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ENVIRONMENTAL APPROACHES IN ANIMAL AND AQUATIC SYSTEMS

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AUTHORS
BARDHAN Avishek
MAITI Binayak
BRAHMA Aritra
SENGUPTA Sourashish
HALDER Soumili
ANASO Emmanuel Ugochukwu
OKONKWO Henry Onyebuchi
CHIMA Uzoma Darlington
NSIEN Iniobong Bruno
BABALOLA Olumide Tade

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PREFACE

This volume brings together a collection of scholarly contributions that explore the complex interactions between animal production systems, environmental sustainability, and biological research. As global demands for food continue to rise, ensuring the sustainability of both terrestrial and aquatic animal systems has become a critical priority.

The chapters in this book address key themes related to monitoring, management, and ecological balance within animal-based production systems. The application of environmental DNA (eDNA) in aquaculture highlights innovative tools for monitoring biodiversity and improving sustainability in aquatic environments. The discussion on antimicrobial resistance in livestock production emphasizes emerging public health risks and the need for sustainable alternatives in animal agriculture. In addition, the study of reproductive ecology and plant-based integration reflects the importance of biodiversity and ecological approaches in supporting resilient production systems.

By adopting an interdisciplinary perspective, this volume integrates insights from animal science, environmental biology, aquaculture, and sustainability studies. It contributes to academic discourse while also offering practical implications for researchers, practitioners, and policymakers working to develop environmentally responsible and sustainable animal production systems.

It is hoped that this book will serve as a valuable resource for scholars and professionals interested in animal systems, environmental biology, and sustainability, while encouraging further research on innovative and integrated approaches to ecological and agricultural challenges.

Editorial Team
April, 2026
Türkiye

CHAPTER 1

ENVIRONMENTAL DNA (EDNA) IN AQUACULTURE: AN APPROACH FOR MONITORING, MANAGEMENT AND SUSTAINABILITY

[1]BARDHAN Avishek
[2]MAITI Binayak
[3]BRAHMA Aritra
[4]SENGUPTA Sourashish
[5]HALDER Soumili

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[1] Division of Fisheries, The Neotia University, Sarisha, Diamond Harbour, West Bengal, India, avishek.bardhan@tnu.in, ORCID ID: 0000-0003-3087-5927
[2] Division of Fisheries, The Neotia University, Sarisha, Diamond Harbour, West Bengal, India
[3] Division of Fisheries, The Neotia University, Sarisha, Diamond Harbour, West Bengal, India
[4] Division of Fisheries, The Neotia University, Sarisha, Diamond Harbour, West Bengal, India
[5] Division of Fisheries, The Neotia University, Sarisha, Diamond Harbour, West Bengal, India

INTRODUCTION

Aquaculture is the farming of aquatic organisms with significant commercial importance, contributing substantially to global food production. In India, aquaculture production has reached approximately 19.77 million tonnes (2024–25) (FAO, 2024). Environmental DNA (eDNA) has become an important tool in fisheries science, offering a novel approach to studying aquatic systems. eDNA refers to genetic material released by organisms into their environment through processes such as defecation, secretion, reproduction, and decay. These DNA fragments persist in water, sediments, or other environmental matrices and can be collected and analysed without capturing organisms. The concept of using DNA from environmental samples originated in microbiology and paleoecology, where DNA was extracted to study microbial communities and ancient biological records (Chouhan et al. 2023). Its application to aquatic organisms became feasible with the development of molecular techniques such as polymerase chain reaction (PCR), quantitative PCR (qPCR), and next-generation sequencing (NGS). In aquaculture, eDNA supports improved monitoring and management practices. It enables detection of fish populations, identification of harmful or invasive species, and early detection of pathogens. This contributes to better disease management and helps reduce economic losses. Additionally, eDNA allows continuous monitoring of aquatic environments and improves the efficiency of water quality assessment compared to traditional methods. Another important feature of eDNA is its ability to detect rare or cryptic species that may not be captured through conventional sampling methods such as nets or traps. Thus, it enhances biodiversity assessment and supports ecosystem-based fisheries management. Overall, eDNA provides a fast and cost-efficient method for studying aquatic organisms and holds strong potential for future applications in fisheries science.

1. PRINCIPLES AND METHODOLOGY OF EDNA ANALYSIS

1.1. Sample collection

Sample collection is the foundational phase of eDNA analysis and is perhaps the most critical determinant of downstream data quality. Water samples are typically collected using sterile, pre-cleaned collection vessels such as polypropylene bottles or Nalgene containers at multiple sites within a water body. Volume collected generally ranges from one to several liters, depending on the target organism's density and the turbidity of the environment. Filtration is the predominant method for capturing eDNA from water samples. Glass fibre filters (GFF), cellulose nitrate membranes, and polyether sulfone (PES) filters with varying pore sizes (0.2–3 µm) are commonly employed. Chouhan et al. (2023) noted that the choice of filter material, pore size, and sample volume significantly influences eDNA recovery efficiency. Sediment sampling is an alternative approach for benthic species, where surface sediment is collected using grabs or corers. Regardless of matrix type, strict contamination-control protocols are mandatory: field personnel must wear gloves, use disposable equipment, and maintain separate zones for sampling and processing. Field blanks and negative controls must accompany every sampling event to detect and account for environmental or procedural contamination.

DNA extraction

Following sample collection, DNA extraction is performed to isolate genetic material from the captured eDNA (Fig. 1). Filters or sediment samples are subjected to chemical and mechanical cell lysis to release DNA from cells and extracellular matrices. The most widely adopted extraction approaches include the cetyl trimethylammonium bromide (CTAB) method, phenol-chloroform extraction, and commercially available silica-column-based kits such as the DNeasy Blood and Tissue Kit (Qiagen) or the Power Water DNA Isolation Kit (MoBio). Bohara et al. (2022) emphasized that kit-based extraction methods are preferred in aquaculture pathogen detection studies due to their consistency, speed, and ability to remove PCR inhibitors present in water samples such as humic acids, tannins, and heavy metals.

DNA yield and purity are assessed using spectrophotometry (Nano Drop) or fluorometry (Qubit), with A260/A280 ratios between 1.7 and 2.0 considered acceptable. Proper storage conditions (−20°C to −80°C) are essential for preserving extracted DNA integrity until downstream analysis.

DNA amplification

DNA amplification is the process by which specific target sequences in the extracted eDNA are exponentially replicated for detection. Polymerase Chain Reaction (PCR) and its quantitative variant, quantitative PCR (qPCR), are the most widely employed amplification techniques in eDNA research. Species-specific primers and probes are designed to target conserved genomic regions such as the mitochondrial cytochrome oxidase I (COI) gene, the 12S or 16S rRNA gene, or the internal transcribed spacer (ITS) regions, depending on the organism group of interest. Chouhan et al. (2023) described how qPCR not only confirms the presence or absence of a target species but also provides quantitative estimates of DNA concentration, which can be used as a proxy for relative abundance or biomass. Droplet digital PCR (ddPCR) is an emerging alternative that offers superior precision and sensitivity, particularly when eDNA concentrations are extremely low. Bohara et al. (2022) demonstrated the utility of qPCR in detecting fish pathogens such as *Aphanomyces invadans* (the causative agent of epizootic ulcerative syndrome) in aquaculture water samples, with detection limits as low as a few copies of target DNA per reaction. Strict use of negative controls, no-template controls (NTCs), and positive controls in all amplification runs is essential to validate results and rule out false positives caused by contamination.

DNA sequencing

Sequencing is the final analytical step that provides definitive taxonomic identification and community-level information from eDNA samples. Sanger sequencing is used for single-species confirmation of amplified PCR products, whereas Next Generation Sequencing (NGS) technologies, such as Illumina MiSeq and Oxford Nanopore Technologies (ONT), enable metabarcoding approaches for simultaneous detection of multiple taxa from a single environmental sample.

In eDNA metabarcoding, universal primers are used to amplify broad taxonomic groups (e.g., all fish species via 12S rRNA), and the resulting amplicon library is sequenced to generate millions of short reads. These reads are then processed through bioinformatics pipelines that include quality filtering, chimera removal, clustering into Operational Taxonomic Units (OTUs) or Amplicon Sequence Variants (ASVs), and taxonomic assignment against reference databases such as NCBI GenBank, BOLD, or SILVA. Bohara et al. (2022) highlighted that NGS-based eDNA approaches can identify pathogen communities in aquaculture ponds with unprecedented resolution, enabling early warning systems for disease outbreaks. Chouhan et al. (2023) further noted that bioinformatic standardization and reference library completeness remain key challenges in achieving consistent taxonomic resolution across different aquatic ecosystems.

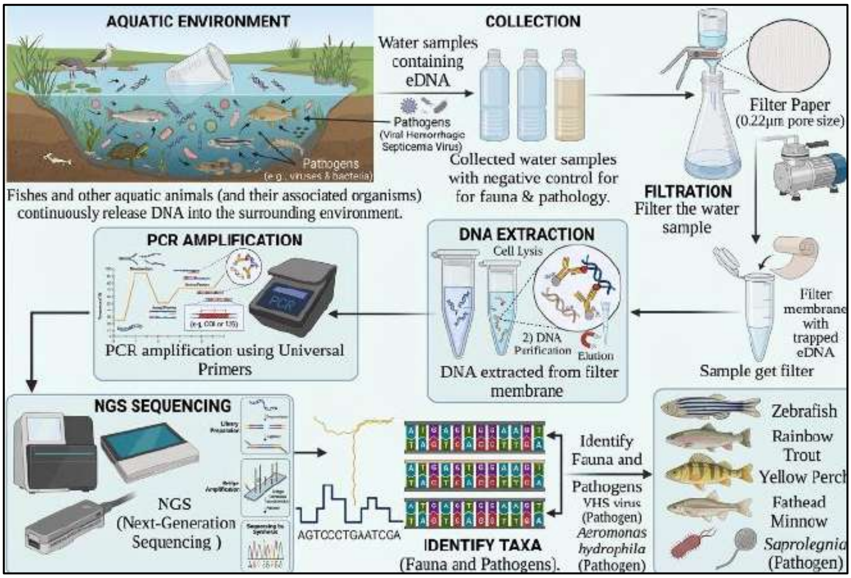

Figure 1 Workflow of eDNA analysis in aquatic systems, from sample collection and filtration to DNA extraction, amplification, sequencing, and species identification.

2. EDNA APPLICATIONS IN FISHERIES

eDNA has transformed fisheries science by offering non-invasive, cost-effective methods for monitoring aquatic ecosystems.

Building on foundational work demonstrating that eDNA concentrations correlate with species abundance (Lacoursière-Roussel et al., 2016), recent research has expanded applications across biodiversity assessment, endangered species conservation, invasive species detection, and pathogen surveillance.

Biodiversity assessment

Early biodiversity monitoring relied heavily on traditional methods like gillnetting, electrofishing, and visual surveys, which were labor-intensive, costly, and often harmful to target populations. Lacoursière-Roussel et al. (2016) demonstrated that eDNA concentrations in lake water significantly correlated with catch per unit effort (CPUE) for Lake Trout, establishing that eDNA could inform not just presence/absence but relative abundance. Metabarcoding approaches now enable simultaneous detection of entire fish communities from single water samples, replacing species-specific assays with broader surveys. Seemani et al. (2025) applied eDNA metabarcoding in the Mweru-Luapula fishery and detected five rare species (including *Marcusenius senegalensis* and *Synodontis schoutedeni*) not previously recorded through conventional methods. Spatial heterogeneity of eDNA distribution has been shown to mirror actual spatial variation in fish abundance, allowing researchers to map population distributions across water bodies without extensive netting efforts. Seasonal and temporal dynamics are now better understood, with studies showing that eDNA signals fluctuate with spawning activity, water temperature, and flow conditions, enabling timing-specific surveys that capture population dynamics.

Endangered species monitoring

Traditional monitoring of endangered fish species posed ethical and practical problems: electrofishing and netting stressed already vulnerable populations, and cryptic or low-density species often evaded detection entirely. Nolan et al. (2023) validated eDNA technology for brook trout (*Salvelinus fontinalis*), a species of conservation concern in Southwestern Ontario.

Their collaborative study between academia, industry, and NGOs demonstrated that eDNA detected brook trout at all sampling locations in Hanlon Creek and at 5 of 6 locations in Twelve Mile Creek, including sites where the species was previously unreported. Importantly, stronger eDNA signals in November compared to September suggested spawning activity, demonstrating eDNA's capacity to infer reproductive behavior without direct observation. Schumer et al. (2019) showed that eDNA could reliably detect a single brook trout up to 500 meters downstream, providing managers with tools to monitor threatened bull trout (*Salvelinus confluentus*) populations and assess the effectiveness of invasive species removal efforts. Because eDNA requires only water collection, endangered species can be monitored repeatedly without the handling, stress, or mortality associated with traditional capture methods, which is a critical consideration for ESA-listed species.

Invasive species monitoring and pathogen tracking

Detecting invasive species at low densities, before populations establish, has historically been extremely difficult. Similarly, tracking aquatic pathogens required intensive sampling of host organisms. eDNA enables detection of invasive species at densities below the threshold of traditional methods. Riaz et al. (2023) used quantitative eDNA assays to assess predator-prey interactions between invasive fishes (*Lepomis gibbosus*, *Pseudorasbora parva*) and native amphibians in Germany, finding negative correlations between predator and prey eDNA concentrations, confirming that invasive fish were contributing to amphibian declines. Schumer et al. (2019) demonstrated that eDNA sampling provides rapid, reliable confirmation of whether eradication efforts have succeeded, replacing weeks of electrofishing with water sampling that can detect survivors within days. Seemani et al. (2025) revealed invasive *Parachanna* species in three of four strata of the Mweru-Luapula fishery, compared to only two strata previously known through traditional methods, demonstrating eDNA's superior sensitivity for mapping invasion fronts.

3. ADVANTAGES AND LIMITATIONS OF EDNA IN AQUACULTURE

eDNA has emerged as a powerful modern tool in fisheries science, referring to genetic material released by organisms into the environment through skin cells, mucus, faeces, or gametes, which can be collected from water samples and analysed to detect species presence without physical capture (Fig. 2). One of its major advantages is that it is a non-invasive and eco-friendly method that avoids handling or disturbing fish populations, thereby reducing stress and mortality, and making it especially suitable for endangered or protected species. eDNA methods are highly sensitive and can detect species even at very low abundance, which is useful for identifying rare, invasive, or cryptic species. Additionally, metabarcoding allows detection of multiple species from a single sample, enabling biodiversity assessment, ecosystem monitoring, and understanding species interactions. The method is also cost-effective and time-saving, requiring minimal equipment and manpower, with faster sampling and the ability to process multiple samples simultaneously. Sampling is relatively simple and can be standardized across locations, improving comparability of results. Furthermore, eDNA provides better biodiversity coverage by detecting species that may be missed by traditional methods, such as deep-water or fast-swimming fishes, and supports conservation and fisheries management by providing information on species distribution, habitat use, and invasive species presence.

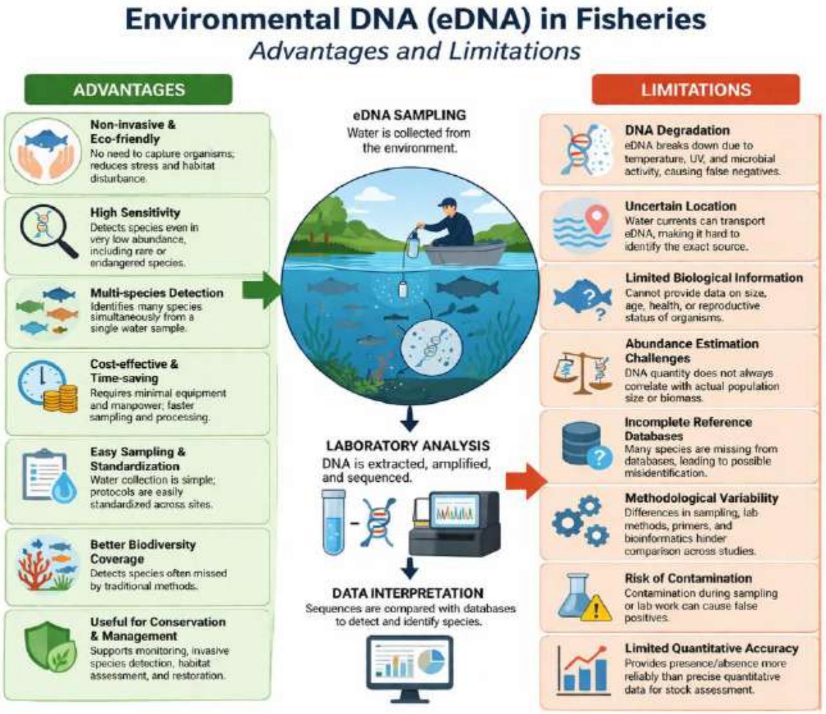

Figure 2. Overview of eDNA in fisheries showing sampling and laboratory analysis workflow, along with key advantages and limitations

However, eDNA also has several limitations that must be considered. DNA degrades rapidly due to environmental factors such as temperature, UV radiation, and microbial activity, which may reduce detection success. In addition, water movement can transport DNA away from its source, making it difficult to determine the exact location of organisms. Unlike conventional methods, eDNA cannot provide detailed biological information such as size, age, growth rate, or reproductive status. Estimating abundance or biomass is also challenging because DNA shedding rates vary among species and environmental conditions influence DNA concentration. The reliability of results is further affected by incomplete or inaccurate reference databases, as well as methodological variability in sampling, extraction, amplification, and bioinformatics analysis. High sensitivity of eDNA also increases the risk of contamination during sampling and laboratory processing, which may lead to false positives.

Finally, while eDNA is effective for detecting presence or absence, its quantitative accuracy is still limited, restricting its application in precise stock assessment.

4. RECENT DEVELOPMENTS OF EDNA IN FISHERIES AND AQUACULTURE

Edna has rapidly become a key tool for non-invasive, cost-effective monitoring of fish and aquatic ecosystems. Recent work shows eDNA can support fisheries stock assessment, invasive species detection, health and pathogen surveillance, and ecosystem-based management in both wild fisheries and aquaculture settings. Recent research positions eDNA as a powerful complement to traditional fisheries and aquaculture monitoring, enabling broad-scale biodiversity surveys, emerging biomass indices, disease and invasive species surveillance, and ecosystem-based management (Table 1). At the same time, studies stress the need for standardized methods, better understanding of eDNA dynamics, careful validation, and stronger integration with stock assessment and policy frameworks before full operational adoption.

Table 1 Detailed tabulation of recent developments of eDNA in aquaculture

Application	Purpose	Key Points	References
Biodiversity monitoring using metabarcoding (MiFish)	Assess species richness and community composition	High-throughput metabarcoding (e.g., MiFish primers) enables simultaneous detection of diverse fish communities; improves detection of rare species; reveals spatial and temporal patterns in ecosystems	Miya et al. 2022; Yao et al. 2022
eDNA-based stock assessment and biomass estimation	Develop fishery-independent indices and improve stock monitoring	eDNA concentration shows correlation with abundance/biomass, though influenced by environmental factors; workflows developed for large-scale marine surveys;	Rourke et al. 2025; Yao et al. 2022

		requires calibration and standardization	
Salmon monitoring and aquaculture applications	Track wild and cultured salmon populations and health	eDNA applied for distribution mapping, pathogen detection, and monitoring of farm-wild interactions; useful in hatcheries and open-water systems	Chouhan et al. 2023
Pathogen detection, ARGs, and biosecurity in aquaculture	Early detection of diseases and resistance genes	Enables monitoring of fish pathogens, harmful algal blooms, and antibiotic resistance genes; supports biosecurity and reduces disease outbreaks in farms	Wang et al. 2025; Chouhan et al. 2023
Invasive and rare species detection	Early warning and conservation monitoring	Highly sensitive detection at low densities; allows rapid identification of invasive species and supports conservation of endangered taxa	Miya et al. 2022; Bernos et al. 2023
Methodological advances (qPCR, ddPCR, multiplex, CRISPR, meta-omics, eRNA)	Improve detection accuracy and expand applications	Development of species-specific assays (qPCR/ddPCR), multiplex detection, CRISPR-based diagnostics, and integration with eRNA and meta-omics for functional insights beyond presence/absence	Pochon et al. 2025
eDNA in marine fisheries survey design	Improve large-scale monitoring strategies	Optimized sampling design, replication strategies, and integration with conventional surveys enhance reliability for marine stock assessments	Ramírez-Amaro et al. 2022

Policy integration and fisheries management frameworks	Incorporate eDNA into decision-making systems	Increasing adoption in national monitoring programs; development of guidelines and frameworks for integrating eDNA into fisheries management	Baetscher et al. 2025; Bernos et al. 2023
Understanding eDNA dynamics (shedding, decay, transport)	Improve interpretation of abundance and spatial patterns	Studies on DNA shedding rates, degradation kinetics, particle size, and environmental influences help refine quantitative models and reduce uncertainty	Kirtane et al. 2021
Addressing uncertainty and limitations in eDNA applications	Improve reliability and acceptance in fisheries science	Highlights challenges in quantification, environmental variability, and methodological standardization; emphasizes need for calibration with traditional methods	Yao et al. 2022

CONCLUSION AND FUTURE PERSPECTIVES

Environmental DNA has steadily established itself as a practical and informative approach for understanding aquatic systems, particularly within aquaculture. By allowing detection of species, pathogens, and community shifts without direct handling of organisms, it offers a clear advantage in terms of efficiency and minimal disturbance. Across this chapter, it is evident that eDNA can support a wide range of applications, from routine monitoring of farm environments to early detection of disease risks and assessment of biodiversity. At the same time, it is important to recognize that eDNA is not without its limitations. Factors such as DNA degradation, environmental variability, and challenges in quantitative interpretation require careful consideration. Rather than replacing conventional methods, eDNA works best when used alongside them, adding another layer of insight that can improve decision-making.

Looking ahead, continued improvements in molecular techniques, data analysis, and standardization will likely make eDNA more reliable and accessible for aquaculture practitioners. As the field progresses, its role in supporting sustainable aquaculture and responsible resource management is expected to grow, making it an increasingly valuable component of modern fisheries science.

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CHAPTER 2

ANTIMICROBIAL RESISTANCE IN LIVESTOCK PRODUCTION: CHALLENGES, PUBLIC HEALTH RISKS, AND THE STRATEGIC ROLE OF PHYTOGENIC FEED ADDITIVES IN SUSTAINABLE ANIMAL AGRICULTURE

[1]ANASO Emmanuel Ugochukwu

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[1]Department of Animal Science, Faculty of Agriculture, Federal University of Agriculture Mubi, Adamawa, Nigeria, dranasoeub@gmail.com, ORCID ID: 0009-0001-6886-8557

INTRODUCTION

Livestock production is an essential component of global agri-food systems, ensuring the supply of high-quality animal protein, micronutrients, and industrial raw materials while also providing a critical source of income for millions of smallholder farmers and pastoral communities. Beyond its direct contribution to food security, the sector plays a crucial role in socioeconomic development by creating jobs, accumulating assets, and mitigating risk in vulnerable rural economies. Livestock serves as a source of financial capital and socio-cultural richness in developing countries, notably in Sub-Saharan Africa, emphasizing its varied importance (FAO, 2013; Anaso, 2024; Anaso and Anaso, 2025; Anaso and Chibuogwu, 2026).

However, the progressive intensification and commercialization of livestock systems, which include larger stocking densities, genetic selection for productivity, and increased confinement, has resulted in increased disease pressure and production stress. To address these issues and maintain production, antimicrobial medicines have been widely used in animal husbandry methods, not only for therapeutic objectives, but also for prevention and growth promotion. These sub-therapeutic treatments, which are frequently provided over long periods of time, provide perfect selection conditions for the growth of resistant microbial strains (Van Boeckel et al., 2015; Marshall and Levy, 2011).

The consequence of this widespread and frequently unregulated antimicrobial use is the accelerated emergence and dissemination of antimicrobial resistance (AMR), now recognized as one of the most pressing global public health threats. AMR arises through genetic adaptations in microorganisms such as mutation or horizontal gene transfer that enable them to withstand previously effective antimicrobial compounds. This phenomenon compromises the efficacy of standard treatments, resulting in persistent infections, increased morbidity and mortality, and escalating healthcare and production costs (WHO, 2020; Anaso et al., 2024a-d). In livestock production systems, the implications are particularly profound, as resistant pathogens can compromise animal health, reduce productivity, and undermine the sustainability of the sector.

AMR has a significant influence on human health via many transmission channels, in addition to animal populations. Zoonotic transmission of resistant bacteria can occur through direct contact with animals, occupational exposure among farm workers, and ingestion of contaminated animal-derived products such as meat, milk, and eggs. Furthermore, environmental dispersion via manure, wastewater, and runoff promotes the spread of resistance genes into soil and aquatic habitats, increasing the public health risk (Landers et al., 2012; Anaso et al., 2025a,d). This connection is consistent with the One Health paradigm, which acknowledges the inextricable link between animal health, human health, and environmental integrity.

Projections of the global burden of AMR are worrying, with estimates indicating that, in the absence of effective intervention, antimicrobial-resistant illnesses could account for up to 10 million deaths yearly by 2050, surpassing mortality from major diseases such as cancer. This impending catastrophe needs a rapid shift to sustainable and responsible livestock production systems that reduce dependency on conventional antibiotics while maintaining productivity and animal welfare.

In this context, phytogenic feed additives (PFAs) have emerged as potentially beneficial alternatives to antibiotic growth promoters. PFAs are derived from plants and include herbs, spices, essential oils, and plant extracts. They contain a wide range of bioactive chemicals including as phenolics, flavonoids, terpenoids, and alkaloids. These chemicals have a variety of biological actions, including antibacterial, antioxidant, anti-inflammatory, and digestive stimulatory properties. PFAs can change gut microbiota composition, improve intestinal integrity, boost endogenous enzyme production, and increase nutrition consumption efficiency. Furthermore, their natural origin and well accepted safety profile make them promising candidates for incorporation into sustainable cattle feeding regimens (Windisch et al., 2008; Patra and Saxena, 2010; Anaso et al., 2025a-g).

Importantly, the use of PFAs corresponds with global efforts to limit antimicrobial use in animal agriculture, which are supported by international regulatory and advisory groups. Their multifunctional features not only improve animal health and performance, but also help to prevent the formation and spread of AMR.

As a result, ongoing study into the efficacy, appropriate inclusion levels, and molecular routes of PFAs, particularly in region-specific production systems, is critical for expanding their practical implementation and guaranteeing the long-term viability of livestock systems.

1. ANTIMICROBIAL USE IN LIVESTOCK PRODUCTION

1.1 Drivers of Antimicrobial Use

The use of antimicrobials in livestock production is underpinned by a complex interplay of biological, managerial, and economic drivers that collectively shape decision-making at the farm level. Fundamentally, antimicrobials are employed to safeguard animal health, optimize productivity, and ensure economic viability within increasingly demanding production systems (Aarestrup, 2015). Their applications broadly span three domains: therapeutic use for the treatment of clinically ill animals, prophylactic use to prevent disease outbreaks in at-risk populations, and sub-therapeutic use as growth promoters to enhance feed efficiency and weight gain.

The structural and environmental factors of intensive livestock production systems predispose animals to increased illness risk. High stocking numbers, restricted space, and continuous production cycles promote rapid pathogen transmission and raise the risk of endemic diseases. Furthermore, animals in such systems are routinely subjected to a variety of stressors, including heat stress, transportation, weaning, food transitions, and social rivalry, all of which can impair immune function and reduce disease resistance. Under these situations, prophylactic antimicrobial medication becomes a standard management method for maintaining herd or flock health and avoiding economically disastrous disease outbreaks. While this method may result in short-term productivity benefits, it also puts ongoing selective pressure on microbial populations, hastening the establishment of resistant species.

Antimicrobials have long been used as growth promoters, which has contributed to their extensive use. Certain antibiotics boost growth performance at subtherapeutic doses by altering the gut microbiota, lowering subclinical infections, and increasing nutrient absorption efficiency. This method has proven particularly appealing in commercial operations where small increases in feed conversion ratio (FCR) translate into significant economic returns.

However, non-therapeutic antibiotic usage has been extensively criticized for contributing significantly to antimicrobial resistance, leading regulatory limits or outright bans in many affluent nations.

Economic considerations support antimicrobial use throughout animal systems. Disease outbreaks can cause substantial financial losses due to death, reduced growth rates, higher feed costs, and veterinarian expenses. As a result, farmers frequently regard antimicrobials as cost-effective insurance measures that reduce production risks and stabilize output. In highly competitive marketplaces with tight profit margins, the temptation to maintain steady production may trump concerns about long-term public health consequences, especially in the absence of immediate regulatory enforcement or viable alternatives.

The issues connected with antibiotic use are significantly more severe in underdeveloped countries due to systemic and institutional constraints. Weak regulatory frameworks frequently fail to effectively oversee the distribution, prescription, and administration of veterinary medications. As a result, antimicrobials are frequently available without a prescription, allowing farmers with inadequate technical competence to freely acquire and utilize them. This lack of control is exacerbated by poor veterinary infrastructure, which includes a scarcity of educated veterinarians, inadequate diagnostic facilities, and limited extension services. Consequently, farmers frequently turn to self-prescription, poor drug selection, incorrect dose, and failure to observe withdrawal periods (Anaso and Salihu, 2025).

Moreover, the informal nature of many livestock production systems in developing countries exacerbates the problem. Smallholder farmers, who constitute a significant proportion of livestock producers, often operate under resource constraints that limit their ability to implement biosecurity measures, vaccination programs, and proper housing systems. In such contexts, antimicrobials become a convenient and readily accessible substitute for comprehensive herd health management practices. The use of counterfeit or substandard drugs an issue prevalent in some low- and middle-income countries further complicates the situation by exposing pathogens to sub-lethal concentrations of active ingredients, thereby accelerating resistance development.

Knowledge gaps and limited awareness regarding antimicrobial resistance also play a critical role. Many farmers are unaware of the mechanisms and consequences of AMR, including its implications for human health and long-term livestock productivity. This lack of awareness, coupled with aggressive marketing by pharmaceutical vendors and inadequate policy enforcement, fosters a culture of misuse and overdependence on antibiotics (Anaso and Dikki, 2025).

Collectively, these factors create a high-risk environment for the emergence and dissemination of antimicrobial resistance within livestock systems, particularly in developing regions. Addressing this challenge requires a multifaceted approach, including strengthening regulatory frameworks, enhancing veterinary service delivery, promoting farmer education, and encouraging the adoption of integrated disease management strategies. Such strategies should prioritize preventive measures such as improved nutrition, biosecurity, vaccination, and the use of sustainable alternatives to reduce reliance on antimicrobials while maintaining productivity and animal welfare.

1.2 Patterns of Use

Antibiotics routinely deployed in livestock production encompass several major pharmacological classes, notably tetracyclines, macrolides, β-lactams, and sulfonamides, each characterized by distinct mechanisms of action and spectra of antimicrobial activity (Van Boeckel et al., 2015). Their widespread use reflects their relative affordability, broad-spectrum efficacy, and historical success in controlling bacterial diseases in food-producing animals.

Tetracyclines, for instance, are among the most extensively used antimicrobials in animal agriculture due to their ability to inhibit bacterial protein synthesis by binding to the 30S ribosomal subunit. They are commonly administered for the treatment and prevention of respiratory, enteric, and systemic infections across multiple species, including poultry, swine, and ruminants. Similarly, macrolides such as tylosin and erythromycin target the 50S ribosomal subunit and are particularly effective against Gram-positive bacteria and certain intracellular pathogens, making them valuable in managing respiratory diseases and mycoplasma infections (Anaso and Salihu, 2025).

β-lactam antibiotics, which include penicillins and cephalosporins, function by disrupting bacterial cell wall synthesis, leading to cell lysis. These drugs are widely used in both therapeutic and prophylactic contexts, especially in the treatment of mastitis, septicemia, and other bacterial infections in livestock. Sulfonamides, often used in combination with trimethoprim, act by inhibiting folic acid synthesis in bacteria and are commonly applied in the control of coccidiosis and bacterial enteritis.

While these antimicrobial classes play a crucial role in maintaining animal health and productivity, their extensive and sometimes indiscriminate use in livestock production raises significant public health concerns. A central issue is that many of these antibiotics are classified as critically important for human medicine by global health authorities due to their role in treating serious and sometimes life-threatening infections. For example, macrolides and certain β-lactams (particularly third- and fourth-generation cephalosporins) are essential for managing respiratory tract infections, bloodstream infections, and other invasive bacterial diseases in humans.

The overlap in antimicrobial classes used in both veterinary and human medicine creates a pathway for cross-resistance, a phenomenon whereby resistance developed in animal-associated bacteria can compromise the effectiveness of the same or structurally related drugs in human pathogens. Mechanistically, this occurs through shared resistance determinants such as efflux pumps, enzymatic degradation (e.g., β-lactamases), and target site modifications, which can be encoded by mobile genetic elements like plasmids, transposons, and integrons. These elements facilitate horizontal gene transfer between bacterial populations, enabling resistance traits to spread across species and ecological niches.

From a One Health perspective, the implications are profound. Resistant bacteria originating in livestock can be transmitted to humans through multiple routes, including the food chain, direct animal contact, and environmental dissemination via manure and agricultural runoff. Once established in human populations, these resistant strains can limit therapeutic options, leading to treatment failures, prolonged illness, and increased mortality.

The concern is further amplified by the potential for co-selection and multi-drug resistance. For example, the use of tetracyclines in livestock can select for resistance genes that are genetically linked to resistance against other antibiotic classes, even in the absence of direct exposure to those drugs. This genetic linkage accelerates the emergence of multidrug-resistant (MDR) pathogens, which are significantly more difficult and costly to manage.

The continued reliance on antibiotic classes that are critical for human health in livestock production systems necessitates urgent and coordinated interventions. These include stricter regulation of antimicrobial use, prioritization of antibiotics with lower importance to human medicine for veterinary applications, and the development of alternative strategies such as vaccination, improved biosecurity, and the use of non-antibiotic feed additives. Without such measures, the risk of eroding the efficacy of essential antimicrobials and thereby undermining both animal and human health systems remains a significant and escalating global threat.

2. MECHANISMS AND TRANSMISSION OF ANTIMICROBIAL RESISTANCE

2.1 Mechanisms of Resistance

Microbial resistance to antimicrobial agents is a multifactorial and dynamic process driven by genetic adaptability and selective pressure. Bacteria and other microorganisms have evolved a range of sophisticated mechanisms that enable them to survive exposure to antibiotics that would otherwise inhibit or kill them. These resistance strategies may be intrinsic (naturally occurring) or acquired through mutation and horizontal gene transfer, and they often operate synergistically within the same organism, thereby enhancing the overall level of resistance. The principal mechanisms include enzymatic degradation of antibiotics, modification of drug targets, active efflux of antimicrobial agents, and reduced cellular permeability.

Enzymatic degradation of antibiotics represents one of the most direct and effective resistance mechanisms. In this process, microorganisms produce specific enzymes that chemically inactivate antimicrobial agents before they can reach or bind to their intended targets.

A classical example is the production of β-lactamases, which hydrolyze the β-lactam ring of penicillins and cephalosporins, rendering them ineffective. Similarly, aminoglycoside-modifying enzymes—such as acetyltransferases, phosphotransferases, and nucleotidyltransferases—alter the structure of aminoglycoside antibiotics, thereby preventing their interaction with bacterial ribosomes. The genes encoding these enzymes are often located on plasmids, facilitating rapid dissemination across bacterial populations and even between different species.

Modification of drug targets is another critical mechanism by which microorganisms evade antimicrobial action. Antibiotics typically exert their effects by binding to specific cellular targets, such as ribosomal subunits, enzymes involved in cell wall synthesis, or DNA replication machinery. Through genetic mutations or acquisition of resistance genes, bacteria can alter the structure or configuration of these targets, reducing the binding affinity of the drug. For instance, alterations in penicillin-binding proteins (PBPs) can confer resistance to β-lactam antibiotics, as observed in methicillin-resistant *Staphylococcus aureus* (MRSA). Likewise, methylation of ribosomal RNA can prevent macrolide binding, while mutations in DNA gyrase and topoisomerase IV can lead to resistance against fluoroquinolones. These modifications preserve essential cellular functions while diminishing antibiotic efficacy.

Efflux pump systems constitute an active resistance mechanism in which microorganisms expel antimicrobial agents from the cell before they can accumulate to inhibitory concentrations. These membrane-associated transport proteins can be highly specific for certain drugs or function as multidrug resistance (MDR) pumps capable of extruding a wide range of structurally unrelated compounds. Efflux pumps are particularly significant because they contribute not only to resistance but also to reduced intracellular drug accumulation, which may allow bacteria to survive sub-lethal antibiotic exposure and subsequently develop additional resistance mechanisms. In Gram-negative bacteria, efflux systems such as the AcrAB-TolC complex play a major role in resistance to tetracyclines, chloramphenicol, and fluoroquinolones.

Reduced permeability to antimicrobial agents further limits the effectiveness of antibiotics, particularly in Gram-negative bacteria, which possess an outer membrane that acts as a selective barrier. Alterations in membrane proteins, such as porins, can decrease the uptake of antibiotics into the cell. For example, downregulation or structural modification of porin channels can significantly reduce the entry of β-lactams and other hydrophilic antibiotics. In addition, changes in membrane lipid composition can affect drug diffusion and permeability. This mechanism is often coupled with efflux pump activity, creating a dual barrier that both prevents drug entry and enhances drug expulsion.

Importantly, these resistance mechanisms rarely occur in isolation. Many pathogenic bacteria harbor multiple resistance determinants simultaneously, often encoded on mobile genetic elements such as plasmids, transposons, and integrons. This genetic organization facilitates the co-selection of resistance traits, meaning that the use of one antibiotic can inadvertently select for resistance to several others. In livestock production systems, where antimicrobial exposure may be continuous or sub-therapeutic, such conditions provide an ideal environment for the selection, amplification, and dissemination of multidrug-resistant organisms.

The cumulative effect of these mechanisms is the progressive erosion of antimicrobial efficacy, complicating disease management in both veterinary and human medicine. Understanding these resistance pathways is therefore essential for designing targeted interventions, developing novel therapeutics, and implementing effective antimicrobial stewardship strategies.

Horizontal gene transfer via plasmids, transposons, and integrons plays a crucial role in spreading resistance genes (Davies and Davies, 2010).

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3. PUBLIC HEALTH AND ENVIRONMENTAL IMPLICATIONS

The implications of antimicrobial resistance (AMR) extend far beyond the boundaries of livestock production, constituting a systemic threat to global public health, environmental sustainability, and economic stability. What begins as a management practice within animal agriculture can cascade through interconnected biological and ecological systems, ultimately compromising the effectiveness of life-saving therapies in human medicine.

At the human health level, resistant infections significantly alter clinical outcomes and healthcare dynamics. When pathogens become resistant to first-line or even last-resort antibiotics, treatment options become limited, less effective, and often more toxic. This leads to prolonged illness, increased risk of complications, and higher case fatality rates. Routine medical procedures such as surgeries, chemotherapy, organ transplantation, and neonatal care also become riskier, as they depend heavily on effective antimicrobial prophylaxis. Moreover, resistant infections often require extended hospital stays, the use of more expensive second- or third-line drugs, and intensive care interventions, thereby substantially increasing healthcare costs and placing additional strain on already burdened health systems, particularly in low- and middle-income countries (WHO, 2020).

Beyond direct clinical impacts, AMR exerts significant socio-economic consequences. Loss of productivity due to prolonged illness, increased out-of-pocket healthcare expenditures, and the burden on public health infrastructure collectively contribute to economic decline. In severe cases, AMR can undermine progress toward global development goals, especially those related to poverty reduction, food security, and health equity.

The environmental dimension of AMR is equally critical and often underappreciated. The widespread use of antimicrobials in livestock production results in the excretion of unmetabolized drug residues and resistant microorganisms through urine and feces. These contaminants are subsequently introduced into the environment via manure application on agricultural land, runoff into water bodies, and improper waste disposal practices.

Once in the environment, antibiotic residues can persist and exert selective pressure on native microbial communities, promoting the proliferation and maintenance of resistance genes even outside clinical or farm settings (Kümmerer, 2009; Anaso, 2026a,b).

This environmental exposure disrupts natural microbial ecosystems, which play essential roles in nutrient cycling, soil fertility, and ecosystem resilience. Antibiotics and resistance determinants can alter microbial diversity and community structure, potentially impairing ecosystem functions such as nitrogen fixation, organic matter decomposition, and biogeochemical cycling. Over time, such disruptions may contribute to reduced soil productivity and broader biodiversity loss, particularly among microbial taxa that are sensitive to antimicrobial compounds.

Livestock waste, in particular, serves as a major reservoir and conduit for antimicrobial resistance genes (ARGs). Manure from treated animals often contains high concentrations of both antibiotic residues and resistant bacteria. When applied as fertilizer, this manure introduces ARGs into the soil microbiome, where they can be taken up by environmental bacteria through horizontal gene transfer mechanisms such as transformation, transduction, and conjugation. These genes can then persist, proliferate, and potentially re-enter human and animal populations through contaminated water, crops, or direct environmental exposure.

Aquatic systems are especially vulnerable to this form of contamination. Runoff carrying antibiotics and resistant bacteria can pollute rivers, lakes, and groundwater, creating hotspots for resistance evolution. In such environments, diverse microbial communities interact closely, facilitating the exchange of genetic material and accelerating the spread of resistance across different bacterial species, including potential human pathogens.

The interconnected nature of these processes underscores the importance of the One Health framework, which recognizes that human health, animal health, and environmental health are inextricably linked. Addressing AMR therefore requires coordinated, cross-sectoral interventions that encompass prudent antimicrobial use in livestock, improved waste management systems, environmental monitoring, and strengthened public health infrastructure.

In summary, AMR is not merely a veterinary or clinical issue but a global ecological crisis with far-reaching implications. The role of livestock systems in amplifying and disseminating resistance highlights the urgent need for sustainable production practices, integrated surveillance systems, and the adoption of alternative strategies that minimize antimicrobial dependence while preserving ecosystem integrity and public health.

4. PHYTOGENIC FEED ADDITIVES AS ALTERNATIVES TO ANTIBIOTICS

Overview of Phytogenic Feed Additives

Phytogenic feed additives (PFAs) are plant-derived compounds including:

- Essential oils
- Tannins
- Saponins
- Flavonoids
- Alkaloids

These compounds exhibit antimicrobial, antioxidant, and anti-inflammatory properties (Windisch et al., 2008; Patra and Saxena, 2010; Anaso et al.,2025a-e).

Mechanisms of Action

PFAs exert their effects through:

- Disruption of microbial cell membranes
- Inhibition of enzyme activity
- Modulation of gut microbiota
- Reduction of pathogen colonization

Essential oils such as thymol, carvacrol, and eugenol have demonstrated strong antimicrobial activity against pathogenic bacteria (Burt, 2004; Anaso et al., 2025a-g).

Effects on Animal Performance

Studies have shown that PFAs:

- Improve feed efficiency

- Enhance nutrient digestibility
- Boost immune response
- Reduce disease incidence

Plant-based additives such as *Piliostigma thonningii* and *Daniellia oliveri* have shown promising results in ruminant nutrition (Anaso et al., 2025a-g).

Methane Reduction and Environmental Benefits

PFAs can also reduce enteric methane emissions by altering rumen fermentation pathways, thereby contributing to climate change mitigation (Patra and Saxena, 2010; Anaso and Olafadehan, 2025).

5. CHALLENGES IN ADOPTION OF PHYTOGENIC ADDITIVES

Despite their potential, several constraints limit widespread adoption:

- Variability in efficacy due to plant composition
- Lack of standardization and dosage optimization
- High cost of extraction and processing
- Limited awareness among farmers
- Regulatory uncertainties

Addressing these challenges requires multidisciplinary research and policy support (Anaso and Dikki, 2025).

6. POLICY AND REGULATORY FRAMEWORKS

Global efforts to combat antimicrobial resistance (AMR) have coalesced around coordinated, multi-sectoral frameworks, most notably the World Health Organization Global Action Plan on Antimicrobial Resistance. This strategy is anchored in the One Health paradigm, recognizing the interdependence of human, animal, and environmental health systems. It outlines priority interventions aimed at curbing the emergence and spread of AMR while safeguarding the efficacy of existing antimicrobial agents.

Reduction in antimicrobial use

A central pillar of global AMR mitigation strategies is the rationalization and reduction of antimicrobial use across all sectors, particularly in livestock production where non-therapeutic applications have historically been widespread. This involves transitioning from routine prophylactic and growth-promoting uses toward evidence-based, therapeutic applications under strict veterinary oversight. Antimicrobial stewardship programs are being promoted to ensure appropriate drug selection, dosing, and duration of treatment. Additionally, the prioritization of critically important antimicrobials for human medicine such as certain macrolides and advanced β-lactams has led to restrictions or bans on their use in animal agriculture. Reducing overall antimicrobial consumption not only decreases selective pressure on microbial populations but also slows the evolution and dissemination of resistance (Anaso, 2026).

Surveillance and monitoring

Robust surveillance systems are essential for tracking antimicrobial usage patterns and the prevalence of resistant pathogens across human and animal populations. Global initiatives advocate for the establishment of integrated surveillance networks that collect, analyze, and share data on AMR trends. These systems enable early detection of emerging resistance, identification of high-risk practices, and evidence-based policymaking. In livestock systems, surveillance extends to monitoring drug residues in animal products, resistance genes in microbial populations, and environmental contamination pathways. Harmonized data collection protocols and international collaboration are critical for ensuring comparability and reliability of surveillance outputs.

Promotion of alternatives to antimicrobials

Recognizing that sustainable livestock production cannot rely indefinitely on conventional antibiotics, global frameworks emphasize the development and adoption of viable alternatives. These include phytogenic feed additives (PFAs), probiotics, prebiotics, organic acids, vaccines, and improved management practices such as enhanced biosecurity, hygiene, and nutrition.

Research and innovation are being actively encouraged to validate the efficacy, safety, and economic feasibility of these alternatives. The integration of such strategies reduces dependency on antimicrobials while maintaining animal health and productivity.

A landmark policy intervention in this domain is the ban on antibiotic growth promoters implemented under EU Regulation 1831/2003, which came fully into force in 2006. This regulatory action by the European Union marked a significant shift in livestock production practices, eliminating the routine use of antibiotics for growth enhancement and catalyzing the adoption of non-antibiotic alternatives. The EU experience demonstrates that, with appropriate management adjustments and innovation, it is possible to sustain productivity while significantly reducing antimicrobial inputs. It has also set a precedent that has influenced policy reforms in other regions globally.

Contextual challenges and priorities in Africa

In the African context, the implementation of AMR control strategies faces unique structural and institutional challenges that necessitate tailored interventions. Strengthening veterinary services is a foundational requirement. This includes increasing the availability of trained veterinarians and para-veterinary professionals, improving diagnostic infrastructure, and expanding extension services to reach smallholder farmers. Effective veterinary oversight ensures that antimicrobial use is guided by accurate diagnosis and appropriate prescription practices.

Improving legislative and regulatory frameworks is equally critical. Many African countries currently face gaps in policy enforcement, allowing uncontrolled access to veterinary drugs and the proliferation of informal markets. Strengthening legislation to regulate the importation, distribution, and use of antimicrobials coupled with effective enforcement mechanisms will significantly reduce misuse and overuse.

Farmer education and capacity building represent another key intervention point. A substantial proportion of livestock producers in Africa operate within smallholder or informal systems, where awareness of AMR and best management practices is often limited.

Targeted training programs, participatory extension approaches, and community-based advisory systems can enhance knowledge on responsible antimicrobial use, withdrawal periods, biosecurity, and alternative health management strategies. Empowering farmers with this knowledge not only improve animal health outcomes but also contributes to broader public health goals (Anaso et al., 2026a,b).

8. FUTURE PERSPECTIVES AND RESEARCH DIRECTIONS

Advancing the role of phytogenic feed additives (PFAs) as sustainable alternatives to conventional antimicrobials requires a coordinated and multidisciplinary research agenda that integrates phytochemistry, microbiology, nutrition, systems biology, and digital agriculture. The following priority areas represent critical frontiers for innovation and translational impact:

Identification of novel phytogenic compounds

Future research should intensify the bioprospecting of underutilized plant species, particularly those indigenous to diverse agro-ecological zones, for bioactive compounds with antimicrobial, antioxidant, immunomodulatory, and digestive-enhancing properties. Advanced analytical techniques such as high-performance liquid chromatography (HPLC), gas chromatography–mass spectrometry (GC-MS), and nuclear magnetic resonance (NMR) should be leveraged to isolate, characterize, and standardize these compounds. Emphasis should also be placed on understanding structure activity relationships, dose-response dynamics, and stability under feed processing conditions. This will enable the development of targeted, reproducible, and commercially viable phytogenic formulations.

Synergistic effects of combined additives

Single-compound interventions may have limited efficacy due to the complexity of the gut ecosystem and host physiology. Therefore, investigating synergistic interactions among PFAs and between PFAs and other feed additives (e.g., probiotics, prebiotics, organic acids, enzymes) is essential.

Such combinations may exert additive or multiplicative effects on gut health, nutrient utilization, and pathogen suppression. Mechanistic studies should explore how these interactions influence microbial ecology, epithelial integrity, and host immune responses. Factorial experimental designs and systems modeling approaches can help optimize combinations and inclusion levels for maximal efficacy while minimizing antagonistic effects.

Genomic and metabolomic studies on gut microbiota

The gut microbiome is central to animal health, productivity, and resistance to pathogens. Integrating omics technologies particularly metagenomics, transcriptomics, proteomics, and metabolomics will provide deeper insights into how PFAs modulate microbial communities and metabolic pathways. Metagenomic sequencing can identify shifts in microbial diversity and functional gene profiles, including antimicrobial resistance genes (ARGs), while metabolomic analyses can reveal changes in key metabolites such as short-chain fatty acids, bile acids, and secondary plant metabolites. These approaches will facilitate a more precise understanding of host–microbe–diet interactions and support the design of microbiome-targeted feeding strategies.

Development of precision feeding strategies

Precision nutrition represents a paradigm shift from generalized feeding regimens to data-driven, individualized or group-specific dietary interventions. Future research should focus on integrating animal-level data—such as genetics, physiological status, health indicators, and production metrics—with real-time environmental and feed composition data to optimize nutrient delivery and additive inclusion. PFAs can be incorporated into such systems as dynamic components, with dosages adjusted based on disease risk, stress levels, or production stage. This approach not only enhances feed efficiency and animal performance but also reduces unnecessary input use, thereby minimizing environmental impact and antimicrobial reliance.

Integration of PFAs into climate-smart agriculture

As the livestock sector faces increasing pressure to reduce its environmental footprint, PFAs offer potential contributions to climate-smart production systems. Research should evaluate how phytogenic compounds influence enteric methane emissions, nitrogen utilization efficiency, and overall greenhouse gas outputs. Additionally, the role of PFAs in improving resilience to climate-induced stressors such as heat stress and fluctuating feed quality should be explored. Integrating PFAs into circular and regenerative agricultural models, where plant-derived inputs are sustainably sourced and waste streams are minimized, will further enhance their relevance in sustainable livestock systems.

Application of digital technologies and artificial intelligence

The incorporation of digital tools and artificial intelligence (AI) into livestock management systems represents a transformative opportunity to enhance the efficacy and scalability of PFAs. Sensor technologies, wearable devices, and automated monitoring systems can generate real-time data on animal health, behavior, feed intake, and environmental conditions. AI-driven analytics can process these large datasets to detect early signs of disease, predict performance outcomes, and recommend optimized feeding strategies, including the strategic use of PFAs. Machine learning models can also be applied to identify patterns in microbiome data, forecast antimicrobial resistance trends, and guide decision-making at both farm and policy levels (Anaso, 2026a,b).

In addition, digital traceability platforms can improve transparency and accountability in antimicrobial use and feed additive application across the value chain. This is particularly relevant for meeting regulatory standards and consumer demand for sustainably produced animal products.

Collectively, these research directions emphasize a shift toward integrative, data-driven, and sustainability-oriented livestock production systems. By combining advances in phytogenic science with cutting-edge technologies in omics and digital agriculture, it is possible to develop robust alternatives to antibiotics that support animal health, safeguard public health, and promote environmental stewardship.

CONCLUSION

Antimicrobial resistance represents a complex and multifaceted challenge requiring urgent and coordinated action across livestock systems. The overuse of antibiotics in animal agriculture has significantly contributed to the emergence and spread of resistant pathogens, posing serious threats to public health, food safety, and environmental sustainability.

Phytogenic feed additives offer a viable and sustainable alternative to conventional antibiotics, with demonstrated benefits in improving animal health, enhancing productivity, and reducing environmental impacts. However, their successful integration into livestock systems depends on overcoming technical, economic, and regulatory barriers.

A holistic approach that combines improved management practices, biosecurity measures, policy interventions, and innovative feed solutions is essential for mitigating AMR. Transitioning toward antibiotic-free livestock production systems will not only safeguard human and animal health but also contribute to sustainable agricultural development and global food security.

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CHAPTER 3

REPRODUCTIVE ECOLOGY, REGENERATION BIOLOGY, AND SILVICULTURAL INTEGRATION OF GARCINIA KOLA IN TROPICAL FOREST SYSTEMS

[1]OKONKWO Henry Onyebuchi
[2]CHIMA Uzoma Darlington
[3]NSIEN Iniobong Bruno
[4]BABALOLA Olumide Tade

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[1] Swamp Forest Research Station Onne, Forestry Research Institute of Nigeria, Nigeria, richychrist4ever@gmail.com, ORCID ID: 0000-0001-8270-6952

[2] Department of Environmental Forestry and Wildlife Management, Faculty of Agriculture, University of Port Harcourt, Port Harcourt, Nigeria, uzoma.chima@uniport.edu.ng,
ORCID ID: 0000-0002-0832-5155

[3] Swamp Forest Research Station Onne, Forestry Research Institute of Nigeria, Nigeria, inibruno@gmail.com, ORCID ID: 0009-0004-9547-8564

[4] Swamp Forest Research Station Onne, Forestry Research Institute of Nigeria, Nigeria, olubabs2003@gmail.com

INTRODUCTION

Tropical forests are among the most biologically diverse and functionally complex ecosystems on Earth, providing critical ecosystem services that sustain both global environmental stability and local livelihoods. They hold a substantial proportion of the world's terrestrial biodiversity, regulate climate through carbon sequestration, and support hydrological cycles and soil fertility (FAO, 2020; Pan et al., 2011). In many parts of sub-Saharan Africa, tropical forests also serve as vital socio-economic systems, supplying food, medicine, and income through timber and non-timber forest products (NTFPs) (Sunderland et al., 2011). The sustainability of these ecosystems is therefore closely linked to the management and conservation of indigenous tree species that underpin their ecological integrity and productivity.

Indigenous fruit trees constitute a particularly important component of tropical forest ecosystems and agroforestry systems. These species contribute to biodiversity conservation, enhance structural complexity, and provide essential ecosystem services, including nutrient cycling and habitat provision (Leakey, 2012). Within agroforestry landscapes, indigenous fruit trees support food security and income diversification while maintaining ecological functions such as soil stabilization and microclimate regulation (Okonkwo et al., 2014). Their integration into managed systems represents a key strategy for achieving sustainable land use and climate-resilient agriculture in tropical regions.

Garcinia kola (Heckel), commonly known as bitter kola, is of significant ecological and economic importance in West and Central Africa. The species is valued for its medicinal properties, cultural significance, and role as a high-value NTFP in local and regional markets (Okonkwo et al. 2020). Ecologically, *G. kola* contributes to forest structure and diversity and is adapted to humid tropical environments, often occurring in lowland rainforests and forest, mangrove transition zones (Okonkwo 2023). Despite its importance, the species remains largely undomesticated, and its cultivation is constrained by limited ecological and silvicultural knowledge (Okonkwo et al., 2024a).

A major challenge in the management and domestication of *G. kola* is the desiccation sensitivity of the seed.

The species exhibits recalcitrant seed behaviour, characterized by rapid loss of viability from moisture loss, which severely limits seed storage and large-scale propagation (Okonkwo et al., 2020a). In addition, it is predominantly dioecious, and in some cases trioecious, reproductive system introduces further constraints to cultivation, as sex ratios and spatial distribution of male and female trees directly influence pollination success and fruit yield (Okonkwo et al., 2022a; Okonkwo & Omokhua, 2022). These biological limitations, combined with anthropogenic pressures such as overharvesting and habitat degradation, contribute to low regeneration rates in natural and managed populations. Addressing these challenges requires a comprehensive and integrated approach that links reproductive ecology, regeneration biology, and silvicultural practices. Reproductive ecology provides insights into flowering phenology, pollination mechanisms, and fruiting patterns, which are essential for understanding reproductive success and yield variability. Regeneration biology focuses on seed behavior, germination processes, and seedling establishment, offering pathways to overcome constraints associated with recalcitrant seeds and poor natural regeneration. Silviculture, in turn, translates these ecological insights into practical management strategies, including propagation techniques, plantation design, and resource management interventions aimed at optimizing growth and productivity.

Despite increasing research attention on *G. kola,* existing studies are largely fragmented, often addressing isolated aspects such as seed germination, vegetative propagation, or reproductive phenology. There is a clear need for a holistic synthesis that integrates these domains within a forest ecological framework to support evidence-based cultivation and conservation strategies. Such an approach is essential for advancing the domestication of *G. kola* and enhancing its contribution to sustainable forest-based production systems. This review therefore aims to: (i) synthesize current knowledge on the reproductive ecology and regeneration biology of *G. kola*; (ii) identify key ecological constraints limiting its cultivation and sustainable management; and (iii) propose silvicultural pathways that integrate ecological principles with practical interventions to enhance its domestication, conservation, and productivity in tropical forest systems.

1. *GARCINIA KOLA* ECOLOGY AND DISTRIBUTION

Garcinia. kola Heckel belongs to the family Clusiaceae (formerly Guttiferaea), a group of predominantly tropical trees and shrubs known for their ecological and economic importance (Dao et al., 2025). The genus Garcinia comprises over 200 species, many of which produce edible fruits and bioactive compounds (Okonkwo, 2023). *G. kola* is a medium-sized evergreen tree that can attain heights of 12–20 m under favorable conditions. It is characterized by a straight bole, dense crown, and leathery, opposite leaves. The species exhibits sexual dimorphism, with male and female flowers borne on separate individuals in predominantly dioecious populations, although cases of sexual polymorphism have been reported. The fruits are typically large, orange to yellow drupes containing few seeds embedded in a fleshy pulp, with seeds being the primary economic product due to their medicinal and stimulant properties (Okonkwo et al., 2022a).

Geographically, *Garcinia kola* is widely distributed across the humid forest zones of West and Central Africa. Its natural range includes countries such as Nigeria, Cameroon, Ghana, Côte d'Ivoire, and extends into parts of the Congo Basin (Dao et al., 2020). In Nigeria, the species is commonly found in the southern rainforest belt, including lowland and coastal forest ecosystems (Agwu et al., 2020). Despite its broad distribution, natural populations are often fragmented due to deforestation, land-use change, and overexploitation, leading to localized declines in abundance (Dao et al., 2020). The species thrives in humid tropical environments, particularly in lowland rainforests and transitional zones between rainforest and mangrove ecosystems. It is frequently associated with areas of high annual rainfall (typically >2000 mm) and relatively stable temperatures (Okonkwo et al., 2025). *G. kola* demonstrates a preference for well-drained, loamy to sandy-loam soils rich in organic matter, although it can tolerate a range of soil conditions provided moisture availability is adequate. It is often found in secondary forests, fallow lands, and agroforestry systems, indicating a degree of ecological plasticity (Babalola & Agbeja,2010).

Ecologically, *G. kola* is considered a shade-tolerant to moderately shade-demanding species, particularly during its early growth stages (Akintan et al., 2020).

Seedlings establish more successfully under partial canopy cover, where reduced light intensity and moderated microclimatic conditions enhance survival and growth. As the tree matures, it can tolerate increased light exposure, allowing it to persist within mixed-species forest stands and managed plantations (Okonkwo et al., 2026). This shade response has important implications for its integration into agroforestry systems and enrichment planting designs. Within forest ecosystems, *G. kola* plays a significant role as a non-timber forest product (NTFP) species. Its seeds are widely harvested for medicinal, cultural, and commercial purposes, contributing to rural livelihoods and local economies. The species also supports biodiversity by providing food resources for wildlife and contributing to forest structural diversity. However, increasing demand for its seeds has led to unsustainable harvesting practices, often involving destructive extraction methods that compromise regeneration and long-term population viability (Babalola and Agbeja, 2010; Okonkwo et al., 2024a). Hence, the ecological characteristics of *G. kola*, including its distribution, habitat preferences, and functional role, underscore its importance in tropical forest systems. Understanding these ecological attributes is essential for developing effective conservation strategies and designing silvicultural interventions that support both sustainable utilization and ecosystem integrity.

2. REPRODUCTIVE ECOLOGY OF *GARCINIA KOLA*

Sexual Systems and Population Structure

Garcinia kola exhibits a predominantly dioecious sexual system, with male and female reproductive organs borne on separate individuals (Manourova et al., 2019). This condition imposes inherent constraints on the reproductive success, as effective pollination and fruit set depend on the spatial proximity and relative abundance of male and female trees. However, emerging evidence indicates the occurrence of sexual polymorphism in some populations, including the presence of bisexual individuals, suggesting a trioecious system under certain ecological contexts (Figure 1) (Okonkwo & Omokhua, 2022). Such variability in sexual expression may represent an adaptive strategy to enhance reproductive assurance in environments where pollination is limited. Sex ratios in natural and plantation populations are often skewed, typically favouring male trees (Okonkwo & Omokhua, 2022.

This imbalance has significant implications for plantation design and productivity, as fruit yield is directly dependent on the proportion of reproductively active female trees. A high male-to-female ratio may ensure adequate pollen supply but can reduce overall fruit output per unit area. Conversely, insufficient male representation may limit pollination success. Therefore, optimizing sex ratios, commonly suggested within a range that balances pollen availability and fruit production, is critical for maximizing yield in managed systems. From a functional perspective, reproductive allocation in *G. kola* reflects a source–sink dynamic, where assimilates produced through photosynthesis are partitioned between vegetative growth and reproductive structures. Female trees, which bear the energetic cost of fruit and seed development, often exhibit higher resource demands compared to male trees. This differential allocation can influence growth rates, physiological performance, and survival, potentially contributing to observed patterns of sexual dimorphism in morphology and function (Okonkwo et al., 2022). Understanding these allocation strategies is essential for managing nutrient inputs and optimizing plantation productivity.

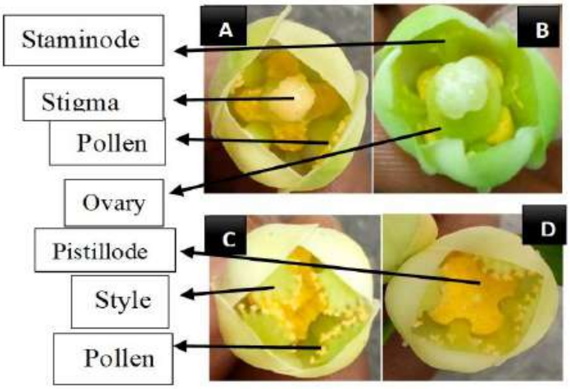

Figure 1. Flower polymorphism in Garcinia kola. (A) Bisexual flower; (B) Invariant female flower; (C) Inconstant male flower; (D) Bisexual tree male flower.

Flowering Phenology and Climatic Drivers

The flowering phenology of *Garcinia kola* is closely linked to seasonal climatic patterns characteristic of humid tropical environments (Okonkwo et al., 2024). Flowering typically occurs during specific periods of the year, often coinciding with the onset or peak of the rainy season (Figure 1).

This synchronization ensures favorable conditions for pollinator activity and subsequent fruit development. However, the timing and intensity of flowering can vary among individuals and across years, reflecting both genetic and environmental influences. Rainfall is a primary driver of phenological events in *G. kola,* influencing bud initiation, development, and flowering duration. Adequate soil moisture promotes physiological processes necessary for reproductive development, while prolonged dry periods may suppress flowering or delay its onset. Temperature and relative humidity also play critical roles by affecting metabolic rates and floral longevity. Optimal temperature ranges support pollen viability and stigma receptivity, whereas extreme conditions may impair reproductive success. Inter-annual variability in climatic conditions introduces additional complexity to flowering dynamics. Variations in rainfall distribution, temperature fluctuations, and the increasing unpredictability associated with climate change can lead to asynchronous flowering among individuals within a population. Such asynchrony may reduce effective pollination and ultimately limit fruit set. Consequently, *G. kola* exhibits a degree of climate sensitivity, highlighting the need for adaptive management strategies that account for changing environmental conditions (Okonkwo and Omokhua, 2024).

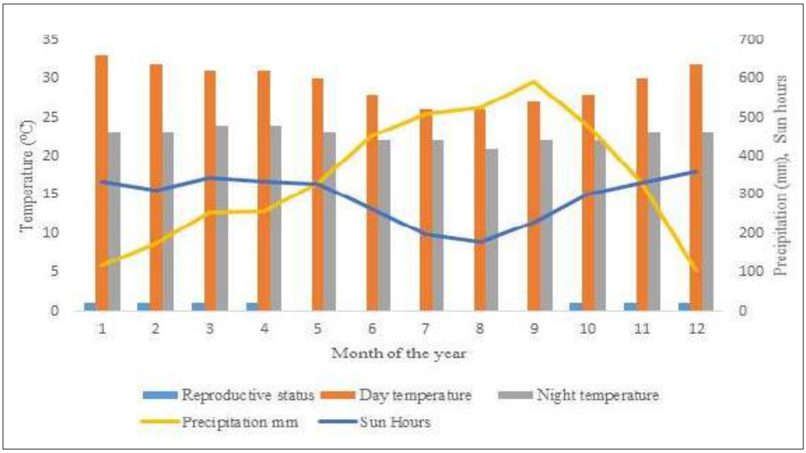

Figure 2. Seasonal phenological variation in Garcinia kola.

Pollination Ecology

Pollination in *Garcinia kola* is primarily mediated by biotic agents, indicating an entomophilous pollination system. A range of insect pollinators has been associated with the species, including bees (e.g., *Apis mellifera*), butterflies (e.g., *Danaus chrysippus*), wasps, and ants, which visit flowers in search of nectar and pollen (Okonkwo et al., 2023). These pollinators play a crucial role in transferring pollen from male to female flowers, thereby facilitating fertilization and fruit development. The effectiveness of pollination depends on several factors, including pollinator abundance, diversity, and foraging behaviour. Bees are often considered the most efficient pollinators due to their mobility and ability to carry large quantities of pollen. However, the contribution of other insects should not be underestimated, particularly in diverse tropical ecosystems where pollination networks are complex and interdependent (Bascompte et al., 2003; Memmott et al., 2004; Blüthgen et al., 2007). In fragmented forest landscapes, pollination efficiency may be significantly reduced due to habitat loss and declining pollinator populations. Fragmentation can disrupt pollinator movement and reduce visitation rates, leading to pollen limitation and lower fruit set. Additionally, increased distances between male and female trees in degraded habitats can further constrain successful pollination. These challenges underscore the importance of maintaining habitat connectivity and conserving pollinator communities as part of sustainable forest management strategies.

Fruit Set, Seed Development, and Yield Variability

Fruit set in *Garcinia kola* is the culmination of successful pollination and fertilization, followed by a period of fruit and seed development that may span several months. The maturation timeline is influenced by environmental conditions and tree physiology, with fruits typically developing during the rainy season when water and nutrient availability are high. Mature fruits contain a limited number of seeds, which are the primary economic product of the species (Figure 1). Significant tree-to-tree variation exists in fruit and seed characteristics, including size, number, and biochemical composition. Genetic factors, environmental conditions, and management practices influence this variability.

Studies have demonstrated that differences in tree size, age, and health status can affect reproductive output, with larger and more vigorous trees generally producing higher yields (Okonkwo et al., 2023).

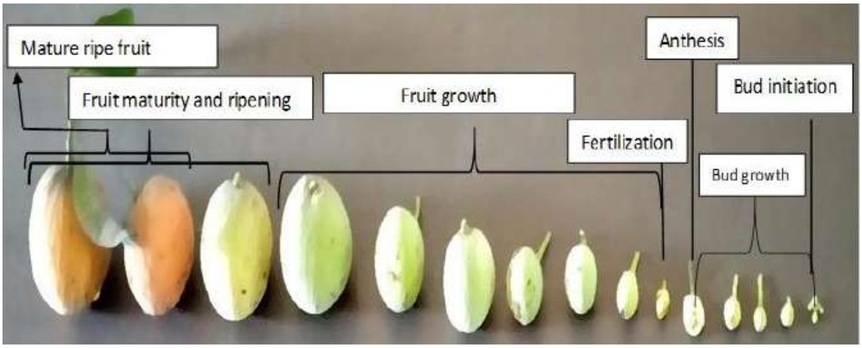

Figure 3. Reproductive phenological stages in Garcinia kola.

Sex also plays a fundamental role in yield dynamics, as female trees mostly contribute directly to fruit production (Okonkwo and Omokhua, 2022; Okonkwo et al.,2024). However, the presence and proximity of male trees remain essential for ensuring adequate pollen supply. Environmental factors such as soil fertility, moisture availability, and light conditions further interact with biological traits to determine overall productivity (Chapin et al., 2002; Lambers et al., 2008; Reich, 2014). Yield variability in *G. kola* plantations is therefore a product of complex interactions among reproductive biology, environmental conditions, and management practices. Understanding these interactions is critical for developing strategies to enhance fruit production, including selecting high-yielding genotypes, optimizing plantation structure, and improving resource management practices.

3. REGENERATION BIOLOGY

Seed Biology and Germination Ecology

The regeneration of *Garcinia kola* is strongly governed by its seed biology, which presents both ecological adaptations and significant constraints to propagation. A defining characteristic of the species is its recalcitrant seed behavior, meaning that seeds are highly sensitive to desiccation and cannot withstand drying or prolonged storage (Asomaning et al., 2011).

Unlike orthodox seeds, which can be stored at low moisture content and temperature, *G. kola* seeds retain high moisture content at maturity and rapidly lose viability when exposed to unfavorable environmental conditions (Okonkwo et al., 2020). This recalcitrance poses a major limitation to large-scale propagation, germplasm conservation, and seed distribution systems. Seed viability in *G. kola* is typically short-lived, often declining significantly within a few weeks after harvest if not properly handled. Evidence (Anegbeh et al., 2006; Yakubu et al., 2014) shows that maintaining seeds under moist conditions and moderate temperatures can slightly extend viability, but storage beyond short durations remains problematic. This limitation necessitates immediate sowing after seed extraction (Okonkwo et al., 2020), which restricts flexibility in nursery operations and plantation establishment. The inability to store seeds also complicates breeding programs and ex situ conservation efforts.

Germination in *G. kola* follows a hypogeal pattern, where the cotyledons remain below the soil surface during seedling emergence (Okonkwo & Omokhua, 2022). This strategy may confer protection to the embryonic tissues from environmental stress and herbivory. However, germination is often slow and irregular, with considerable variation in germination time and percentage among seed lots. Such variability is influenced by seed maturity, size, and physiological condition at the time of sowing (Fenner & Thompson, 2005; Bewley et al., 2013). To enhance germination performance, several pre-germination treatments have been explored. Mechanical scarification, seed pricking, and removal of the seed coat have been shown to improve water uptake and accelerate germination (Okonkwo et al., 2020). Furthermore, soaking seeds in water before sowing can help to activate metabolic processes (Yakubu et al., 2014). Despite these interventions, achieving uniform and rapid germination remains a challenge, which shows the need for further refinement of seed handling protocols.

Seedling Establishment and Early Growth Dynamics

Successful regeneration of *Garcinia kola* extends beyond germination to include seedling establishment and early growth stages, which are highly sensitive to environmental conditions (Agwu et al., 2018; Ochia & Mbaekwe, 2019).

Light availability plays a crucial role, as *G. kola* seedlings are generally shade-tolerant during their early developmental stages. Moderate shading promotes better survival and growth by reducing evapotranspiration and protecting seedlings from excessive radiation (Agyeman et al., 1999; Poorter, 2001; Onyekwelu et al., 2008; Ogunjemite & Oladele, 2011). However, prolonged deep shade may limit photosynthetic activity and slow growth, indicating the need for balanced light conditions. Moisture availability is another critical factor influencing seedling establishment. Given the species' adaptation to humid environments, consistent soil moisture is essential for maintaining physiological processes and preventing stress-induced mortality. Water deficits, particularly during the early stages, can significantly reduce survival rates (Agyememan et al., 1999; Engelbrecht & Kursar, 2003). Similarly, soil properties such as texture, structure, and nutrient content affect root development and overall seedling vigor. Well-drained, fertile soils with adequate organic matter are generally favorable for optimal growth (Okonkwo et al., 2025).

Although species-specific provenance trials for *G. kola* remain limited, evidence from related tropical tree species suggests clear genetic variation among seed sources (Nsien et al., 2024). This variation can significantly influence early growth performance and stress tolerance. It also reinforces the need for careful selection of provenances in domestication programs (Okonkwo et al.2025). Differences between nursery and field performance further highlight the complexity of seedling establishment. While controlled nursery conditions often promote higher survival and uniform growth, transplanting seedlings to field environments introduces stress factors such as fluctuating moisture, temperature extremes, and biotic interactions. Effective hardening-off practices and site-specific management are therefore essential to ensure successful field establishment (Landis et al., 2010; Grossnickle & MacDonald, 2018; Riikonen & Luoranen, 2018).

Vegetative Propagation and Clonal Regeneration

Given the limitations associated with seed-based regeneration (Yakubu et al., 2014; Okonkwo et al., 2021), vegetative propagation has emerged as a critical strategy for the domestication and large-scale cultivation of *Garcinia* *kola* (Dao et al., 2025). Techniques such as marcotting (air layering), grafting, and budding enable the production of genetically uniform planting material and bypass the challenges of seed recalcitrance (Okonkwo et al., 2020a&b). Marcotting has been widely investigated as a propagation method for *G. kola* (Okonkwo et al., 2020). This technique involves inducing root formation on a branch while it is still attached to the parent tree. Studies indicate moderate success rates, although rooting efficiency can be influenced by factors such as the physiological state of the parent plant, environmental conditions, and the use of rooting hormones (Okonkwo et al., 2020b). A key limitation of marcotting is the relatively low multiplication rate and the potential for poor root system development, which may affect long-term stability and growth (Asaah, 2012).

Grafting and budding techniques offer additional opportunities for clonal propagation (Ibukun, 2016). Successful grafting depends on rootstock–scion compatibility, which influences vascular connection, nutrient transport, and overall plant survival. Morphological characteristics such as stem diameter, age, and physiological vigor of both rootstock and scion play critical roles in determining graft success. Recent studies have highlighted the importance of matching rootstock and scion sizes and selecting appropriate grafting methods (e.g., cleft grafting, chip budding) to improve success rates (Nsien et al., 2025a). Coppicing and the use of wildlings also represent viable regeneration pathways. Coppicing exploits the natural ability of *G. kola* to produce shoots from cut stumps, while wildlings (naturally regenerated seedlings collected from the forest) can be transplanted into nurseries or plantations. Root pruning and proper handling of wildlings have been shown to enhance survival and growth (Nsien et al., 2021). These approaches are particularly useful in resource-limited settings where advanced propagation technologies may not be readily available.

Constraints to Natural and Artificial Regeneration

Despite the availability of multiple regeneration pathways, several constraints continue to limit the successful propagation of *Garcinia kola*. The desiccation sensitivity of seeds remains one of the most significant challenges, restricting storage, transport, and large-scale planting efforts (Asomaning et al., 2011; Okonkwo et al., 2020a). Closely related to this is the issue of low germination uniformity, which complicates nursery management and reduces the efficiency of plantation establishment (Okonkwo et al., 2021). The species polymorphic reproductive system introduces additional constraints by reducing the effective number of fruit-producing individuals and complicating plantation design. Without prior knowledge of sex at the seedling stage, plantations may develop suboptimal sex ratios, leading to reduced productivity. This reproductive inefficiency underscores the need for early sex identification techniques and strategic planting designs (Okonkwo et al., 2022).

Anthropogenic pressures further exacerbate regeneration challenges (Agwu et al., 2020). Overharvesting of seeds for commercial and medicinal purposes often reduces the availability of viable propagules for natural regeneration. In many cases, destructive harvesting methods damage parent trees and impair their reproductive capacity. Habitat loss and fragmentation, driven by agricultural expansion and urbanization, also reduce suitable regeneration sites and disrupt ecological processes such as pollination and seed dispersal. Collectively, these constraints highlight the need for integrated management approaches that combine ecological understanding with practical interventions. Addressing seed biology limitations, improving propagation techniques, and mitigating anthropogenic impacts are essential steps toward enhancing the regeneration and sustainable utilization of *G. kola* in tropical forest systems.

4. FUNCTIONAL TRAITS, VARIABILITY, AND DOMESTICATION POTENTIAL

Functional trait variability in *Garcinia kola* provides a critical foundation for understanding its ecological performance, regeneration dynamics, and potential for domestication (Lavorel & Garnier, 2002; Okonkwo et al., 2026). Traits expressed at the levels of morphology, physiology, and biochemistry influence how the species interacts with its environment and responds to both natural and managed conditions (Albert et al. 2010). In tropical forest systems, where environmental heterogeneity is high, such variability represents both an adaptive advantage and an opportunity for targeted selection and improvement (Zhang et al., 2012).

Morphological Variation

Substantial morphological variation exists in *Garcinia kola* across individuals and populations, particularly in fruit, seed, and tree architectural traits (Okonkwo, 2023). Fruit characteristics such as size, shape, pulp thickness, and seed number exhibit considerable tree-to-tree variability, reflecting both genetic differences and environmental influences. Similarly, seed traits, including size, weight, and cotyledon structure, vary widely and have direct implications for germination behavior and seedling vigor. Larger seeds, for instance, often contain greater nutrient reserves, which can enhance early seedling establishment and survival under suboptimal conditions (Kenule, 2024). Tree architectural traits, including height, crown structure, branching pattern, and stem form, also show notable variability. These traits influence light interception, competitive ability, and overall productivity in both natural forests and plantation systems (Okonkwo et al., 2023). For example, trees with well-developed crowns and efficient branching architecture may exhibit higher photosynthetic capacity and reproductive output. Such morphological diversity provides a basis for selecting superior phenotypes suited to specific silvicultural objectives.

Biochemical Variability

Beyond morphology, *Garcinia kola* exhibits significant biochemical variation, particularly in seed composition. The seeds are rich in bioactive compounds, including flavonoids, alkaloids, and phenolic substances, which contribute to their medicinal and economic value. Variability in the concentration and composition of these compounds has been observed among different trees and provenances, suggesting underlying genetic diversity as well as environmental modulation (Okonkwo et al., 2025). This biochemical heterogeneity has important implications for both ecological function and domestication. From an ecological perspective, variation in secondary metabolites may influence resistance to pests and diseases, as well as interactions with herbivores and pathogens (Diverkar et al., 2022; Okonkwo et al., 2025). From a utilization standpoint, selecting genotypes with desirable phytochemical profiles can enhance the commercial value of *G. kola* products.

Thus, biochemical traits represent a key dimension of functional diversity that should be incorporated into domestication strategies.

Provenance Effects and Environmental Gradients

Provenance variation plays a significant role in shaping the expression of functional traits in *Garcinia kola*. Differences among populations originating from distinct ecological zones, such as variations in rainfall, soil type, and temperature, can lead to localized adaptations that influence growth performance, reproductive capacity, and stress tolerance (Agwu et al., 2020). Although comprehensive provenance trials for *G. kola* are still limited, evidence from related tropical species and emerging studies suggests that selecting appropriate seed sources can markedly improve plantation outcomes (Nsien et al., 2024). Environmental gradients further interact with genetic factors to influence trait expression. For instance, soil fertility and moisture availability can affect fruit size, seed quality, and overall tree vigor, while light conditions may influence crown development and reproductive allocation (Marschner, 2012). Understanding these genotype–environment interactions is essential for optimizing site-species matching and improving the success of cultivation efforts.

Linkages Between Traits, Regeneration, and Productivity

Functional traits (Wright et al., 2004) in *Garcinia kola* are closely linked to both regeneration success and productivity. Seed traits (Poschlod et al., 2026) such as size and viability directly affect germination rates and seedling establishment, while vegetative traits (Wright et al., 2004) influence growth dynamics and survival. For example, seedlings derived from larger seeds or vigorous parent trees often exhibit enhanced growth and resilience, increasing their likelihood of successful establishment in both nursery and field conditions (Kenule, 2024). Reproductive traits (Poschlod et al., 2026), including flowering intensity, fruit set, and seed output, are key determinants of productivity. These traits are influenced by both intrinsic factors (e.g., tree size, age, and sex) and extrinsic conditions (e.g., climate and soil fertility). The integration of these trait dimensions provides a holistic understanding of how *G. kola* performs across different ecological contexts and management regimes.

Implications for Selection, Breeding, and Domestication

The observed (Okonkwo et al., 2023; Okonkwo et al., 2026) variation in functional traits offers significant opportunities for the selection and improvement of *Garcinia kola.* Identifying and propagating superior genotypes with desirable characteristics, such as high fruit yield, large seed size, favorable biochemical composition, and robust growth, can accelerate the domestication process (Okonkwo et al., 2026). Vegetative propagation techniques, including grafting and marcotting, enable the clonal multiplication of selected individuals, ensuring the retention of desirable traits in subsequent generations (Dao et al., 2025). For breeding programs, the integration of morphological, physiological, and biochemical trait data is essential for developing improved varieties. Provenance selection and the establishment of seed orchards can further enhance genetic gains and ensure the availability of high-quality planting material. Additionally, incorporating trait-based approaches into domestication programs can facilitate the development of ideotypes (Leakey & Page, 2006) tailored to specific ecological conditions and production goals. In summary, the functional trait diversity of *G. kola* represents a valuable resource for advancing its domestication and sustainable utilization. By linking trait variation to ecological performance and management outcomes, it is possible to design more efficient and resilient cultivation systems that support both conservation and livelihood objectives.

5. SILVICULTURAL INTEGRATION AND PLANTATION DEVELOPMENT

The successful domestication and large-scale cultivation of *Garcinia kola* depend on the effective integration of ecological knowledge into silvicultural systems. Given the species' biological constraints, particularly recalcitrant seed behavior and sexual polymorphism, plantation development requires carefully designed interventions spanning nursery practices, stand establishment, reproductive management, and long-term resource sustainability.

Nursery and Plantation Establishment Techniques

The propagation of *G. kola* begins with careful seed handling, as seeds are highly sensitive to desiccation (Asomaning et al., 2011) and must be sown shortly after extraction. Maintaining seed moisture through storage in humid substrates (e.g., moist sawdust or sand) can help preserve viability for short periods before sowing (Okonkwo et al., 2021). The selection of appropriate sowing media is critical, with well-drained, fertile substrates, such as loamy soil mixed with organic matter, providing optimal conditions for germination and early growth. Studies (Kenule, 2024; Onyekosi et al., 2026) have shown that media composition significantly influences germination success and seedling vigor, particularly in recalcitrant tropical species (Onyekosi et al., 2026). Effective seedling management practices are essential to ensure uniform growth and high survival rates. These include regular watering to maintain consistent soil moisture, shading to reduce heat stress during early growth stages, and gradual hardening-off before field transplantation. Given the species' moderate shade tolerance, partial canopy cover or shade nets are recommended during nursery phases (Akintan et al., 2022). At the plantation level, site selection should prioritize areas with high rainfall, good soil fertility, and well-drained conditions, consistent with the species' natural habitat. Avoidance of waterlogged or highly degraded soils is important to reduce establishment failure. Spacing regimes must balance resource availability with canopy development and reproductive efficiency. Wider spacing may enhance crown expansion and fruit production per tree, while moderate spacing can optimize land use efficiency in mixed systems (Okonkwo et al., 2025).

Managing Sexual Systems in Plantations

The polymorphic nature of *G. kola* presents a unique silvicultural challenge, as mostly female trees produce economically valuable seeds. Consequently, male: female ratio optimization is a key consideration in plantation design. While male trees are necessary for pollen production, excessive numbers reduce overall productivity. Empirical observations suggest that maintaining a balanced ratio, often skewed toward females (e.g., 1 male:4–6 females), can enhance fruit yield while ensuring adequate pollination (Okonkwo et al., 2024).

Spatial arrangement of trees is equally important for effective pollination. Male trees should be strategically distributed within plantations to maximize pollen dispersal and ensure proximity to female individuals. Clustered or systematic planting patterns may improve pollinator efficiency and reduce the likelihood of pollen limitation. These reproductive considerations have direct implications for yield maximization. Plantations established without regard to sex ratios may experience reduced productivity due to insufficient female representation or poor pollination. Advances in early sex identification, if developed, would significantly enhance plantation planning and efficiency.

Soil Fertility and Nutrient Management

Soil fertility plays a central role in the growth and productivity of *G. kola*. The application of organic amendments, such as compost, and manure, has been shown to improve soil structure, enhance microbial activity, and increase nutrient availability (Onyekosi et al., 2026). Organic inputs are particularly beneficial in tropical systems, where nutrient leaching and soil degradation are common challenges. Nutrient cycling within *G. kola* plantations is influenced by litter production and decomposition processes. Leaf litter contributes to the return of essential nutrients to the soil, supporting long-term fertility and ecosystem sustainability (Nsien et al., 2020). The incorporation of litter into soil management practices can reduce dependence on external inputs and enhance nutrient-use efficiency. Integration into agroforestry systems further enhances nutrient dynamics (Palm et al., 1997). For example, combining *G. kola* with crops or other tree species can promote complementary resource use and improve overall system productivity. Agroforestry systems also facilitate nutrient recycling through diversified litter inputs and root interactions, contributing to soil health and resilience.

6. KNOWLEDGE GAPS AND FUTURE RESEARCH DIRECTIONS

Despite growing interest in *G. kola* cultivation, significant knowledge gaps remain, constraining its effective domestication and integration into tropical forest management systems.

One of the most critical limitations is the lack of long-term ecological data. Existing studies are largely short-term and site-specific, providing limited insight into temporal dynamics such as growth trajectories, reproductive cycles, population structure, and responses to environmental variability. Long-term monitoring across ecological gradients is essential to understand the species' life-history strategies and to inform sustainable management under changing climatic conditions.

There is also a pressing need for genetic improvement studies aimed at enhancing key traits such as fruit yield, seed quality, growth rate, and stress tolerance. Although evidence (Okonkwo et al., 2026) of substantial phenotypic and biochemical variability exists, systematic breeding programs remain underdeveloped. Research should prioritize provenance trials, genetic diversity assessments, and the establishment of seed orchards and clonal banks. Such efforts would support the selection of superior genotypes and accelerate the domestication process. The application of trait-based approaches, particularly within the framework of the Leaf Economics Spectrum (LES), represents another promising research frontier. Integrating functional traits, such as specific leaf area, leaf dry matter content, and nutrient-use efficiency, into studies of *G. kola* could provide mechanistic insights into its growth strategies, resource use, and adaptability across environments. This would enable the development of predictive models linking trait expression to performance under different silvicultural regimes.

Given increasing environmental variability, climate change response studies are urgently needed. Research should focus on how shifts in temperature, rainfall patterns, and extreme events affect phenology, pollination, regeneration, and productivity. Experimental and modeling approaches can help identify climate-resilient genotypes and inform adaptive management strategies for plantations and natural populations. Another key priority is the scaling of propagation techniques. While methods such as grafting, marcotting, and improved seed handling have shown promise, their application remains largely at experimental or smallholder levels. Research should address the standardization, cost-effectiveness, and scalability of these techniques to support large-scale plantation development and restoration programs.

Finally, the integration of ecological modeling and remote sensing technologies offers significant potential for advancing research and management. Spatial modeling can be used to predict suitable habitats, optimize site selection, and assess landscape-level dynamics, while remote sensing tools can facilitate monitoring of growth, health, and productivity over large areas. Combining these approaches with field-based data will enhance decision-making and support the sustainable management of *G. kola* in tropical forest systems. Addressing these knowledge gaps through interdisciplinary research will be critical for unlocking the full ecological and economic potential of Garcinia kola and ensuring its resilience in the face of environmental change.

CONCLUSION

This review synthesizes current knowledge on the reproductive ecology, regeneration biology, and silvicultural integration of *G. kola*, highlighting the complex interactions that govern its performance in tropical forest systems. Evidence shows that the species' regeneration and productivity are strongly shaped by its reproductive traits, particularly polymorphism, phenological patterns, and pollination dynamics, as well as by constraints associated with recalcitrant seed biology and variable germination behavior. At the same time, opportunities exist through vegetative propagation, functional trait selection, and improved nursery and plantation management practices to enhance its cultivation potential. A central argument emerging from this synthesis is that the successful cultivation and domestication of *G. kola* cannot be achieved through isolated interventions but must be grounded in the integration of ecological understanding with silvicultural practice. Reproductive ecology provides the basis for managing sex ratios and pollination efficiency; regeneration biology informs seed and seedling management; and silviculture translates these insights into practical strategies for plantation establishment, nutrient management, and yield optimization. Such a systems-based approach is essential for overcoming current biological and environmental constraints. Ultimately, advancing the sustainable domestication of *G. kola* offers significant opportunities for both conservation and development.

By promoting its integration into agroforestry systems and restoration programs, it is possible to reduce pressure on natural populations while enhancing biodiversity, ecosystem resilience, and carbon sequestration. At the same time, the species' economic value as a non-timber forest product can support rural livelihoods and strengthen local economies. Harnessing these dual benefits requires coordinated efforts in research, management, and policy to ensure that Garcinia kola contributes meaningfully to sustainable forest management and livelihood enhancement in tropical regions.

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