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Signatures of selection underlying adaptation and production performances in tropical *Bos indicus* cattle: A systematic review

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Systematic Review

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Abstract

Tropical *Bos indicus* (zebu) cattle are essential for livestock production in tropical regions because of their adaptation to heat, parasites, and low-quality feed. Natural and artificial selection leave detectable genomic footprints, yet evidence from signatures of selection studies remains fragmented across breeds, geographies, and analytical methods. This systematic review synthesizes genome-wide selection-signature evidence in tropical *Bos indicus* to identify consistently reported candidate genes associated with adaptation and production traits and assess methodological trends across genome-wide selection-signature studies. Following PRISMA 2020 guidance, Scopus was searched via Watase Uake (completed April 2026) using predefined keyword combinations related to selection signatures, selective sweeps, and zebu/indicine cattle. After focusing on publications from 2012–2026 and applying eligibility criteria requiring validated selection-signature methods and trait-linked candidate genes in tropical *Bos indicus*, 58 original studies were retained for qualitative synthesis. Whole-genome sequencing was the predominant platform (22/58), and multi-statistic designs were common (39/58). Adaptation-related signatures yielded 512 gene–trait entries (429 unique genes) across 54 studies, dominated by immunity/parasite resistance and thermotolerance annotations. The most recurrent adaptation candidates included *DNAJC18*, *KIT*, BoLA/MHC genes, *HOXC13*, *HSPA4*, *HSPA9*, *PDGFRA*, and *SOD1*, with *HELB* recurring as a DNA-maintenance locus under tropical selection. Production-related signatures yielded 497 entries (444 unique genes) across 46 studies, mainly for milk, reproduction, and growth/carcass traits; *HMGA2* was the most repeatedly reported production gene, followed by *SLC4A4*, *GHR*, *KCNIP4*, *NCAPG*, *NCKAP5*, *RXFP2*, and *SLC24A3*. Thirty-three genes overlapped both domains, nominating targets at the adaptation–productivity interface. These recurrent loci consistently point to biological pathways related to heat stress response, immune regulation, and tissue development. Selection signatures in tropical zebu are highly polygenic, yet a reproducible core of stress-response, integument, immune, growth, dairy, and fertility genes emerges across studies. These consensus loci provide priority targets for functional validation, genomic selection, and conservation strategies aimed at improving climate resilience without compromising productivity.

INTRODUCTION

Domestic cattle are broadly categorized into two lineages, i.e. humpless taurine (*Bos taurus*) and humped zebu or indicine (*Bos indicus*). While taurine cattle were domesticated in the Fertile Crescent roughly 10,000 years ago, indicine cattle originated independently in the Indus Valley of the Indian subcontinent approximately 6,000 to 8,000 years before present (YBP) (Chen et al., 2010; Felius et al., 2015; Utsunomiya et al., 2019). Genomic evidence suggests these two lineages diverged from a common aurochs ancestor (*Bos primigenius*) hundreds of thousands of years ago, with estimates ranging between 100,000 and 850,000 YBP (Magee et al., 2014). Following domestication, zebu cattle dispersed across Africa, Asia, Latin America, and Oceania, becoming integral to livestock production systems in tropical and subtropical regions worldwide (Diamond and Bellwood, 2003; Utsunomiya et al., 2019). The current African and East to South-East Asian zebu cattle populations are the result of multiple introductions (Pérez-Pardal et al., 2018; Wang et al., 2025). In Africa, indicine cattle hybridized with native taurine populations to form resilient sanga breeds (Hanotte et al., 2000). While in the 19th and 20th centuries, Indian cattle breeds were introduced to Brazil (Sanders, 1980; Genuíno et al., 2025), significantly shaping the commercial livestock landscape in the tropics.

The global success of *Bos indicus* is primarily due to its superior adaptation to environmental stressors that limit taurine productivity. Tropical regions are characterized by high temperatures, intense ultraviolet radiation, and high parasite burdens (Mohammed, 2023). Zebu cattle have evolved specialized physiological and morphological traits to mitigate these challenges, including a prominent hump, a pendulous dewlap, and a high density of sweat glands for efficient thermoregulation (Mavunga et al., 2025). Their light-colored, shiny hair coats further reflect solar radiation. Beyond heat tolerance, zebu cattle exhibit remarkable resilience to ectoparasites, particularly ticks, and vector-borne diseases such as trypanosomiasis and theileriosis. Furthermore, their ability to maintain metabolic and reproductive functions on low-quality forage distinguishes them as essential for sustainable agriculture in developing nations (Utsunomiya et al., 2019). Due to their large global population, indicine cattle play an important role in global food security (Mavunga et al., 2025), producing milk and meat in Asia, Africa, and Latin America. Beyond production, they provide draught power for plowing and transportation, and serve as vital cultural and ritual assets (Lodrick, 2005; Ibeagha-Awemu, 2019). However, the genetic capacity of many zebu breeds remains underutilized compared to high-yielding exotic breeds, necessitating a deeper understanding of their genomic potential.

The processes of natural selection (for environmental survival) and artificial selection (for human-desired traits) leave detectable imprints on the genome known as selection signatures or selective sweeps (Jensen et al., 2016). When a beneficial mutation is selected, its frequency increases, often "hitchhiking" linked neutral alleles and resulting in regions of reduced genetic diversity and high autozygosity (Fay and Wu, 2000). Identifying these regions allows researchers to pinpoint candidate genes associated with adaptation as well as production traits. In livestock species, identification of selection signatures can inform breeding strategies, facilitate marker-assisted selection, and enhance our understanding of genotype-environment interactions (Saravanan et al., 2020). Over the past two decades, dense Single Nucleotide Polymorphism (SNP) panels and increasingly accessible Whole-Genome Sequencing (WGS) have made genome-wide scans for selective sweeps routine. A family of complementary statistics targets allele-frequency differentiation, site-frequency spectrum distortions, extended haplotype homozygosity, and composite likelihood contrasts, among other signatures. Applied thoughtfully, these methods can nominate chromosomal intervals and genes for follow-up (Saravanan et al., 2020). Recent advancements favor composite methods like the De-correlated Composite of Multiple Signals (DCMS), which integrate multiple univariate statistics to improve detection power and resolution while accounting for covariance (Ma et al., 2015).

The sustainability of tropical cattle is threatened by climate change, which intensifies thermal stress and disease outbreaks, and by indiscriminate crossbreeding with exotic breeds, which risks the erosion of unique adaptive alleles (Passamonti et al., 2021; Mohammed, 2023; Mavunga et al., 2025). While numerous studies have identified selective sweeps in various indicine cattle breeds, the literature remains fragmented across different geographic regions and methodologies. There is an urgent need for a systematic synthesis to provide a consensus on the genomic architecture of zebu resilience. Here, we systematically survey published genome-wide selection scans focused on *Bos indicus* cattle, summarize methodological choices and recurrent candidate regions, and discuss what consistency across studies implies given demography and technical heterogeneity. From an applications perspective, these themes connect to global priorities around food security, health, and climate resilience (SDGs 2, 3, and 13). The objective of this systematic review is to integrate current genomic evidence regarding selection signatures in tropical *Bos indicus* cattle. Specifically, this review aims to: 1) Catalog major genomic regions or candidate genes consistently identified for tropical adaptation and production traits, 2) Synthesize the methodological evolution and current state of the art in zebu genomics, 3) Identify research gaps and technical biases that limit our understanding of the zebu genome, and 4) Propose future directions for the conservation and sustainable improvement of indigenous cattle. By providing a comprehensive overview, this systematic review serves as a foundation for future breeding strategies that balance productivity with environmental robustness in a warming world.

SYSTEMATIC LITERATURE REVIEW

Overview of Methods

In this systematic review, we followed a process for identifying, screening, and evaluating the eligibility of papers, using the PRISMA (Preferred Reporting Items for Systematic Reviews and Meta-analyses) reporting technique (Page et al., 2021) (Fig. 1). Scopus was a major database searched, assisted by using the web-based application Watase Uake (Wahyudi, 2024). We identified the research problem, the search term, the inclusion and exclusion criteria, and conducted a standard systematic literature search to collect relevant papers. This approach involves several major stages, i.e. 1) identify literature using academic database searches, 2) screening articles based on the title and abstract, 3) eligibility is determined through full-text reading after document retrieval, and 4) selection of articles that fit the requirements for further investigation.

Literature Search

The literature search followed four sequential stages: identification, screening, eligibility assessment, and selection. In the identification stage, a comprehensive literature search was conducted in the Scopus database using the Watase Uake tool (Wahyudi, 2024). The search employed combinations of the following keywords: “genomic signatures of selection *Bos indicus*”, “selection signatures adaptation zebu cattle”, “selection signatures in tropical cattle”, “selective sweep *Bos indicus*”, and “gene under selection *Bos indicus*”. To capture the broadest possible range of relevant studies, no publication date restrictions were initially applied. The database search was completed in April 2026 and retrieved 220 publication records spanning the years

2002–2026 (Fig. 2). Considering the annual publication trend, only studies published during the last 15 years (2012–2026) were retained, as the number of publications has consistently exceeded three per year since 2012.

In the screening stage, duplicate records were removed, and the remaining articles were screened based on their titles and abstracts according to predefined inclusion and exclusion criteria (Table 1). Studies were considered potentially eligible if they focused on *Bos indicus*, indicine, or zebu cattle adapted to tropical environments; employed validated genomic methods for detecting selection signatures as described by Saravanan et al. (2020), including Tajima's D, FST, iHS, Rsb, XP-EHH, XP-CLR, ROH, and DCMS; and investigated associations between identified selection signatures (including candidate genes) and adaptation or production traits.

Table 1
Inclusion and exclusion criteria

No	Parameters	Inclusion criteria	Exclusion criteria
1.	Population	*Bos indicus*, indicine, zebu	*Bos taurus*, taurine, hybrid, non cattle
2.	Investigation	Validated methods in signatures of selection study	Not using signatures of selection analysis
3.	Context	Adaptation and production traits	Not related to adaptation and production traits
4.	Output	Lists of candidate gene related to selection signatures	There is no candidate gene lists related to signatures of selection
5.	Article type	Original article in peer-reviewed journal, scopus indexed, included in tier Q1-Q4	Review, not in peer-reviewed journal, not indexed by scopus, not included in tier Q1-Q4
6.	Time	Published in the last 15 years (2012–2026)	Published not in 2012–2026
7.	Language	English	Not in English
8.	Retrieval	Retrieved through Watase Uake tools	Not retrieved through Watase Uake tools

During the eligibility stage, the full texts of the screened articles were retrieved through the Watase Uake application and evaluated against the complete eligibility criteria. Eligible studies were required to be original research articles published in English in peer-reviewed journals ranked Q1–Q4, with full-text access successfully obtained. Studies were excluded if they focused exclusively on *Bos taurus*, hybrid cattle, or non-cattle species; did not investigate genomic selection signatures or failed to associate identified signatures with specific traits; were review articles without original data; were published in languages other than English or in non-reputable journals; or if their full texts could not be retrieved through Watase Uake. Finally, in the selection stage, only articles that fulfilled all inclusion criteria and none of the exclusion criteria were included for further investigation and qualitative synthesis.

RESULTS

A Description of the Included Studies

The literature search in Scopus via Watase Uake retrieved 220 publication records spanning 2002–2026 (Fig. 2). After restricting the corpus to the last 15 years (2012–2026), when annual output consistently exceeded three papers, and applying the predefined inclusion and exclusion criteria (Table 1), 58 original studies met all eligibility requirements and were retained for qualitative synthesis (Fig. 1; Table 2). These studies collectively represent the contemporary evidence base for genome-wide selection signature analyses in tropical *Bos indicus* cattle.

Table 2
Summary of the selection signatures studies included in this systematic literature review

No	Study	Reference genome	Genotyping platform	Number of analyzed SNPs / genotypes	Number of regions considered	*Bos indicus* cattle breeds	Analysis methods
1.	Dixit et al. (2020)	UMD3.1	HD-chip	n.a.	170	Sahiwal, Tharparkar, Gir, Ongole, Hariana, Kangayam, Vechur	ROH
2.	Carrara et al. (2023)	ARS-UCD1.2	50K-chip	50,641	15,660	Guzera	ROH
3.	Nayak et al. (2025)	UMD3.1	50K-chip, 70K-chip	n.a.	87 (Tajima's D), 119 (iHS), 155 (Rsb), 152 (XP-EHH)	Tharparkar, Gir	Tajima's D, iHS, Rsb, XP-EHH
4.	Liao et al. (2013)	UMD3.1	WGS	9,990,773	79	Gir	Pooled heterozygosity
5.	Naval-Sanchez et al. (2020)	ARS-UCD1.2, UMD3.1	WGS	23,494,872	72	Nelore, Gir, Sahiwal, Ogaden, Boran	F_{ST}
6.	Peripolli et al. (2020)	UMD3.1	WGS	33,328,447	499	Gir	DCMS
7.	Mauki et al. (2022)	ARS-UCD1.2, UMD3.1	GBS, WGS	3,282,427	6 (PBS), 4 (CLR)	Nigerian zebu cattle: Kaduna, Kano, Katsina, Oyo, Plateau, Sokoto, Taraba, Zamfara	PBS, CLR
8.	Kim et al. (2017)	UMD3.1	WGS	37,460,739	130 (XP-EHH), 165 (XP-CLR)	Boran, Kenana, Ogaden	XP-EHH, XP-CLR
9.	Randhawa et al. (2016)	UMD3.1	Multiple paltforms	varies	1 (Brahman), 1 (Gir), 4 (Nellore)	Brahman, Gir, Nellore	Meta Selection Score
10.	Bahbahani et al. (2018)	UMD3.1	HD-chip	703,901	Butana: 8 (iHS), 79 (Rsb); Kenana: 2 (iHS), 59 (Rsb)	Butana, Kenana	iHS, Rsb
11.	Maiorano et al. (2018)	UMD3.1	50K-chip	23,275	142 (F_{ST}), 66 (iHS), 101 (XP-EHH)	Gir	F_{ST}, iHS, XP-EHH
12.	Cortez et al. (2022)	n.a.	RNA-seq	n.a.	2,500 orthologous groups	Nellore	dN/dS ratio
13.	Braga et al. (2025)	ARS-UCD1.2	WGS	31,253,205 (Gir India), 31,264,796 (Gir Brazil)	Gir India: 252 (iHS), 232 (Tajima's D), 268 (F_{ST}), 131 (XP-EHH);	Gir	Tajima's D, iHS, F_{ST},, XP-EHH

No	Study	Reference genome	Genotyping platform	Number of analyzed SNPs / genotypes	Number of regions considered	*Bos indicus* cattle breeds	Analysis methods
					Gir Brazil: 231 (iHS), 264 (Tajima's D), 288 (F_{ST}), 160 (XP-EHH)		
14.	Zavarez et al. (2015)	UMD3.1	HD-chip	668,589	3	Nellore	ROH
15.	Bahbahani et al. (2017)	UMD3.1	HD-chip	649,611	101	East African Shorthorn Zebu	iHS, Rsb, CMS
16.	Alshawi et al. (2019)	UMD3.1	HD-chip	680,124	19 (iHS), 17 (Rsb)	Jenoubi	iHS, Rsb
17.	Taye et al. (2017)	UMD3.1	WGS	37,000,000	233 (XP-EHH), 245 (XP-CLR)	Boran, Ogaden, Kenana	XP-EHH, XP-CLR
18.	Liu et al. (2020)	UMD3.1	HD-chip	568,129	Lufeng: 251 (iHS), 184 (Rsb), 76 (F_{ST}) Leiqiong: 270 (iHS), 174 (Rsb), 76 (F_{ST}) Hainan: 256 (iHS), 146 (Rsb), 76 (F_{ST})	Lufeng, Leiqiong, Hainan	iHS, Rsb, F_{ST}
19.	Illa et al. (2021)	UMD3.1, ARS-UCD1.2	Indus-chip	53,648	14	Sahiwal	DCMS
20.	Zhang et al. (2021)	ARS-UCD1.2	WGS	49,094,970	1,243 (F_{ST}), 1,301 (π-ratio), 644 (XP-CLR), 273 (XP-EHH)	Dianzhong	F_{ST}, π-ratio, XP-CLR, XP-EHH
21.	Naji et al. (2022)	n.a.	WGS	332,110,000 to 346,430,000	5 (iHS), 1,648 (iSAFE)	Dabieshan, Dehong, Dengchuan, Fujian, Guanling, Liping, Wenling	iHS, iSAFE
22.	Ayalew et al. (2023)	ARS-UCD1.2	WGS	23,963,154	83	Abigar	Nucleotide diversity, F_{ST}
23.	Wang et al. (2024)	ARS-UCD1.2	WGS	10,205,360	5,210 (CLR), 1,972 (Tajima's D), 1,290 (ROH)	Hainan Yellow	CLR, Tajima's D, ROH
24.	Dominguez et al. (2026)	ARS-UCD1.2	50K-chip	27,980	7	Visayan	ROH, Tajima's D, his, XP-EHH, F_{ST}
25.	Luo et al. (2022)	ARS-UCD1.2	WGS	5,300,000	2,297 (Nucleotide diversity), 539 (CLR)	Dehong	Nucleotide diversity, CLR

No	Study	Reference genome	Genotyping platform	Number of analyzed SNPs / genotypes	Number of regions considered	*Bos indicus* cattle breeds	Analysis methods
26.	Terefe et al. (2023)	ARS-UCD1.2	WGS	25,600,000	154 (Pooled heterozygosity), 258 (iHS), 152 (F_{ST}), 236 (XP-CLR)	14 Ethiopian indigenous cattle: Afar, Arsi, Bagaria, Bale, Begait, Boran, Choke, Fogera, Goffa, Horro, Mursi, Ogaden, Semien, Sheko	Pooled heterozygosity, iHS, F_{ST}, XP-CLR
27.	Senczuk et al. (2022)	UMD3.1	50K-chip	23,313	2	Bhagnari, Dajal, Guzerat, Hariana, Hissar, Kankrej, Tharparkar, Sahiwal	F_{ST}
28.	Neumann et al. (2025)	ARS-UCD1.2	WGS	54,532,198	553	Butana	ROH, XP-EHH
29.	Ayalew et al. (2024)	ARS-UCD1.2	WGS	36,527,967	7 (Pooled heterozygosity), 10 (F_{ST}), 8 (π-ratio)	Barka / Begait	Pooled heterozygosity, F_{ST}, π-ratio
30.	King et al. (2022)	ARS-UCD1.2	80k-chip	29,010	229 (total), 11 (by both F_{ST} and Rsb)	Nguni	F_{ST}, Rsb
31.	Genuino et al. (2025)	ARS-UCD1.2	HD-chip	533,967 (Nellore), 506,520 (Gir), 560,495 (Red Sindhi)	62 (Nellore), 57 (Gir), 72 (Red Sindhi)	Nellore, Gir, Red Sindhi	XP-EHH, Rsb, F_{ST}
32.	Nayak et al. (2025)	n.a.	ddRAD	289,551	44 (Tajima's D), 54 (CLR), 78 (iHS), 24 (ROH)	Red Sindhi	Tajima's D, CLR, iHS, ROH
33.	Okwasiimire et al. (2026)	ARS-UCD1.3	WGS	22,455,225	803 (RAiSD), 49 (ROH)	Ankole, Karamojong, Nganda, Nkedi, Ntuku	RAiSD, ROH
34	Chavan et al. (2025)	UMD3.1	50K-chip	26,889	290 (DCMS), 8 (ROH)	Belahi	DCMS, ROH
35.	Vani et al. (2026)	Bos indicus_1.0 (GCF_000247795.1)	WGS	1,390,449	7,250 (CLR), 806 (F_{ST})	Alambadi, Bargur, Kangayam, Pulikulam, Umblachery	CLR, F_{ST}
36.	Nayak et al. (2024)	UMD3.1	50K-chip	15,606 to 27,474	19 (Gir), 11 (Hariana), 14 (Kankrej), 12 (Nellore), 10 (Ongole),12	Gir, Hariana, Kankrej, Nellore, Ongole, Red Sindhi,	Tajima's D

No	Study	Reference genome	Genotyping platform	Number of analyzed SNPs / genotypes	Number of regions considered	*Bos indicus* cattle breeds	Analysis methods
					(Red Sindhi), 13 (Sahiwal), 13 (Tharparkar)	Sahiwal, Tharparkar	
37.	Venkatesan et al. (2025)	ARS-UCD1.2	ddRAD	1,983,581	300	Kankrej	CLR
38.	Venkatesan et al. (2026)	ARS-UCD2.0	ddRAD	1,939,949	627	Gir	Tajima's D, Nucleotide diversity, iHS, CLR
39.	Bhardwaj et al. (2021)	UMD3.1	HD-chip	191,351	46 (ROH), 3,565 (F_{ST})	Siri, Ladakhi, Kankrej, Hallikar	ROH, F_{ST}
40.	Mengistie et al. (2023)	UMD3.1	80K-chip	67,491	14	Begait, Boran, Fogera	F_{ST}
41.	Montes et al. (2019)	UMD3.1	HD-chip	22,241	39	Nellore	EHH
42.	Goyache et al. (2021)	UMD3.1	HD-chip	543,595	9	Bororo, Zebu Peul	iHS, XP-EHH, nSL
43.	Rajawat et al. (2024)	ARS-UCD1.3	ddRAD	78,193	146	Sahiwal	Tajima's D, CLR, iHS, iHH12, ROH
44.	Tiwari et al. (2025)	ARS-UCD1.2	WGS	8,630,854	1,189 (ROH), 3,616 (F_{ST})	Sahiwal	ROH, F_{ST}
45.	Nayak et al. (2023)	UMD3.1	50K-chip	20,154 to 27,474	106 (Tajima's D), 195 (CLR), 117 (iHS), 34,399 (ROH), 91 (F_{ST}), 110 (XP-EHH), 96 (Rsb)	Gir, Ongole, Red Sindhi, Sahiwal, Tharparkar	Tajima's D, CLR, iHS, ROH, F_{ST}, XP-EHH, Rsb
46.	Maiorano et al. (2022)	ARS-UCD1.2	WGS	82,326	718 (hapFLK), 1,713 (F_{ST}), 346 (overlap between 2 methods)	Nellore	hapFLK, F_{ST}
47.	Tijjani et al. (2022)	ARS-UCD1.2	WGS	4,100,000	59	Kenana, Butana, Aryashai, Baggara, Gash, Fulani, Boran, Ogaden, Gir	Pooled heterozygosity, F_{ST}, XP-EHH
48.	Dixit et al. (2021)	UMD3.1	HD-chip	1,993	553	Sahiwal, Tharparkar, Gir, Vechur, Ongole, Kangayam, Hariana	F_{ST}
49.	Mavunga et al. (2025)	ARS-UCD2.0	60K-chip	43,271	Draught vs Dairy: 6 (XP-EHH), 21 (F_{ST})	29 Asian Zebu from India, Sri Lanka, Bangladesh,	XP-EHH, F_{ST}

No	Study	Reference genome	Genotyping platform	Number of analyzed SNPs / genotypes	Number of regions considered	*Bos indicus* cattle breeds	Analysis methods
					Mini vs Large stature: 3 (XP-EHH), 38 (F_{ST})	Pakistan, Cambodia, Myanmar	
50.	Bitew et al. (2026)	ARS-UCD1.2	50K-chip	33,147	12 (iHS), 109 (Rsb), 107 (XP-EHH)	Adamawa Gudali, Red Fulani, White Fulani, Zebu Bororo, Zebu Fulani	iHS, XP-EHH, Rsb
51.	Bahbahani et al. (2015)	UMD3.1	50K-chip	46,171	24	East African Shorthorn Zebu	F_{ST}, iHS, Rsb
52.	Taye et al. (2018)	UMD3.1	WGS	16,181	257 (XP-EHH), 345 (XP-CLR)	Boran, Ogaden, Kenana	XP-EHH, XP-CLR
53.	Kumar et al. (2024)	ARS-UCD1.2	50K-chip	10,980	112	Ongole, Nellore, Red Sindhi, Gir, Hariana, Kankrej, Sahiwal, Hissar, Tharparkar	Deep Genome Scan
54.	Ge et al. (2026)	ARS-UCD1.2	WGS	104,575	31	Dabieshan	F_{ST}, Nucleotide diversity, Tajima's D, XP-CLR
55.	Mei et al. (2017)	UMD3.1	WGS	57,220,105	2,842	Gir, Nellore, Brahman, Yunnan, Leiqiong	d_i statistics
56.	Somavilla et al. (2014)	UMD3.1	HD-chip	560,565	31	Nellore	EHH
57.	Edea et al. (2018)	n.a.	80K-chip	12,389	285 (F_{ST} Ethiopian), 317 (F_{ST} Zebu)	Begait, Boran, Arsi, Guraghe, Ogaden, Fogera, Arado, Raya Azebo, Deshi, Red Chittagong, Nellore	F_{ST}
58.	Li et al. (2019)	UMD3.1	HD-chip	619,375	327 (F_{ST}), 129 (XP-EHH), 84 (XP-CLR)	Dehong	F_{ST}, XP-EHH, XP-CLR

Publication activity increased markedly over time: five studies were published between 2012 and 2016, 20 between 2017 and 2021, and 33 between 2022 and 2026, reflecting the growing accessibility of dense SNP arrays and WGS in zebu genomics. Geographically, the included literature covers major tropical cattle systems. Brazilian and other Latin American zebu populations (notably Nellore, Gir, Guzerá, Brahman, and Red Sindhi) were frequently investigated, alongside South Asian breeds (e.g., Sahiwal, Tharparkar, Ongole, Hariana, Kankrej, Vechur, and Kangayam), diverse African indicine and sanga/zebu populations (e.g., Boran,

Kenana, Ogaden, Butana, East African Shorthorn Zebu, Nigerian and Ethiopian zebus), and East/Southeast Asian local cattle (e.g., Dehong, Hainan, Leiqiong, and related southern Chinese stocks) (Table 2).

Methodological heterogeneity was substantial but informative. WGS was the most common genotyping platform (22/58 studies), followed by high-density SNP chips (13/58) and medium-density (~ 50K) arrays (10/58), while a minority of studies used reduced-representation sequencing (ddRAD/GBS), specialized chips (e.g., Indus-chip), or RNA-seq-based designs (Table 2). The bovine reference genome UMD3.1 remained the predominant assembly (27 studies), although ARS-UCD1.2 (and related ARS-UCD releases) has been increasingly adopted (19 studies), with a few analyses reporting dual-genome mapping. Selection statistics were likewise diverse: differentiation-based F_{ST} was the most frequently applied method (25 studies), followed by haplotype-based approaches including iHS and XP-EHH (16 studies each), runs of homozygosity (ROH; 13 studies), Tajima's D and Rsb (10 studies each), and composite/likelihood methods such as CLR, XP-CLR, and DCMS. Notably, 39 of 58 studies combined two or more complementary statistics, consistent with current recommendations to improve power and reduce method-specific false positives (Ma et al., 2015; Saravanan et al., 2020). The number of genomic regions reported as under selection ranged from a few intervals to several hundred, depending on marker density, sample design, and significance thresholds (Table 2).

Selection Signatures for Adaptation Traits

Across the eligible literature, adaptation-related selection signatures were reported in 54 studies and yielded 512 gene–trait entries corresponding to 429 unique candidate genes (Supplementary Table S1). After reconciling gene symbols for overlap analysis with production-associated candidates, 428 genes were assigned to the adaptation set, of which 395 were adaptation-exclusive and 33 were shared with production traits (Fig. 3). Trait annotations clustered into several recurrent biological themes. Entries linked to immunity, parasite burden, and disease resistance were the most abundant (~ 211 entries; ~197 unique genes), followed by heat stress, thermotolerance, and oxidative/hypoxic stress responses (~ 142 entries; ~111 genes). Additional recurrent categories included coat colour, pigmentation, and skin/hair morphology (~ 56 entries), feed/metabolic and arid-environment adaptation, behavioural/temperament traits, and high-altitude responses (Supplementary Table S1).

Despite the large catalogue of nominated genes, cross-study recurrence was limited: only 56 adaptation genes were reported in two or more independent studies, 15 in three or more, and eight in four or more studies when BoLA/BOLA locus nomenclature was collapsed at the gene-family level used for ranking (Table 3; Supplementary Table S1). The most repeatedly identified adaptation candidate was *DNAJC18* (seven studies), a DnaJ/HSP40-family chaperone gene repeatedly linked to heat-stress response and cellular proteostasis in African and other tropical zebu populations (Bahbahani et al., 2015; Bahbahani et al., 2017; Tijjani et al., 2022; Ayalew et al., 2023; Terefe et al., 2023; Braga et al., 2025; Bitew et al., 2026). *KIT* ranked second (six studies) and was associated with coat colour/pigmentation, tropical thermoregulation, and, in some reports, immune or spermatogenesis-related signals (Illa et al., 2021; Bhardwaj et al., 2021; Mauki et al., 2022; Terefe et al., 2023; Nayak et al., 2024; Vani et al., 2026).

Table 3
Top 10 candidate genes associated to adaptation traits in *Bos indicus* cattle ranked by number of studies reporting

Gene	Study frequency	Associated traits
DNAJC18	7	Heat stress response; protein folding / chaperone function; cellular stress adaptation
KIT	6	Coat colour and pigmentation; tropical thermoregulation; immune-related / spermatogenesis signals
BOLA	4	MHC immunity; tick and parasite resistance; trypanotolerance; adaptive immune response
HOXC13	4	Hair follicle development; skin thickness; heat tolerance; developmental regulation under disease selection
HSPA4	4	Heat shock protein; heat tolerance / thermotolerance; cellular stress response
HSPA9	4	Heat shock protein; heat stress response; immune response
PDGFRA	4	Coat colour / pigmentation (including reddening phenotype)
SOD1	4	Oxidative stress response; heat tolerance / thermotolerance; high-altitude adaptation
HELB	3	Tropical / harsh-environment adaptation; UV and DNA damage response
HOXC12	3	Hair follicle development; skin thickness; heat tolerance; metabolic homeostasis

Several additional genes formed a coherent thermotolerance and integumentary module. Heat-shock genes *HSPA4* and *HSPA9* (four studies each) and the oxidative-stress gene *SOD1* (four studies) were repeatedly highlighted in African and Asian zebu scans for heat and environmental stress tolerance (Kim et al., 2017; Taye et al., 2017; Edea et al., 2018; Cortez et al., 2022; Mengistie et al., 2023; Tiwari et al., 2025). Hair-follicle and skin-development genes *HOXC13* (four studies) and *HOXC12* (three studies) were linked to skin thickness and heat dissipation phenotypes (Taye et al., 2017; Ayalew et al., 2023; Dominguez et al., 2026; Bitew et al., 2026). Pigmentation genes *PDGFRA* (four studies) and *MC1R* (three studies) further support selection on coat reflectance and melanogenic pathways relevant to solar load in the tropics (Mei et al., 2017; Illa et al., 2021; Bhardwaj et al., 2021; Rajawat et al., 2024; Vani et al., 2026).

Immune adaptation was prominently represented by the bovine MHC (*BOLA*/*BoLA*) complex, which ranked among the top recurrent candidates when counted across studies reporting BoLA or BOLA class II genes (four independent study contexts in the ranking framework of Table 3). These signals were associated with tick and parasite resistance, trypanotolerance, and broader adaptive immunity in African and Brazilian zebu (Kim et al., 2017; Taye et al., 2018; Mauki et al., 2022; Goyache et al., 2021; Maiorano et al., 2022). Complementary innate-immunity candidates such as *IRAK3* (three studies) recurred in East African and Sudanese zebu under pathogen and environmental pressure (Bahbahani et al., 2018; Ayalew et al., 2023; Neumann et al., 2025). Finally, *HELB* (three studies) emerged as a notable tropical-adaptation candidate implicated in DNA damage/UV response. Coding variants enriched in indicine cattle have been proposed as contributors to genomic integrity under high solar radiation and as part of a broader selective sweep on BTA5 that also intersects production-related loci (Naval-Sanchez et al., 2020; Maiorano et al., 2022; Braga et al., 2025). Collectively, the adaptation gene set supports a multilocus architecture in which chaperone/heat-shock, pigmentation–integument, MHC/innate immunity, and DNA-repair pathways are the most reproducible genomic footprints of tropical zebu resilience (Table 3; Supplementary Table S1).

Selection Signatures for Production Traits

Production-related selection signatures were reported in 46 studies, generating 497 gene–trait entries and 444 unique candidate genes (Supplementary Table S2). Of these, 411 genes were production-exclusive and 33 overlapped with adaptation candidates (Fig. 3; Table 5). Functional annotations were dominated by milk yield and composition or mammary/udder morphology (~ 187 entries; ~173 genes), followed by reproduction and fertility (~ 159 entries; ~151 genes) and growth, stature, meat, or carcass traits (~ 120 entries; ~111 genes). Feed-efficiency annotations were comparatively scarce (Supplementary Table S2), suggesting that production scans in zebu have historically emphasized dairy, beef conformation, and reproductive performance more than explicit efficiency phenotypes.

Table 5
Overlapped candidate genes associated to both adaptation and production traits in *Bos indicus* cattle

No	Genes	Adaptation Traits	Production Traits
1.	*ADAMTS17*	Body size; warmer/dry climate and scarce forage	Age at puberty; protein metabolism; embryogenesis
2.	*ATP5MC2*	Heat tolerance; hypoxia/oxidative stress	Milk fat yield; milk protein; milk yield
3.	*CHADL*	Immune signaling; cellular defense	Growth; skeletal/carcass development
4.	*CHCHD7*	Coat colour	Reproduction
5.	*COA1*	Adaptation to tropical environment	Milk production
6.	*COL8A1*	Skin structural integrity; tick resistance	Muscle development
7.	*CPVL*	Tick infestation resistance; tropical adaptation	Sperm motility; desert/arid adaptation
8.	*EIF2AK3*	Adaptation to tropical environment	Conception rate; puberty age; pregnancy rate (Gir)
9.	*EPHA5*	Feed conversion; local feed adaptation	Milk production; reproduction
10.	*EPHA6*	Temperament; stress response in tropical environments	Milk fat percentage
11.	*ERBB3*	Coat color / pigmentation	Mammary development
12.	*FTO*	Feed intake; energy homeostasis under heat	Milk composition; production traits
13.	*GABRA4*	Behavioural control	Milk production and meat redness
14.	*GABRG1*	Adaptation to tropical environment; temperament; behavioural control	Milk production
15.	*GRIP1*	Anti-inflammatory immune response; adaptation to tropical environment	Estrus detection; uterine epithelial changes; marbling score
16.	*IGF1*	Heat shock response; embryo thermoprotection	Carcass weight; reproduction; follicular development
17.	*IRAK3*	Immune response; TLR signaling; immune signaling; disease resistance; inflammation control; innate immunity	Intramuscular fat deposition; domestication
18.	*ITGB1BP1*	Convergent tropical adaptation; GTPase regulation	Carcass traits
19.	*JAK1*	JAK-STAT immune regulation	Calving ease
20.	*KHDRBS2*	Adaptation to harsh environments	Fertility and reproductive traits; ease of calving
21.	*KIT*	*B*-cell differentiation; eye area pigmentation; somatic cell count; coat colour; skeletal/immune; spermatogenesis; tropical temperature regulation; patterned pigmentation	Spermatogenesis; male fertility
22.	*LRBA*	Immune effector molecule secretion	Dairy form
23.	*LYN*	Grey coat colour; melanogenesis; KIT signaling; innate/adaptive immune response	Body stature and size
24.	*MC5R*	Sebum secretion; thermoregulation; skin integrity / antimicrobial	Meat/lipid metabolism in indicine
25.	*PDGFRA*	Coat colour; reddening phenotype	Growth factor binding
26.	*PRKG1*	Tick resistance	Milk fatty acid traits
27.	*PRKN*	Adipose metabolism; energy balance under tropical stress	Fertility traits
28.	*RAB31*	Adaptation to tropical environment; coat colour	Metabolic pathway; milk performance QTLs

No	Genes	Adaptation Traits	Production Traits
29.	*RXFP2*	Heat tolerance via horn thermoregulation	Teat placement; udder structure; teat length; Testicular descent; fertility; male reproduction / fertility under heat stress
30.	*TCF25*	Immune response	Meat quality
31.	*TOX*	Health; meat and carcass traits	Reproduction
32.	*TRAPPC9*	Mastitis susceptibility	Milk composition; reproduction
33.	*VAV3*	High-altitude adaptation	Bone growth

Cross-study recurrence for production genes was even more sparse than for adaptation: 41 genes appeared in ≥ 2 studies, eight in ≥ 3 studies, and only *HMGA2* reached six independent reports (Table 4). *HMGA2* was consistently associated with growth and body stature, including the distinctive short-stature phenotype of Vechur cattle, and with conformation traits such as muscling and navel/sheath score in commercial zebu (Dixit et al., 2020; Dixit et al., 2021; Naval-Sanchez et al., 2020; Maiorano et al., 2022; Tijjani et al., 2022; Braga et al., 2025). Its genomic neighbourhood on BTA5, which also harbours *HELB* and other adaptation-linked genes, illustrates how a single selective landscape can jointly affect morphology and environmental fitness (Naval-Sanchez et al., 2020).

Table 4
Top 10 candidate genes associated to production traits in *Bos indicus* cattle ranked by number of studies reporting

Gene	Study frequency	Associated traits
HMGA2	6	Growth and stature (including short stature in Vechur cattle); body conformation; navel/sheath score; muscling
SLC4A4	4	Milk production and quality; rumen development; reproduction (conception, puberty, pregnancy rate); somatic cell score
GHR	3	Milk yield; milk casein percentage; reproduction
KCNIP4	3	Milk composition and production; udder morphology; puberty and conception traits
NCAPG	3	Growth, stature, meat and carcass traits; dairy traits; reproduction
NCKAP5	3	Milk yield and production; feed efficiency linked to reproduction
RXFP2	3	Udder/teat morphology; testicular descent and male fertility (including under heat stress)
SLC24A3	3	Fertility traits; growth; milk production
ACER3	2	Milk yield; mammary gland development
ADAMTS17	2	Age at puberty; protein metabolism; embryogenesis

Among dairy-oriented candidates, *SLC4A4* ranked highly (study frequency = 4 in Table 4) and was linked to milk production/quality, rumen development, reproductive performance (conception, puberty, pregnancy rate), and somatic cell score in Gir, Iraqi, and Ethiopian zebu contexts (Alshawi et al., 2019; Montes et al., 2019; Ayalew et al., 2024; Nayak et al., 2025). *GHR* (three studies) was associated with milk yield, casein percentage, and reproduction (Illa et al., 2021; Rajawat et al., 2024; Venkatesan et al., 2025), while *KCNIP4* (three studies) recurred for milk composition, udder morphology, and puberty/conception traits (Maiorano et al., 2018; Nayak et al., 2023; Nayak et al., 2025). Additional recurrent production genes included *NCAPG* (growth, carcass, and dairy-linked signals), *NCKAP5* (milk yield and reproduction-linked feed efficiency), *RXFP2* (udder/teat morphology and male fertility, including under heat stress), and *SLC24A3* (fertility, growth, and milk traits) (Table 4). Classic casein genes (e.g., *CSN3*) appeared in dairy ROH islands of Indian zebu (Dixit et al., 2020; Mei et al., 2017), reinforcing that artificial selection for milk composition has left detectable autozygosity footprints in tropical dairy breeds.

The overlapped genes

The 33 genes shared between adaptation and production catalogues (Fig. 3; Table 5) constitute a particularly informative subset for dual-purpose tropical breeding. Several encode functions at the interface of environmental stress and economic performance. For example, *IGF1* was annotated for heat-shock/embryo thermoprotection as well as carcass weight and reproductive follicular development; *ATP5MC2* for heat/hypoxia tolerance and milk yield components; *KIT*, *PDGFRA*, *LYN*, and *RXFP2* for pigmentation or thermoregulatory morphology alongside fertility or growth; *PRKG1* and *COL8A1* for tick resistance or skin integrity alongside milk fatty-acid or muscle traits; and *IRAK3*, *JAK1*, *TRAPPC9*, and *LRBA* for immune regulation with secondary links to carcass, calving, dairy form, or mastitis-related milk traits (Table 5). Although overlap represented only ~ 4% of the combined unique gene pool (33 of 839 genes when summing adaptation-only, production-only, and shared sets), these loci are priority candidates for follow-up because they may capture genetic correlations between resilience and productivity under tropical production systems.

DISCUSSION

This systematic review consolidates genome-wide selection signature evidence from 58 studies of tropical *Bos indicus* cattle and provides a cross-study map of candidate genes for adaptation and production (Tables 2–5; Supplementary Tables S1–S2; Fig. 3). Three overarching messages emerge. First, the genomic architecture of zebu tropical fitness is polygenic and pathway-structured rather than dominated by a small set of universally replicated loci. Second, production selection signatures are abundant but even less cross-replicated than adaptation signals, reflecting breed-specific breeding goals and heterogeneous trait definitions. Third, a compact set of overlapping genes suggests biological coupling between environmental resilience and productivity, an observation with direct implications for climate-smart breeding and conservation of indigenous zebu genetic resources (Passamonti et al., 2021; Mavunga et al., 2025).

Methodological Landscape and Limits to Cross-Study Consensus

The included studies span a rapid technological transition from medium-density SNP arrays to WGS and composite statistics (Table 2). This progress has improved resolution, particularly for detecting coding and regulatory variants in genes such as *HELB* (Naval-Sanchez et al., 2020), but it also complicates meta-synthesis. Differences in reference genomes (UMD3.1 versus ARS-UCD1.2), marker density, window sizes, significance thresholds, and whether analyses were within-population (e.g., iHS, ROH, Tajima's D) or between-population (e.g., F_{ST}, XP-EHH, XP-CLR, Rsb) all influence which intervals are declared significant. Demography further confounds interpretation: many African zebu populations are admixed with African taurine ancestry (Bahbahani et al., 2015; Bahbahani et al., 2017; Kim et al., 2017), Brazilian commercial zebu have undergone intense recent artificial selection (Maiorano et al., 2022; Genuíno et al., 2025), and Asian local breeds often retain complex introgression histories (Dixit et al., 2021; Mavunga et al., 2025; Wang et al., 2025). Consequently, non-replication of a candidate gene across studies does not necessarily imply biological irrelevance; it may reflect population-specific selection, insufficient power, or technical discordance.

Against this background, the genes that do recur across independent designs and geographies, especially *DNAJC18*, *KIT*, *HMGA2*, heat-shock and oxidative-stress genes, BoLA/MHC signals, and the BTA5 *HELB–HMGA2* neighbourhood, deserve elevated confidence as consensus candidates (Tables 3–4). The frequent use of multi-statistic frameworks in recent studies is encouraging; continued adoption of composite approaches (e.g., DCMS) and explicit reporting of overlapping signals across methods should further stabilize candidate lists (Ma et al., 2015; Peripolli et al., 2020; Saravanan et al., 2020).

Genomic Signatures of Tropical Adaptation

The adaptation catalogue is dominated by immunity/parasite resistance and thermotolerance pathways, in agreement with the ecological pressures that define tropical livestock systems, i.e. high temperature, intense ultraviolet radiation, and heavy ectoparasite and vector-borne disease burdens (Mohammed, 2023; Mavunga et al., 2025). Recurrent detection of *DNAJC18*, *HSPA4*, *HSPA9*, and *SOD1* supports a model in which proteostasis and redox buffering are central to zebu heat resilience (Bahbahani et al., 2015; Kim et al., 2017; Taye et al., 2017; Tijjani et al., 2022). Parallel selection on coat and skin biology (*KIT*, *PDGFRA*, *MC1R*, *HOXC12*/*HOXC13*, *MC5R*) is consistent with morphological adaptations that reduce radiative heat gain and maintain skin barrier function (Illa et al., 2021; Senczuk et al., 2022; Dominguez et al., 2026).

Immune-related sweeps, particularly at BoLA/MHC and innate-immunity genes such as *IRAK3*, align with long-standing phenotypic evidence for superior tick and parasite resistance in indicine cattle (Kim et al., 2017; Taye et al., 2018; Goyache et al., 2021; Neumann et al., 2025). Ancient autozygous segments enriched for immune functions in West African cattle further suggest that pathogen-driven selection has been a persistent evolutionary force (Goyache et al., 2021). The repeated nomination of *HELB* adds a DNA-maintenance dimension to tropical adaptation: indicine-enriched coding variants in this helicase have been interpreted as responses to environmental genotoxic stress and as part of a broader selective landscape shared with growth-related variation (Naval-Sanchez et al., 2020). Together, these findings indicate that zebu adaptation is not a single "heat-tolerance gene" phenomenon but a coordinated genomic response across cellular stress, integument, immunity, and genome integrity.

Selection for Production Performance in Indicine Cattle

Production signatures reflect both traditional and commercial selection histories. In dairy-oriented Indian and West Asian zebu, casein loci, *GHR*, *SLC4A4*, and *KCNIP4* illustrate selection on lactation and mammary biology (Dixit et al., 2020; Illa et al., 2021; Alshawi et al., 2019; Nayak et al., 2025). In Brazilian Nellore and related beef zebu, growth and carcass-oriented candidates such as *HMGA2* and *NCAPG* are consistent with decades of selection for body weight and conformation under tropical ranching systems (Maiorano et al., 2018; Maiorano et al., 2022; Braga et al., 2025). Reproductive candidates (*RXFP2*, *SLC24A3*, *ADAMTS17*, *NCKAP5*) highlight fertility as a limiting economic trait in heat-exposed herds (Montes et al., 2019; Bahbahani et al., 2015; Nayak et al., 2025).

The lower cross-study replication of production genes relative to adaptation genes likely has biological and operational causes. Production goals differ sharply among dairy Sahiwal, draft Kangayam, miniature Vechur, and beef Nellore populations (Dixit et al., 2020; Dixit et al., 2021), so true shared targets are expected to be few. Moreover, production annotations in selection-scan papers are often inferred from QTL databases or gene ontology rather than from within-study phenotypic association, which can inflate gene lists while reducing reproducibility. Even so, *HMGA2* stands out as a robust, repeatedly validated stature/growth locus with relevance across both indigenous and commercial indicine contexts (Naval-Sanchez et al., 2020; Dixit et al., 2021).

Overlapping Genes: Bridging Adaptation and Productivity

The 33 overlapping genes (Table 5; Fig. 3) provide a practical shortlist for breeding programmes that must improve yield without eroding climatic and disease resilience. Pleiotropic or closely linked selection is biologically plausible for several of these loci. *KIT* and related pigmentation pathway genes influence coat traits that modulate heat load while also intersecting fertility and immune signalling annotations. *RXFP2*, classically associated with horn and reproductive morphology, was linked here both to heat-related thermoregulation and to udder/testicular traits under heat stress (Bahbahani et al., 2015; Bahbahani et al., 2017; Nayak et al., 2025). Metabolic and stress-axis genes (*IGF1*, *FTO*, *ATP5MC2*, *PRKN*, *EPHA5*) connect energy homeostasis under heat or poor forage to milk, carcass, or reproductive outcomes. Immune genes with production annotations (*IRAK3*, *TRAPPC9*, *PRKG1*) warn that selection against disease susceptibility can co-affect lactation or carcass quality traits, and vice versa.

From an applied perspective, these overlapping candidates are attractive for multipurpose marker panels and for monitoring genetic diversity during upgrading or crossbreeding. Indiscriminate introgression of exotic taurine genetics can dilute locally adaptive alleles (Passamonti et al., 2021; Mavunga et al., 2025); conversely, intensive selection on a few production QTLs could inadvertently reduce adaptive haplotype diversity. Balancing these pressures will require genomic tools that jointly track adaptation- and production-linked regions identified in this review.

Research Gaps and Future Directions

Several gaps limit translation of selection-signature catalogues into breeding practice. First, functional validation remains rare: most candidates are nominated from sweep statistics without experimental confirmation of causal variants, expression changes, or physiological effects. Second, phenotype–genotype integration is uneven; future studies should couple selection scans with heat-challenge, parasite-load, feed-efficiency, and fertility phenotypes in the same cohorts. Third, geographic and breed coverage is still skewed toward a subset of commercial Brazilian zebu and a limited number of African and Indian breeds, leaving many Southeast Asian and island populations under-represented despite their importance for regional food security (Wang et al., 2025; Dominguez et al., 2026). Fourth, standardized gene nomenclature (especially for BoLA/*BOLA* genes), mandatory reporting of genome build and coordinate lifts, and deposition of full candidate lists would greatly improve future meta-analyses.

Priority next steps include: (i) targeted resequencing and functional assays of high-confidence recurrent genes (*DNAJC18*, *KIT*, *HMGA2*, *HELB*, *HSPA4*/*HSPA9*, *SOD1*, BoLA class II genes, *SLC4A4*, *GHR*, and the Table 5 overlap set); (ii) multi-population meta-scans using harmonized ARS-UCD coordinates and composite statistics; (iii) incorporation of validated adaptive markers into genomic selection indices that explicitly weight resilience; and (iv) community conservation strategies that maintain haplotype diversity around adaptation loci while enabling genetic gain for milk, meat, and reproduction. Such an agenda aligns with global priorities for food security, animal health, and climate action.

CONCLUSION

This systematic review of 58 genome-wide selection signature studies shows that tropical *Bos indicus* cattle harbour a rich but highly polygenic repertoire of candidate genes for environmental adaptation and production performance. Adaptation signals most consistently implicate cellular stress/proteostasis (*DNAJC18*, *HSPA4*, *HSPA9*, *SOD1*), integument and pigmentation (*KIT*, *PDGFRA*, *HOXC12*/*HOXC13*), pathogen defence (BoLA/MHC and innate-immunity genes), and DNA maintenance (*HELB*). Production signals most repeatedly involve growth/stature (*HMGA2*, *NCAPG*) and dairy or reproductive physiology (*SLC4A4*, *GHR*, *KCNIP4*, *RXFP2*, among others). A focused set of 33 genes overlaps both domains, offering concrete targets for dual-purpose, climate-resilient breeding. Although methodological and demographic heterogeneity currently limits strict meta-analytic replication, the recurrent candidates synthesized here provide a consensus foundation for functional validation, marker development, and conservation of indigenous zebu genetic resources in a warming world.

Declarations

Ethical statement

There is no ethical approval was required.

Competing interests

The authors declare that they have no competing interests exist.

Declaration of Generative AI and AI-assisted technologies in the writing process

During the preparation of this work the authors used Watase Uake tool in order to search, filter, and retrieve literatures. After using this tool/service, the authors reviewed and edited the content as needed and take full responsibility for the content of the publication.

Author contributions

DM, PS, SB, and TSMW were contributed to the study conception and design. Project financial support was secured by DM. Literature collection and systematic review analyses were performed by PS. The manuscript was written by PS. Initial reviews of the manuscript were provided by DM, SB, TSMW, and MW. All authors read and approved the final manuscript.

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Data availability

The datasets analysed during the current study are available from the corresponding author on reasonable request.

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Figures

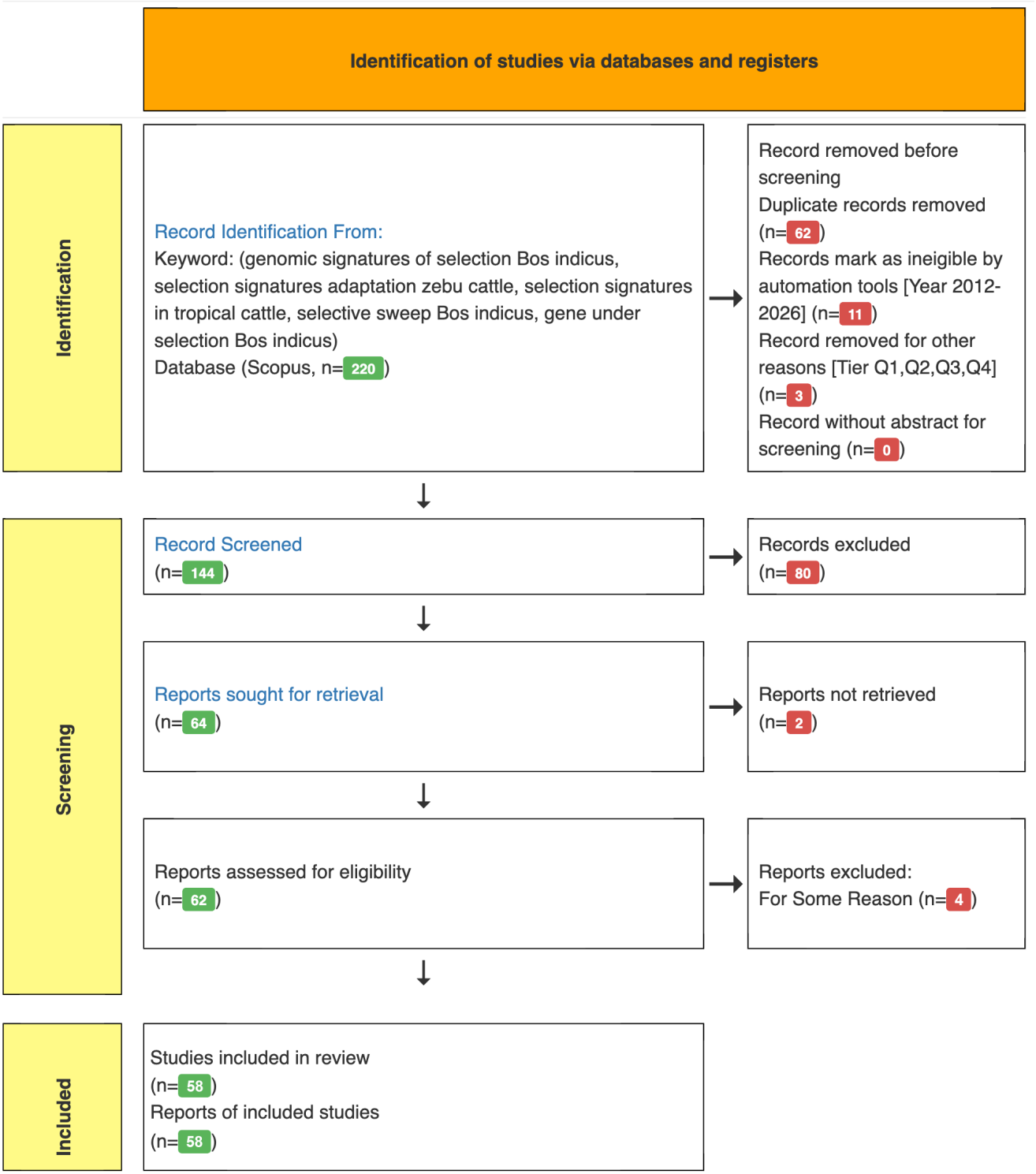


Figure 1

Figure 1. Flow diagram of manuscript retrieval and study selection based on PRISMA (Preferred Reporting Items for Systematic Review and Meta-Analysis) 2020 statement

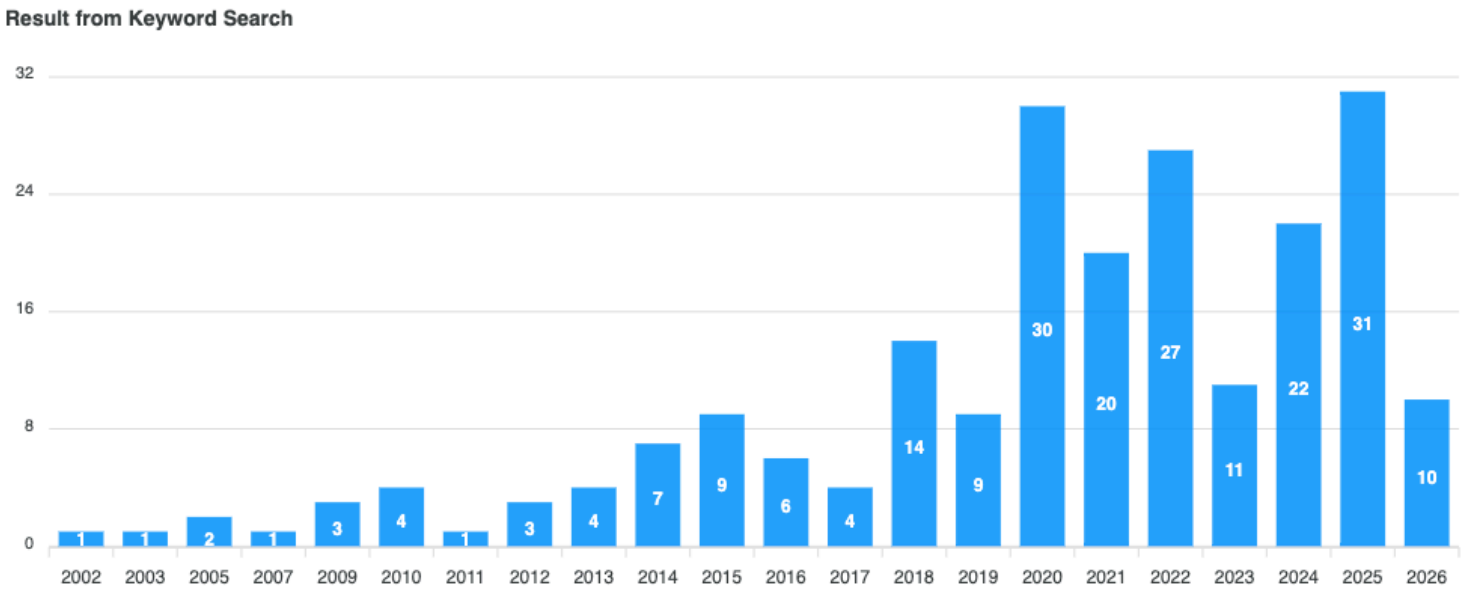


Figure 2

Figure 2. Distribution of publication number resulted from keyword search in Scopus databases with Watase Uake tools

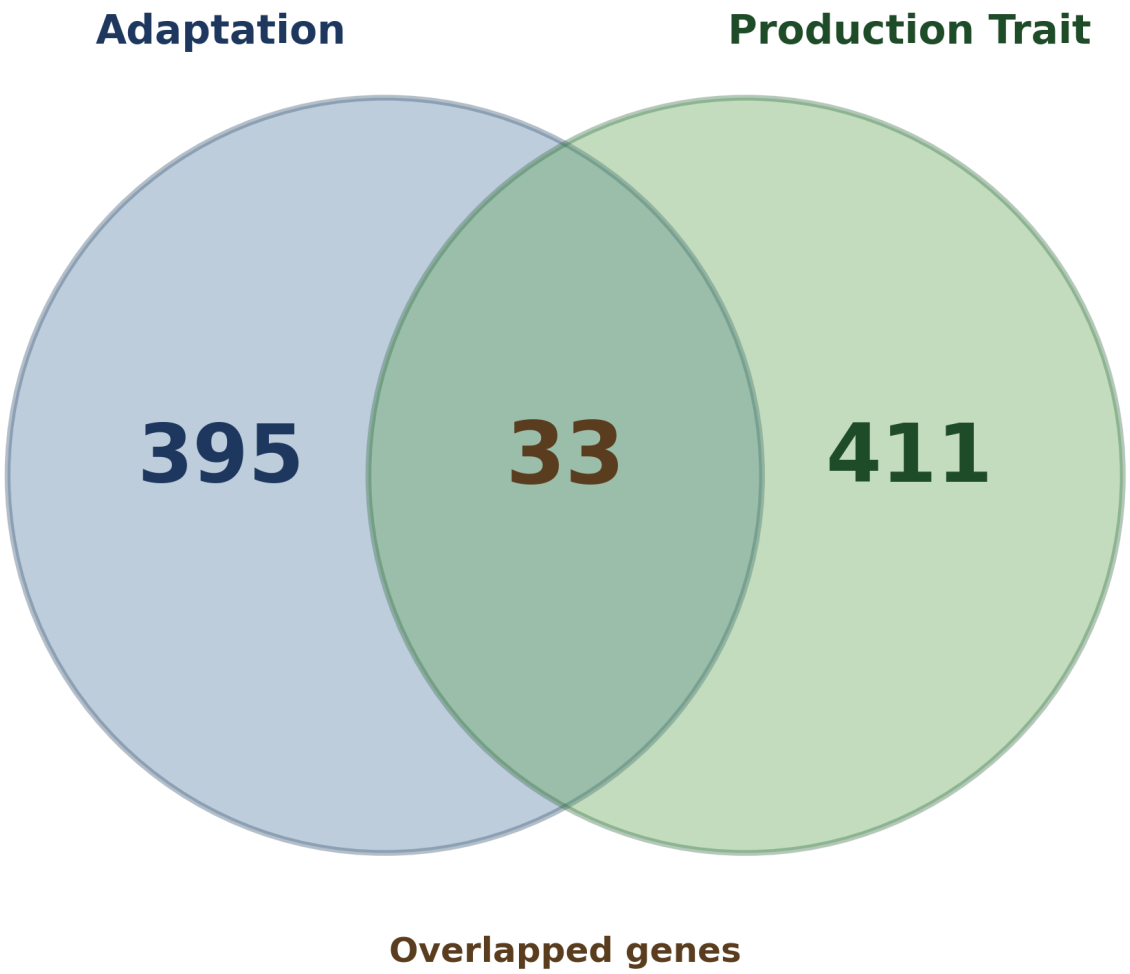


Figure 3

Figure 3. Venn diagram showing the number of candidate genes associated with adaptation and production traits as well as their overlap

Supplementary Files

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- SupplTableS1Adaptationrelatedgenes.docx
- SupplTableS2Productionrelatedgenes.docx