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REVIEW

Application of DNA barcoding for ensuring food safety and quality

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Abstract
With increasing international food trade, food quality and safety are high priority worldwide. The consumption of contaminated and adulterated food can cause serious health problems such as infectious diseases and allergies. Therefore, the authentication and traceability systems are needed to improve food safety. The mitochondrial DNA can be used for species authentication of food and food products. Effective DNA barcode markers have been developed to correctly identify species. The US FDA approved to the use of DNA barcoding for various food products. The DNA barcoding technology can be used as a regulatory tool for identification and authenticity. The application of DNA barcoding can reduce the microbiological and toxicological risks associated with the consumption of food and food products. DNA barcoding can be a gold-standard method in food authenticity and fraud detection. This review describes the DNA barcoding method for preventing food fraud and adulteration in meat, fish, and medicinal plants.

Keywords DNA barcoding · Authentication · Food fraud · Adulteration · Meat · Fish · Plant

Introduction

Food additives derived from plants or animals are commonly used as preservatives, antimicrobials, nutritional additives, and colorants to improve sensory attributes, food safety, and quality (Carocho et al., 2014). With increasing consumer demand for healthy food, natural food additives are extensively used in food processing as natural condiments and also regarded as medicinal ingredients with therapeutic properties such as antihypertension, antimicrobial, antioxidant, anti-inflammation, and anti-cancer (Majdalawieh and Fayyad, 2016; Ortega-Ramirez et al., 2014; Parvathy et al., 2014). Due to the health benefits of natural products, the herbal medicines as food additives are becoming increasingly popular across the world (Ekor, 2014). However, adulteration is a major problem concerned with food additives (Carocho et al., 2014). The adulteration or mislabeling of food products can cause serious health problems, leading to cross-contamination and allergic reaction (Li et al., 2020). The adulteration of meat and meat products can lead a major health risk factor for transmission (Amin et al., 2015). The misidentification of food ingredients can trigger allergic reactions in allergen-susceptible consumers (Ortea et al., 2012). Therefore, the food fraud has become a critical risk factor for food safety. However, the adulteration and food fraud are challenging issues in food industry because the international regulation has not been established to control and detect adulterations (Shokralla et al., 2015).

The awareness for food safety and quality has led consumers to request nutrition labeling (Wong and Hanner, 2008). In this regard, the identification of adulteration and the assessment of biodiversity are essential to reduce consumer doubts and improve food safety and quality (Kvie et al., 2012). Recently, food authenticity is assessed using various methods such as morphology-based approaches, ingredient-targeted analyses, and protein-based methods (Hebert and Gregory, 2005; Salihah et al., 2016). However, these methods are time-consuming and less effective in processed foods and require a trained technician for the identification of specific species (Wong and Hanner, 2008). In comparison, DNA-based techniques are more effective, which can be used for various food matrices (Galimberti et al., 2013). However, there are still drawbacks on the poor

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sequencing of total DNA derived from closely related species and food components as inhibitors of DNA amplification (Galimberti et al., 2013). To resolve the limitations of using the DNA-based techniques, DNA barcoding has received great attention as new authentication tool (Hebert et al., 2003). The DNA-barcoding technique has become the most effective method for analyzing DNA in plants and animals, which is used to track raw materials in food products (Kumar et al., 2009). Therefore, this review addresses the application of DNA barcoding technique in food and food products to prevent adulteration and mislabeling.

DNA barcoding as an alternative tool for authentication

The DNA-based methods have widely been used to identify a species, including species-specific PCR, DNA hybridization, single strand conformational polymorphism (SSCP), and random amplified polymorphic DNA (RAPD) (Lockley and Bardsley, 2000). Among these methods, DNA barcoding approach has received considerable interest due to its rapid, accuracy, and cost-efficacy in authenticating food ingredients (Arunraj et al., 2016; Isaacs and Hellberg, 2020; Thongkhao et al., 2020). The DNA barcode can be considered as an alternative identification method to correctly identify animal or plant species in food products (Cawthorn et al., 2012) and used as a successful tool to authenticate fish samples (Barbuto et al., 2010; Cline, 2012). The US Food and Drug Administration (FDA) has established this method as the standard for seafood identification (Yancy et al., 2008). The accurate identification of food fraud is a critical factor for improving food quality and safety (Cutarelli et al., 2014).

The DNA barcoding is a detection, identification, and diagnostic technique using a short standardized DNA marker (Hebert et al., 2003). The genetic region known as a DNA barcode is composed of a small part of genome (< 1000 bp) (Mishra et al., 2016). The gene fragment of target species located at the 5' end of the barcode gene is amplified and sequenced to produce DNA barcodes that can be used as a master key for identifying species (Hebert et al., 2003). The cytochrome *c* oxidase subunit I (COI) isolated from the mitochondrial DNA (mtDNA) genome is considered as a universal barcode marker for the identification of animal species (Hebert et al., 2003; Waugh, 2007). The COI has higher evolutionary rate than other DNA sequences, allowing accurate species-level distinction (Krishnamurthy and Francis, 2012). The animal mitochondrial genome is also suitable for other genomes due to its stability, preventing the formation of unusual DNA sequences and blocking the sequencing of heterozygous alleles (Swartz et al., 2008).

The mitochondrial COI barcode, however, may not be applicable to amphibian and cowrie species due to the high variability of mitochondrial and COI priming sites that interrupt universal COI marker (Vences et al., 2005). Due to the limitation of using the mitochondrial COI genomes, the chloroplast and nuclear genomes are used as alternative DNA barcoding for identifying authentic and substitute components in plant-based food (Hollingsworth et al., 2011). The large subunit of the ribulose 1,5-bisphosphate carboxylase/oxygenase (*rbcL*) and maturase K (*matK*) are recommended as potential DNA barcode of plants by the Consortium for the Barcode of Life (CBOL) and the International Barcode of Life (iBOL) (Mishra et al., 2016). Rapid, accurate, and reliable DNA-based tools are needed to effectively prevent food fraud under food laws and labelling regulations. Therefore, the DNA barcoding technique can be used for rapid and accurate identification of plant-based foods (Arunraj et al., 2016; Thongkhao et al., 2020). The accurate tools for species detection are also essential to enforce food labelling regulations (Fig. 1).

Application of DNA barcoding

Food authenticity and traceability are growing concerns in the food industry. The accurate ingredient information on food products can reduce the risk of allergic reaction (anaphylaxis) and resolve the doubt for vegetarians and haloodies (Ahmed et al., 2010). Particularly, food allergy is considered a growing health problem worldwide (Prado et al., 2016). Recently, World Health Organization (WHO) has listed the allergenic food ingredients that are mandatorily labelled in instant foods including crustaceous, cereals, eggs, fish, milk, peanuts, soybean, walnuts, and whey (Mafra et al., 2008). Therefore, food authentication is high priority to improve food safety and quality for consumer health.

Meat and poultry products

The misidentification of meat or poultry species in food products causes fraud and adulteration (Ali et al., 2012). Expensive food ingredients are replaced by low-cost ingredients; for example, horse meat is used instead of beef (Hellberg et al., 2017). The appearance and sensory properties of meat products are changed after processing (Hellberg et al., 2017). Furthermore, the processed meat products are more likely to be substituted or adulterated with undeclared species. The undeclared species in meat products can cause allergies and interfere with religious practices. The meat adulteration leads to public health threats such as toxification and allergy (Li et al., 2020). The protein-based methods including immunological, electrophoretic, and chromatographic techniques have been used as a species identification and authentication tools (Tnah et al., 2019). Nevertheless,

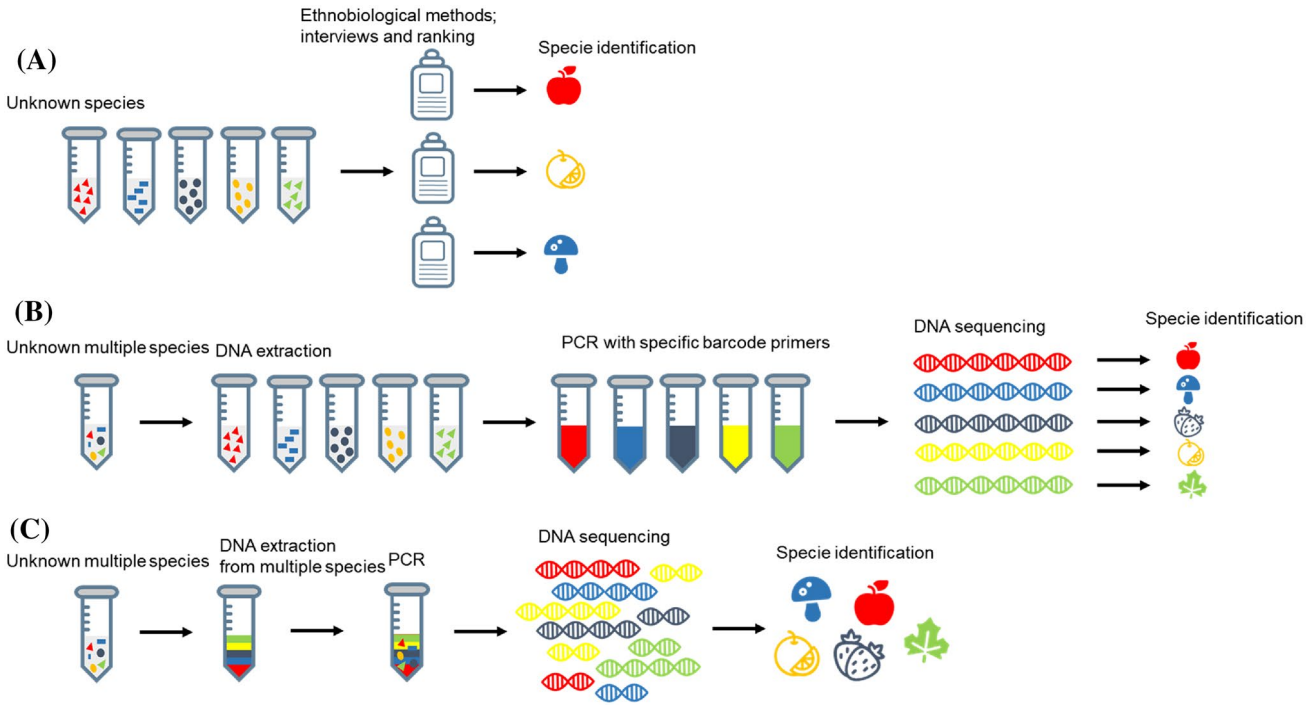

Fig. 1 Traditional (A), which is the standard and conventional method to identify species based on their morphology or external character, DNA barcoding (B), and DNA metacording (C) methods for species identification. (A) The standard and conventional method to identify species based on their morphology or external characteristic. This method should be conducted by a trained technician; (B) There are 3 important steps in DNA barcoding, including DNA extraction, followed by PCR amplification using specific barcode primers and DNA sequencing for species identification. This method can be used to identify a single species at a time. (C) This method involves sequencing of complex bulk samples. The initial steps of this method is total DNA extraction from multiple specie sample, PCR amplification using universal primers, and then DNA sequencing for species identification

there are some limitations of those methods that are unable to identify multiple species simultaneously. Therefore, the DNA barcoding has been considered particular promise to identify a variety of meat or poultry species during the process (Table 1). The DNA barcoding uses short standardized pieces of COI as a universal barcode gene (Hebert et al., 2003). The COI is an appropriate barcode for animal species identification due to the low level of genetic divergence within species and high level of genetic divergence between species (Hellberg et al., 2017). Furthermore, the primer sets have been expanded for the amplification of COI across a broad spectrum of phyla, estimating approximately 200,000 animal species in DNA barcode database (Hellberg et al., 2017). The DNA markers derived from mitochondrial DNA (mtDNA) are used for adulteration detection (Li et al., 2020).

DNA barcoding has been successfully used for the authenticity of meat and poultry (Table 2). DNA barcoding results reported that around 68% of meat products collected from retail stores and butcheries in South Africa contained adulterants that were not declared on product labeling (Cawthorn et al., 2013). DNA barcoding is not applicable for the detection of adulterant in processed meat products due to the DNA degradation and DNA application inhibitors (Hellberg et al., 2017). This can be overcome by developing barcode primer set with high affinity. Soya and gluten are frequently detected as undeclared ingredients, followed by pork and chicken products (Cawthorn et al., 2013). Although food labelling regulations have been responsible for ensuring meat safety and quality, the adulteration and mislabeling are still in a high global concern (Li et al., 2020). Therefore, DNA barcoding plays an important role in fraud detection and food authenticity identification in meat and poultry products (Hellberg et al., 2017).

Fish and seafood products

The annual global consumption of fish, shellfish, and seafood has increased over the last few decades (Fernandes et al., 2021; Pappalardo et al., 2021). With increasing consumer demand, fraud and mislabeling have frequently occurred by substituting high-cost fish for low-cost species, causing microbiological and toxicological risks (Christiansen et al., 2018; Pappalardo et al., 2021). The food mislabeling has been increased over the last decades (Pardo et al., 2016). Mislabeling can occur as a result of unintentional

Table 1 Application of DNA barcoding for fraud detection in meat and poultry products

Locus	Food product	Identification	References
COI	Dried deer tendon	Detection of substitution	Sin et al. (2013)
	Yak jerky	Species substitution	Wang et al. (2016)
	Ground meat	Low-cost meat substitution	Kane and Hellberg (2016)
	Luncheon meats, sausages, patties, ground meats, franks, bacon, jerkies, canned meats, and pet foods	Species in meat and poultry products	Hellberg et al. (2017)
	Dried fins and gill plates	Shark and ray species	Steinke et al. (2017)
	Halal food	Authentication and traceability of meat species	Ahmed et al. (2018)
	Sausages (beef, chicken, pork, turkey)	Species adulteration	Shehata et al. (2019)
	Processed animal-derived food	Mislabeled or undeclared species	Xing R.-R. et al. (2020)
	Burgers, whole cuts/steaks, and hot dogs	Species authentication species	Scales et al. (2021)
Cytochrome b and NADH dehydrogenase subunit 5 (cytb and ND5)	Meatballs	Differentiate beef, buffalo, chicken, duck, goat, sheep, and pork	Uddin and Hossain (2021)
16 s rRNA	Shark fillets from fishmongers and markets	Species substitute	Pazartzi et al. (2019)

Table 2 Application of DNA barcoding for fraud detection in fish and seafood products

Locus	Food product	Identification	References
COI	Fish products	Commercialized seafood (sashimi, salted/dried, frozen fillet, and breaded fillet)	Carvalho et al. (2015)
	Ethnic fishery products (fish, mollusks, and crustaceans)	Ethnic processed and unprocessed seafood products	Armani et al. (2015)
	Sturgeon	Sturgeons from other sturgeon species	Li et al. (2015)
	Fish products	Authentication fraudulent Cod commerce	Calegari et al. (2020)
	Commercialized seafood	Revealing seafood mislabeling in food services from Spain	Pardo and Jiménez (2020)
	Fish	Genetic identification of fish species (genus *Zacco*)	Kim et al. (2020)
16 s rRNA	Roe products	Ingredient of mullet roe products	Kuo et al. (2018)
	Fish	Fish species	Wang et al. (2020)
	Shellfish products	Dried scallop, squid, octopus, and cuttlefish products	Sun et al. (2021)
ITS	Canned tuna fish	Canned tuna species	Mitchell and Hellberg (2016)

or intentional misidentification of seafood species, including toxic substances, parasites, or allergens. In addition, the intentional mislabeling can be abused to hide illegally caught fish. To prevent species substitution, the seafood supply chains need to be standardized at the international level (Pappalardo et al., 2021). The illegal, unreported, and unregulated fishing has become a global issue, which seriously threatens food safety (Pramod et al., 2014). For example, the intestinal disease known as keriorrhea is caused by the consumption of mislabeled oilfish (*Ruvettus pretiosus*) and escolar (*Lepidocybium flavobrunneum*) (Ling et al., 2008). The external morphological features are commonly used to identify seafood species (Christiansen et al., 2018). However, the exterior morphological traits are not a good factor to distinguish adulterants in processed fish products because the specific morphological traits are transformed throughout the processing of fish and seafood species (Cline, 2012; Pappalardo et al., 2021). Therefore, the development of molecular detection methods is necessary to ensure the accurate identification and traceability of seafood. The DNA-based methods can be applied to prevent seafood fraud (Wong and Hanner, 2008).

The DNA barcoding has been used successfully to identify fish and seafood fraud (Table 2) (Cutarelli et al., 2014; Wong and Hanner, 2008). The major advantage of using DNA barcoding is to identify species after fish and seafood processing (Khaksar et al., 2015). The molecular markers such as cytochrome b (Cytb), COI, and mtDNA control

region are generally used for seafood species authentication (Pappalardo et al., 2021). DNA barcoding is applied for species identification and authentication targeting COI gene (Shehata et al., 2018). The DNA barcoding using a 650 bp segment of standard COI gene can distinguish species (Fernandes et al., 2021; Hebert et al., 2003). Over the last decades, the COI has been widely used as a universal barcode in the animal kingdom, especially to identify seafood species (Pappalardo et al., 2021). The COI markers are not suitable to discriminate closely related species because of slow evolution and low sequence divergence (Cawthorn et al., 2015). In this context, NAD genes with sequence variations can alternatively be used for species identification (Ceruso et al., 2019). Furthermore, the mtDNA or nDNA have been also established as DNA barcodes for identification and differentiation of various seafood species (Shokralla et al., 2015). The mtDNA can be used for intraspecific and interspecific discrimination (Miya et al., 2015). The application of DNA barcode for fish and seafood authentication is listed in Table 1. A new commercial platform, FASTFISH-ID kit, is rapid asymmetric DNA amplification tool targeting the COI barcoding gene sequence in the mitochondrial genomes of animals (Pierce et al., 2005). This can convert species-specific DNA sequences into two distinct fluorescence signals (Pierce et al., 2005). The FASTFISH-ID kit can be used for fish species identification with reliable, faster, cheaper, and convenient properties. In addition, the newly developed DNA mini-barcode combined with next-generation sequencing (NGS) can detect cryptic species in mixed raw and processed seafood (Xing et al., 2021). The rapid, sensitive, and accurate methods are required for the detection of fish species substitution and fraud (Xing B. et al., 2020).

Herbs and medicinal plants

Over 7000 species of plants have been used for grains and food ingredients (Galimberti, Labra, et al., 2014). Rice, wheat, potatoes, and maize are the most important agricultural products, providing over 90% of human dietary energy sources, and minor crops such as peach palm and goji are also widely cultivated and consumed locally (Amagase and Farnsworth, 2011; Galimberti, De Mattia, et al., 2014). In addition, the growing demand for plant-based foods that claim to have outstanding nutritional or medical advantages has resulted in high demand for the authentication and adulteration detection of new active metabolites for human health and nutrition (Di Lorenzo et al., 2015). With growing herbal market, the adulteration and fraud in herbal products have become a global concern (Tnah et al., 2019). The use of medicinal plants in pharmaceutical industry can promote health and wellbeing (Mishra et al., 2016). The efficacy of plant-based medications is largely dependent on the appropriate use and their purity (Ekor, 2014). However, the customer confidence towards herbal medicines has been declined due to the unethical business practices such as adulteration, mislabeling, and substitution (Table 3) (Mishra et al., 2016). The average percentage of adulterations has been estimated at more than 20% in black pepper, black cohosh, herbal teas, and ginseng (Tnah et al., 2019). The adulteration is mainly caused by the incorrect identification and intentional substitution (Tnah et al., 2019). The fraudulent herbal medicines can cause the decrease in therapeutic activity and the increase in serious risk to the consumers' safety (Efferth and Greten, 2012). Another quality issue of herbal medicines is the presence of heavy metals such as mercury and arsenic in the plant components (Ernst, 2002).

DNA barcoding has been used to identify and differentiate plant species (Hebert et al., 2003; Kumar et al., 2009). However, plant species are difficult to distinguish due to mitochondrial COI genes with low variability (Fišer Pečnikar and Buzan, 2014). Several DNA regions in plants are used as markers in the DNA barcoding based on their universality and resolution. Chloroplast intergenic spacer *trnH-psbA* and nuclear internal transcribed spacer (ITS) region are commonly used as markers for plant species identification (Kress et al., 2005). The ITS region is amplified in two smaller segments (ITS1 and ITS2) that are particularly beneficial for identifying damaged samples (Kress et al., 2005). However, the limitations of using the ITS region include the reduction in species-level diversity and low quality sequencing data (Álvarez, 2003). Therefore, the plant chloroplast genome is used as an alternative animal mitochondrial genome to find the equivalent DNA barcode. Due to a large number of conserved gene sequences, the chloroplast genome can be useful barcode markers (Fišer Pečnikar and Buzan, 2014). The chloroplast genes such as *rbcL*, *rpoC*$_1$, and *matK* are easier to use for phylogenetic analysis than the nuclear genome (Kress et al., 2005). The chloroplast coding regions including *rbcL* and *matK* are considered as core barcoding regions, whereas non-coding regions such as *psbA-trnH* are classified as an essential supplemental barcode candidate (Fazekas et al., 2008). However, single regional markers do not provide sufficient information for low-level identification. Hence, a mixture of regional markers between ITS, *rbcL*, *matK*, and *psbA-trnH* have been used to detect traceable substances in plant-based products and herbal plant species (Yu et al., 2021). Therefore, the development of DNA barcoding technology has played an important role in the differentiation and identification of plant species.

Advances in DNA barcoding

Food authenticity continues to be high priority due to the increased demand for food safety and quality. DNA barcoding has long been well-proven as molecular technique to

Table 3 Application of DNA barcoding for fraud detection in plants

Locus	Plant source	Identification	References
ITS	Goji samples (*Lycium barbarum*)	Traceability of super food	Xin et al. (2013)
	Banana (*Musaceae*)	Banana cultivars	Dhivya et al. (2020)
	Herbal plant (*Pueraria montana*)	Subspecies and raw materials	Zhang et al. (2020)
	Cudweed herb (*Gnaphalium afne*)	Spices adulterants	Zheng et al. (2021)
	Mushroom samples from southwestern China	Edible mushrooms	Zhang et al. (2021)
matK	Herbal dietary supplements (*Actaea racemose*)	Black cohosh species	Baker et al. (2012)
	Herbal juice	Herbal constituents	Mahadani and Ghosh (2013)
	Sand rice	Rice	Genievskaya et al. (2017)
	Dried berry, fruit jam and fruit juice	Berry authentication in fruit products	Wu et al. (2018)
	Vegetables	Poisonous plant	Thongkhao et al. (2020)
psbA-trnH	Herbal plant (*Illicium verum*)	Toxic adulterants	Meizi (2012)
	Ground cherry (*Physalis*)	Cherry species	Feng et al. (2017)
	Powdered herbal	Herbal dietary supplements	Diaz-Silveira et al. (2021)
rbcL	Cinnamon powder	Adulteration in cinnamon powder	Swetha et al. (2014)
	Aromatic plants	Genetic divergence within and between mint species	Tnah et al. (2019)
	Saffron samples	Adulterants in saffron powder	Khilare et al. (2019)
	Herbal plant (*Aconitum heterophyllum* Wall)	Ayurvedic herb species	Negi et al. (2021)
trnL	Olive and hazelnut oil	Seed admixture and adulteration	Uncu et al. (2017)
	Fruit mixtures	Traceability of commercial processed foods	Bruno et al. (2019)
ITS + *psbA-trnH*	Raw drug samples (*Sida cordifolia*)	Identification of commercial frauds and dangerous substitutions	Vassou et al. (2015)
	Herbal plant products	Identification of *Terminalia* species from commercial drug products	Intharuksa et al. (2020)
matK + *psbA-trnH*	Leaves of selected citrus	Identification of Citrus species	Mahadani and Ghosh (2014)

evaluate food authenticity over morphological identification. However, there are still limitations to the application of DNA barcoding, including the difficulty in designing species-specific universal primers and the low resolution to identify closely-related species (Drouet et al., 2018; Gong et al., 2018; Kwon et al., 2012). Recently, the DNA-based methodologies have been further improved by adopting advanced technologies such as bioinformatics, metagenomics, and next-generation sequencing (NGS), which can increase accuracy, sensitivity, and resolution for identifying ingredients in food products (Delgado-Tejedor et al., 2021; Lumsden et al., 2021). The multibarcode sequencing has been developed to improve reliability for identifying multiple species in mixed and processed food products (Dobrovolny et al., 2019; Mishra et al., 2016; Wu and Shaw, 2022; Yao et al., 2022). The clustered regularly interspaced short palindromic repeats (CRISPR)/CRISPR associated (Cas) (CRISPR-Cas) system has been applied to enhance the detection sensitivity of DNA barcoding for meat adulteration and authentication (Wu et al., 2022). The advances in high-throughput DNA barcoding technologies allow quantitative and qualitative detection, which can be practical tools for routine analyses and promising tools for food safety.

In conclusion, this review demonstrated the DNA barcoding that has a potential for establishing food monitoring system in surveillance authorities and also contributes to the improvement for food safety and protection of consumers. The mislabeling and adulteration of food and food products can cause detrimental impact on consumers' health. The growing concern on food safety and quality has led to the development of authentication and identification tools. The polymorphism-based techniques are commonly used to improve accuracy in species detection. Rapid, accurate, and cost-effective detection methods are essential to effectively supervise mislabeled and adulterated foods, which can eventually enhance food safety and protect consumers' health. However, further study is needed to build DNA barcode database for species detection and identification in raw and processed food products.

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Declarations

Conflict of interest The authors declare no conflict of interest.

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