather than short-cycle project outputs, and it requires the active co-design of genomic tools and breeding programmes with the farming communities they are intended to serve not as end beneficiaries but as essential partners in design, implementation, and governance.

The potential payoff, measured in terms of animal welfare, household food security, environmental sustainability, and rural economic resilience, justifies the investment on every dimension of analysis. Livestock that can maintain productive performance under rising temperatures, sustain fertility through prolonged droughts, withstand shifting disease pressures, and efficiently convert degraded forages into valuable nutrition are not merely a productivity enhancement, they represent a cornerstone of climate adaptation for a billion of the world's most vulnerable people. The science to deliver this future exists and is advancing rapidly. The imperative for the coming decade is to build the institutional, financial, and social architecture that allows this science to reach the animals and the farmers who need it most and who, for too long, have remained at the margins of the global genomics revolution.

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