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Review

Applications of environmental DNA (eDNA) in agricultural systems: Current uses, limitations and future prospects



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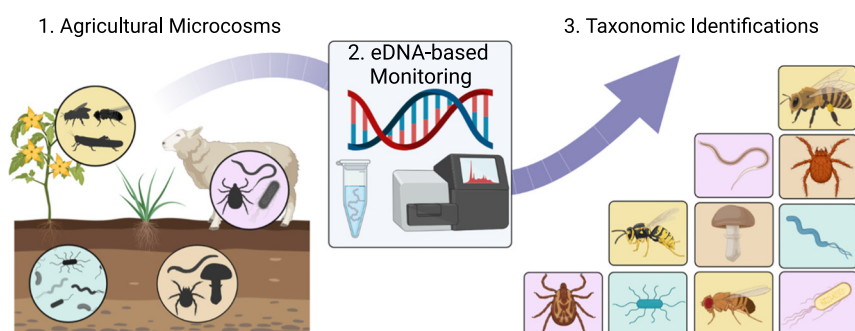
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HIGHLIGHTS

- eDNA is a powerful but underused monitoring tool for agricultural systems.
- eDNA surveys can provide classifications for specific organisms and entire assemblages in substrates ranging from soil to air.
- Monitoring with eDNA can help detect and classify ecologically beneficial and harmful organisms in food production systems.
- In silico, in vitro, and in vivo approaches help overcome limitations and caveats associated with eDNA analysis.
- When combined with traditional techniques, eDNA-based surveys can help improve monitoring for agricultural systems.

GRAPHICAL ABSTRACT



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ABSTRACT

Global food production, food supply chains and food security are increasingly stressed by human population growth and loss of arable land, becoming more vulnerable to anthropogenic and environmental perturbations. Numerous mutualistic and antagonistic species are interconnected with the cultivation of crops and livestock and these can be challenging to identify on the large scales of food production systems. Accurate identifications to capture this diversity and rapid scalable monitoring are necessary to identify emerging threats (i.e. pests and pathogens), inform on ecosystem health (i.e. soil and pollinator diversity), and provide evidence for new management practices (i.e. fertiliser and pesticide applications). Increasingly, environmental DNA (eDNA) is providing rapid and accurate classifications for specific organisms and entire species assemblages in substrates ranging from soil to air. Here, we aim to discuss how eDNA is being used for monitoring of agricultural ecosystems, what current limitations exist, and how these could be managed to expand applications into the future. In a systematic review we identify that eDNA-based monitoring in food production systems accounts for only 4 % of all eDNA studies. We found that the majority of these eDNA studies target soil and plant substrates (60 %), predominantly to identify microbes and insects (60 %) and are biased towards Europe (42 %). While eDNA-based monitoring studies are uncommon in many of the world's food production systems, the trend is most pronounced in emerging economies often where food security is most at risk. We suggest that the biggest limitations to eDNA for agriculture are false negatives resulting from DNA degradation and assay

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biases, as well as incomplete databases and the interpretation of abundance data. These require *in silico*, *in vitro*, and *in vivo* approaches to carefully design, test and apply eDNA monitoring for reliable and accurate taxonomic identifications. We explore future opportunities for eDNA research which could further develop this useful tool for food production system monitoring in both emerging and developed economies, hopefully improving monitoring, and ultimately food security.

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1. Introduction

Global food production faces increasing threats from both environmental and human-induced stressors (Cole et al., 2018; Grafton et al., 2015; Grubisic et al., 2018; Yue et al., 2020). These stressors have curtailed efforts to meet the United Nations Sustainable Development Goal and reduce the 8.9 % of the global population that are currently malnourished (FAO, 2020; United Nation, 2015). The failure to reduce this malnutrition rate has emphasised the challenge of achieving widespread access (physical, social and economic) to safe nutritious food, known as food security (Isvilanonda and Bunyasiri, 2009; Sarkar et al., 2020; Torquebiau, 2016). Improving global food security is a substantial challenge that will become more difficult to achieve as food production systems (used interchangeably with agricultural systems) around the world are threatened by climate change (Lesk and Anderson, 2021), loss of arable land (Hossain et al., 2020), increases in water scarcity (Wada et al., 2016), greater threats from pests and pathogens (Savary et al., 2019), and the loss of pollinating species (Lippert et al., 2021). These threats will likely inflate global food commodity prices, thereby further restricting food security to only those who can afford it (Beydoun et al., 2011; Green et al., 2013; Pollard and Booth, 2019). Responding and adapting to these emerging threats will require a whole systems approach that strengthens current measures by accounting for the inherent biological complexity within food production systems.

Escalating global food demands will need to be met with further intensification of production systems across agricultural and horticultural sectors (FAO, 2020), production which relies upon a combination of soil health/plant nutrition, suppression of disease pressure, and promotion of the presence of beneficial organisms (i.e. nodulating bacteria, pollinators, etc.) (Amari et al., 2021; Mbow and Rosenzweig, 2019; Potts et al., 2016). Detection and identification of these mutualistic and antagonistic species is largely

reliant on labour intensive processes (Kudoh et al., 2020; George et al., 2017; Ashfaq et al., 2016). Indeed, manual identifications have historically been the standard procedure for identifying meso- and macrofauna within soil (Gerlach et al., 2013; Menta and Remelli, 2020), crop and animal pests/pathogens (Tsoi et al., 2020; Vu et al., 2018), as well as pollinating species (Macgregor et al., 2019; Pardo and Borges, 2020). Nevertheless, taxonomic and specialist expertise are becoming increasingly rare, and the effort required to identify organisms to species-level based on morphological characteristics is often time-consuming. Upscaling such detections to large agricultural and horticultural practices is often not economically viable, and some traditional monitoring methods are only effective for a small fraction of the total diversity present (i.e. cultivating bacteria) (Bell et al., 2016; Kudoh et al., 2020; Rappé and Giovannoni, 2003). Consequently, a significant barrier currently exists for efficiently detecting and classifying soil, pest, and beneficial species within food production systems. Increasingly, environmental DNA (eDNA) is being used as a tool to detect taxa from trace DNA deposits, potentially offering a strong complement for monitoring in agricultural ecosystems.

DNA-based approaches offer an efficient means to characterise biodiversity, establish diversity thresholds, and to monitor community changes as a result of activities or management decisions. Trace amounts of intracellular and extracellular DNA isolated and characterised from biological substrates including; soil, scats (faeces), plant material, water, or air are collectively referred to as environmental DNA (eDNA) (Levy-Booth et al., 2007; Taberlet et al., 2012b). This also extends to DNA obtained from bulk samples (e.g. a collection of whole insects from pitfall traps; see Rasmussen et al., 2021; Young et al., 2021) (Taberlet et al., 2012a, 2012b; Taberlet et al., 2018). Once captured, the preserved, but often degraded DNA provides a means to rapidly and accurately identify taxa and survey biological communities (Ficetola et al., 2008; Taberlet et al., 2007). When combined with High-Throughput Sequencing (HTS)

technologies, the large eDNA data volumes can provide a wealth of information on, for example, community composition, food web dynamics, animal diet, the recovery (or otherwise) of ecosystems following restoration, and invasive or pest species presence/absence (Ruppert et al., 2019; Taberlet et al., 2012b). A significant strength of eDNA-based monitoring is the ability to tailor surveys to detect either single species or whole biological communities.

Environmental samples may be targeted and amplified with either a barcoding or metabarcoding approach depending on how many taxa are of interest. DNA barcoding, otherwise known as “targeted-PCR”, provides a single taxon identification and is often used in combination with Sanger sequencing, while eDNA metabarcoding targets many DNA fragments, and therefore many taxa, from mixed biological samples, the amplified fragments are then sequenced on an HTS platform, a process which is sometimes described as “metabarcoding” (Saccò et al., 2022). DNA barcoding is frequently applied to eDNA samples with single-species probe assays (i.e. Valentin et al., 2016), to determine the presence or absence of species via quantitative PCR. In contrast, eDNA metabarcoding uses “universal” primer sets (i.e. assays) to bind to a conserved homologous region of a gene shared by numerous species or groups of taxa using PCR (i.e. Miya et al., 2020) (Saccò et al., 2022). Subsequently, the variable region is amplified (known as an “amplicon”), arranged into libraries and sequenced on an HTS platform (i.e. Illumina MiSeq, Oxford MinION, etc.), the millions of short DNA sequences generated are filtered using a bioinformatics pipeline that can then be used to assess diversity by assigning taxonomic identifications, Operational Taxonomic Units (OTUs) (i.e. Jiang et al., 2014), or Amplicon Sequence Variants (ASVs) (Callahan et al., 2016, 2017) (Fig. 1). The choice of assay for both barcoding and metabarcoding depends on the availability of reference sequences (i.e. Cytochrome c Oxidase subunit I (COI) generally favoured for insects) as well as the presence and suitability of a locus to target (Saccò et al., 2022). Unfortunately, because the genes

containing the homologous regions targeted using universal assays evolve and mutate at different rates (see Kocher et al., 1989), no single universal assay exists that can capture all prokaryotic or eukaryotic diversity within a mixed biological environmental sample (Alexander et al., 2020). Instead, multiple assays are often used to accurately capture the taxonomic diversity and monitor community composition with eDNA samples (i.e. Makiola et al., 2019). eDNA can provide rapid, scalable monitoring which can support current techniques used for food production systems with bulked samples and accurate molecular identifications.

A wide range of studies, mainly in natural ecosystems, have shown eDNA barcoding and metabarcoding to be an effective taxonomic identification tool for both micro- and macroorganisms (Buée et al., 2009; Claret et al., 2021; Miya et al., 2020; Ruppert et al., 2019; Taberlet et al., 2012a). Microbiologists were the first to use DNA barcoding to target uncultivable microorganisms (Hugenholtz and Pace, 1996). By the early 2000's, barcoding of bacterial, fungal and eukaryotic DNA based on cloning technology had become common practice within microbiology, although the term ‘eDNA’ was not used in the discipline until 2009 (Buée et al., 2009; Rolf, 2005; Rondon et al., 2000). While for macroorganisms, the first applications of eDNA helped to reconstruct ancient plant and animal communities from permafrost, ice cores and cave sediment (Haile et al., 2009; Sonstebo et al., 2010; Willerslev et al., 2003). DNA-based assessment of palaeoecological communities (both barcoding and metabarcoding) provided higher taxonomic resolution compared to traditional identification and survey techniques (Haile et al., 2009; Sonstebo et al., 2010; Willerslev et al., 2003). These initial studies established eDNA tools as a fast and efficient means of classifying species assemblages directly from environmental samples (Taberlet et al., 2012b). Such promise made the application of eDNA for detecting extant biodiversity appealing, and it was first used to barcode tadpole DNA from aquarium water samples (Ficetola et al., 2008). Since these initial studies, eDNA-based surveys

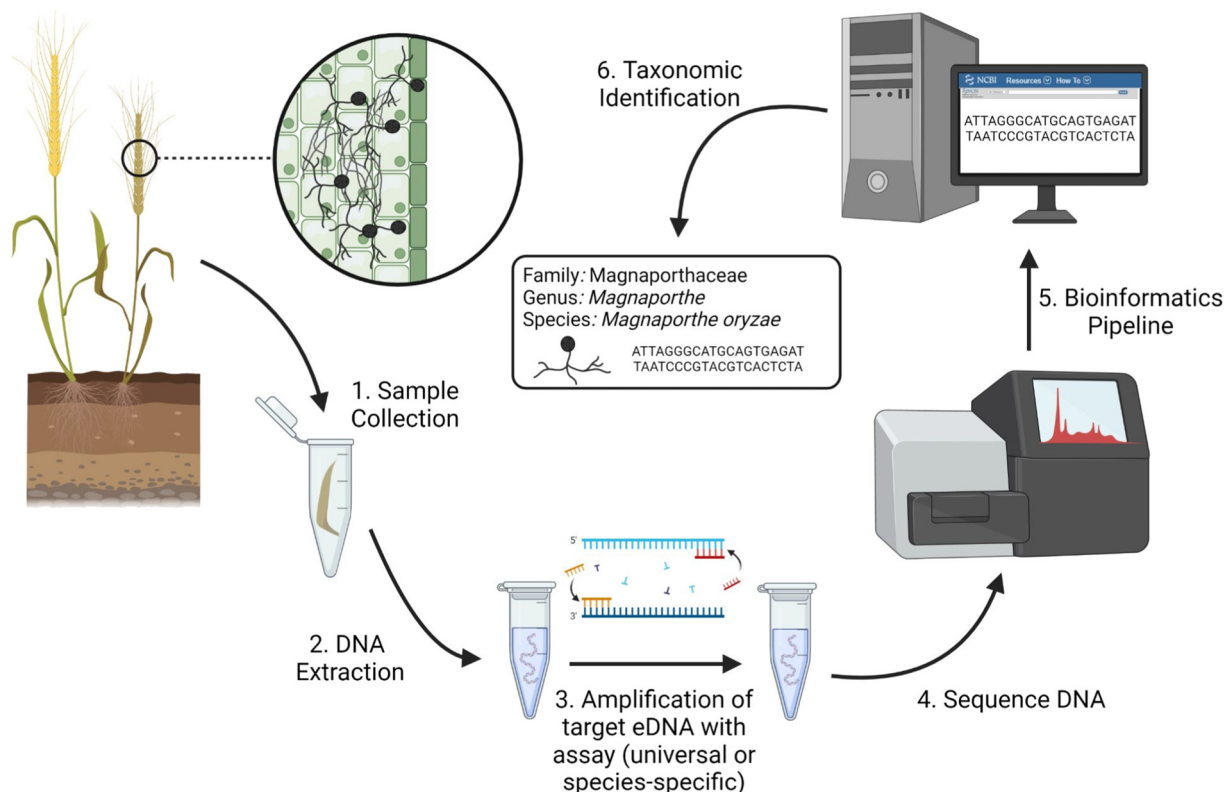


Fig. 1. An example workflow for eDNA-based monitoring to measure the species identity of a fungal pathogen infecting wheat (*Triticum aestivum*). Leaf samples are collected from the infected plants (1), these samples may be placed on ice, or immediately processed for DNA extraction (2). Following extraction, the target DNA of interest, in this case fungal DNA, is amplified with Polymerase Chain Reaction (PCR) using either species-specific or universal primers (3). The amplified products are then cleaned, purified and arranged into libraries prior to sequencing on a High-Throughput Sequencing (HTS) platform (4). The reads generated are then filtered using a bioinformatics pipeline (5) and compared to reads from either online databases, or a custom Barcode Reference Library (BRL) to provide taxonomic identifications (6). Graphic created using BioRender.

have been expanded to monitoring a wide range of animal (Lesk and Anderson, 2021), plant (Yoccoz et al., 2012), fungal (Yan et al., 2018), prokaryotic (Caldwell et al., 2015) and viral communities (Miaud et al., 2019). With this expansion however, an increasing awareness of the limitations of the technology has emerged. For instance, the basic biological processes that “feeds” DNA into the environment and the physical and chemical processes that determine its persistence in terrestrial, aquatic and aerial environments remain largely unexplored (Deiner et al., 2017). Further, not all taxonomic groups can be differentiated with commonly amplified barcoding regions such as COI, and false negatives (taxa present but genetically misclassified as absent), as well as false positives (taxa absent but genetically misclassified as present) are persistent issues in this research field (Deagle et al., 2014; Deiner et al., 2017; Ficetola et al., 2015). These caveats highlight that although eDNA surveys are a powerful molecular tool, they will not apply equally well to all ecosystems (Deiner et al., 2017; Taberlet et al., 2012b). In spite of these limitations, it remains necessary to continually test where eDNA is applicable and what targeted approaches for sampling and species detections are possible to further increase its utility for food production systems.

Traditional monitoring for agriculture has proved challenging to scale and is sometimes impossible because the majority of organisms cannot be cultivated or are difficult to rear (Kudoh et al., 2020; Rappé and Giovannoni, 2003). Detecting species from trace amounts of DNA or from a single bulked environmental sample offers an efficient, reproducible and cost-effective alternative (Kudoh et al., 2020; Valentin et al., 2018; Littlefair et al., 2016). For instance, manually testing individual plants or animals in large consignments for pests and diseases is often logistically impossible given time constraints and associated costs (Brunner, 2020; Ceresini et al., 2019). While for eDNA, one bulked sample (made up of many sub samples) provides a presence/absence measure for the entire consignment, allowing for a rapid general assessment (i.e. targeting Khapra beetle (*Trogoderma granarium*) in shipping containers using a species-specific assay; see DAWE, 2021) (Brunner, 2020; Valentin et al., 2018). eDNA-based detections can also be tailored for economically-important species or entire communities where morphology-based identification has proved problematic (see Aloo et al., 2020; Macgregor et al., 2019), and

where microorganisms cannot be cultured easily using selective media (i.e. $\geq 99\%$ of bacteria are estimated to be unculturable; Rappé and Giovannoni, 2003) (see Sternhagen et al., 2020). Further, because of the high levels of mechanisation in modern agriculture, there are opportunities to integrate these eDNA-based sampling methods with existing machinery and infrastructure to detect these species of interest. Information on these generally ‘invisible’ organisms would enable better monitoring, and potentially better informed management for these species depending on their relationship to the cultivated animal or plant of interest (i.e. controlled pesticide application, reduced fertiliser input, etc.) (Menta and Remelli, 2020; Willcox et al., 2019). The ability to tailor eDNA sampling and specificity according to the species, community or system of interest has enabled non-invasive surveys in an array of different ecosystems and contexts, although despite this promise, eDNA surveys have remained novel for the field of agriculture.

Applications of eDNA surveys have almost exclusively occurred within natural ecosystems (Bohmann et al., 2014; Evans and Kitson, 2020; Ruppert et al., 2019; Taberlet et al., 2012a). Few studies have used eDNA in agricultural systems, although this is beginning to change (Fig. 2). As far as we are aware, no systematic reviews of the applications of eDNA barcoding and metabarcoding for food production systems have been conducted (Figs. 2 & 3); a significant omission given that taxonomic identifications are necessary for monitoring in both natural and human-modified ecosystems (Memmott et al., 2004; Van Elsas et al., 2002; Yue et al., 2020). Here, we conducted a systematic review to identify the current uses of eDNA-based monitoring in agriculture, the substrates and organisms routinely being targeted, and the geographical distribution of these studies. We also stress the most relevant challenges for implementing eDNA methods into food production systems and highlight the current and emerging solutions available. The complexities present within the eDNA workflow have merited numerous reviews over the last decade (i.e. Ruppert et al., 2019; Taberlet et al., 2012b, 2018). Within the constraints of this review we have omitted extensive discussions on eDNA sampling (see Dickie et al., 2018), primer selection (see Schenekar et al., 2020) and bioinformatics (see Mathon et al., 2021), all of which have been reviewed elsewhere. Finally we explore future applications of eDNA-based monitoring, what components

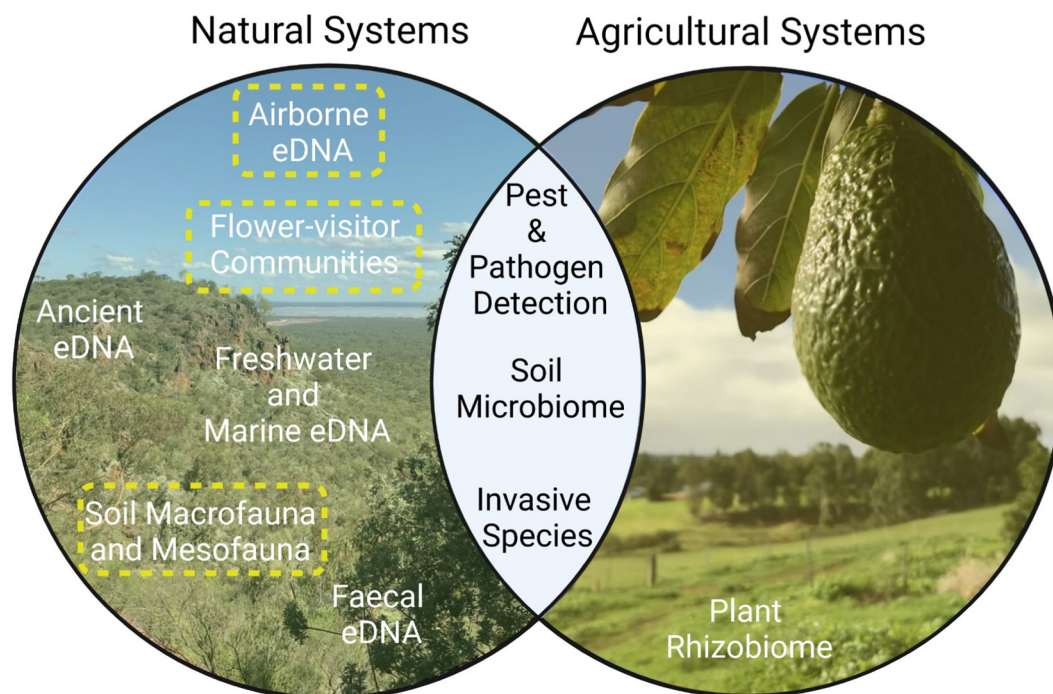


Fig. 2. Applications of eDNA-based surveys in natural and agricultural systems. Applications are based on the papers found during systematic review (Table 1). Yellow boxes designate applications of eDNA which are used in natural systems and are emerging in food production systems. Images captured by Joshua Kestel.

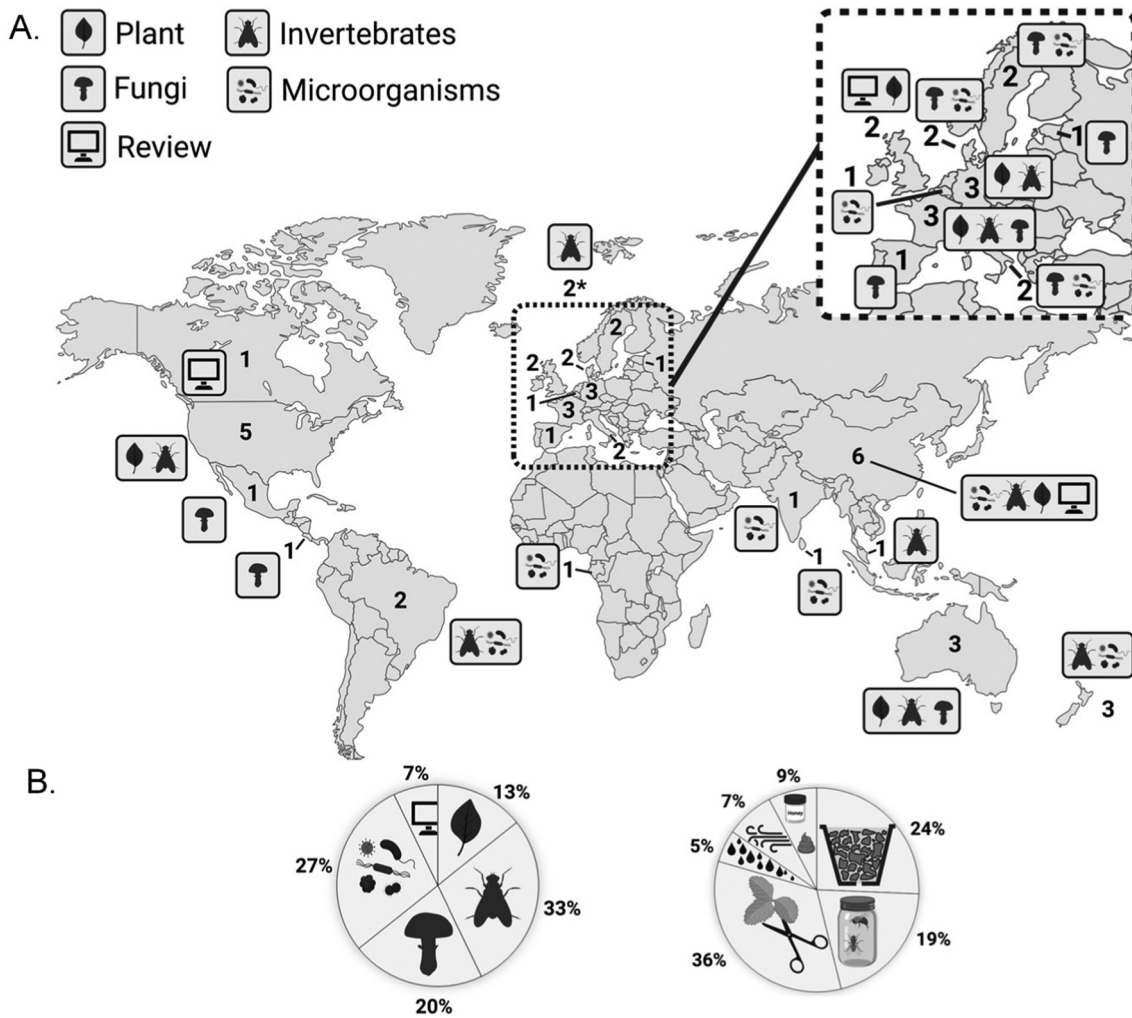


Fig. 3. Panel A; Global distribution of agricultural and horticultural eDNA studies (45). The taxa targeted are symbolised next to the number of studies in each country, not including duplicates. The 2* designates the two studies which used eDNA for agricultural purposes in various countries in Europe. Panel B; left; taxa targeted for each study, clockwise; plants (13%), insects (33%), fungi (20%), microorganisms (27%), and review (7%). Right; substrates sampled for eDNA within agricultural and horticultural context, clockwise; soil (24%), insects (19%), plant material (36%), water (5%), air (7%), and other (9%). Graphic generated in BioRender.

of agriculture are currently unexplored, and how to increase the accessibility of this technology to facilitate greater use in food production systems for both developed and emerging economies.

2. Methods

Literature searches were conducted on SCOPUS up to 6th of January 2022. The SCOPUS database was chosen because it offers greater coverage for the subjects relevant to eDNA, the life sciences and biomedicine, when compared to the Web of Science (Mongeon and Paul-Hus, 2016; Vera-Baceta et al., 2019). The term ‘eDNA’ entered the mainstream scientific literature nearly a decade after DNA metabarcoding became commonplace for the soil sciences (see Buée et al., 2009), where inconsistent and changing terms are used for molecular studies of soil microbial communities (i.e. sed-eDNA, eDNA, metabarcoding, meta-barcoding, amplicon, tag-sequencing, total soil DNA, etc.). It was beyond the scope of this review to classify (e.g. geographic location, target taxa etc.) the many thousands of soil microbial community studies that utilise the eDNA workflow but not the terminology ‘environmental DNA’ or ‘eDNA’ as this is a review in itself, and has been done many times previously (e.g. Imfeld and Vuilleumier, 2012; Pankhurst et al., 1996; Rolf, 2005; Schloter et al., 2018; Trivedi et al., 2016). We therefore caution that this review is non-exhaustive in the context of soil microbial community analysis, but does

provide a snapshot of the trends, emerging research and future directions for the field.

Three searches were undertaken, the first to determine the total number of eDNA studies, the second to specify the number of eDNA studies relevant to food production systems, and the third to identify the number of total soil DNA papers potentially missed from the first two searches. The first search used the terms; (‘eDNA’ OR ‘environmental’) AND ‘DNA’ AND (‘barcode’ OR ‘barcoding’ OR ‘metabarcoding’ OR ‘metabarcoding’) to target all eDNA studies in the literature. For the second search, the terms (‘eDNA’ OR ‘environmental’) AND ‘DNA’ AND (‘barcode’ OR ‘barcoding’ OR ‘metabarcoding’ OR ‘metabarcoding’) AND (‘agriculture’ OR ‘agricultural’ OR ‘horticulture’ OR ‘horticultural’) were used to target eDNA studies relevant to terrestrial food production systems, specifically agriculture and horticulture. Although not included in this review, we sought to quantify the number of soil microbial papers that use the eDNA workflow, but not necessarily the terms ‘eDNA’ or ‘environmental DNA’. As such, a third search using the terms; (‘extracellular’ OR ‘environmental’) AND (‘DNA’ OR ‘eDNA’) AND ‘soil’ AND (‘agriculture’ OR ‘agricultural’ OR ‘horticulture’ OR ‘horticultural’) AND NOT ‘metagenomics’ was conducted in SCOPUS generating 1022 results (Fig. 4).

The first search for all eDNA studies generated 2215 results, and the second search of eDNA studies relevant to food production systems generated 107 results. These results were then checked manually to determine relevance. Of the 2215 results, 1076 (48%) were deemed relevant for eDNA generally (i.e. studies which used eDNA-based surveys, either single species

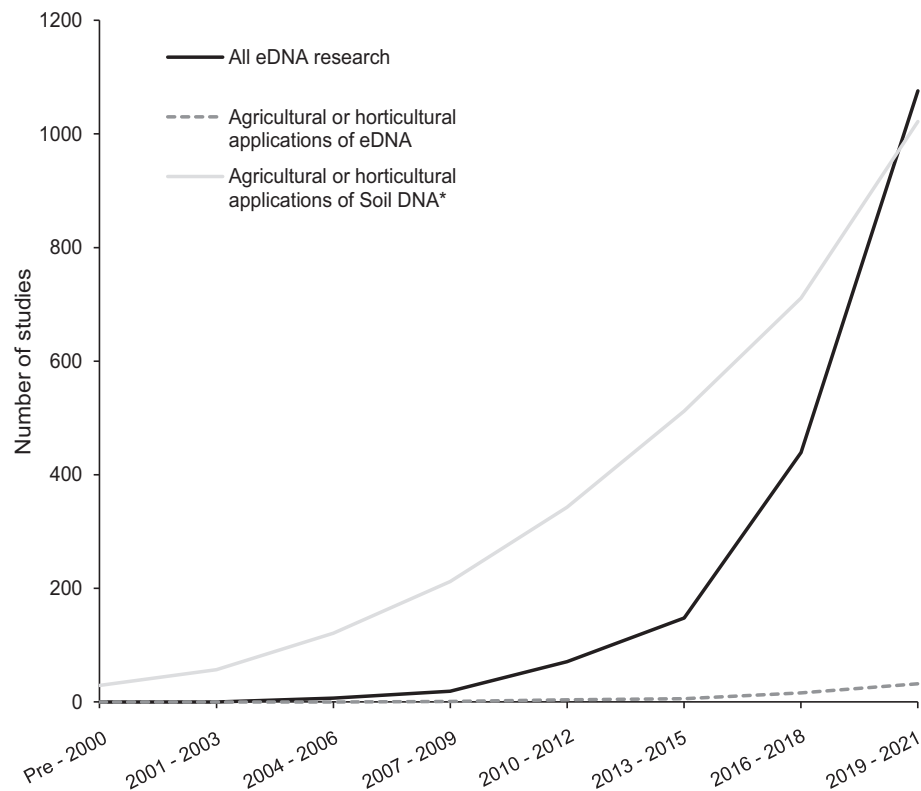


Fig. 4. Cumulative number of eDNA studies in both natural (terrestrial and aquatic) and food production systems ($N = 1076$) (All eDNA research), agricultural eDNA studies ($N = 45$) (Agricultural or horticultural applications of eDNA), and total soil DNA studies (Agricultural and horticultural applications of soil DNA) ($N = 1022$) generated from SCOPUS searches conducted up to 6/01/2022. Agricultural and horticultural applications of soil DNA* studies relevant to agriculture predominantly identified soil microorganisms (81 % of soil studies).

or community, for taxonomic classification) and 45 (4 %) were deemed relevant for eDNA in agriculture (Fig. 3 & Table 1). Papers were grouped according to year of publication, and papers specific to agriculture were graphed separately to the cumulative total of eDNA studies and total soil DNA studies (Fig. 4).

3. Applications of eDNA in food production

The inclusion and further development of eDNA technology to complement species monitoring within food production systems can facilitate the timely detection of emerging pests and pathogens, and establish how new management strategies are affecting local biodiversity. Although, the use of eDNA for agriculture remains an emerging field (4 % of all eDNA studies) (Fig. 3), with a geographical bias towards European countries (42 %). Relatively few records have been published for studies conducted in the Americas (18 %), China (13 %), and Oceania (16 %) despite two of these having the largest economies (America and China), and only one eDNA study was found for food production systems in Africa (Fig. 3 & Table 1.). Our systematic review highlights that relatively few food production systems appear to use eDNA in agriculture, especially those with developing economies (Fig. 3). When used, plant material (36 %), and soil substrates (24 %) are most commonly sampled, while insects (33 %) and microorganisms (27 %) are the most targeted taxa. Further, where eDNA is implemented within food production systems, there is an opportunity to survey more substrates (i.e. honey, faeces; 9 % of substrates measured) and to target a greater breadth of taxa (i.e. plants; 13 % of taxa targeted) than is currently measured. Clearly much research remains to be done across numerous agricultural and horticultural contexts for both broad and narrow ranges of geography in the future. Complementing traditional monitoring with eDNA-based tools is increasingly necessary as stakeholders require identifications and spatial distributions for mutualistic and antagonistic species, both to improve monitoring, and potentially food security

(Weiss et al., 2020). One caveat to these findings is that they largely omit the extensive literature associated with total soil DNA (Fig. 4). It is beyond the scope of this review to retrospectively disentangle the numerous eDNA and metagenomic soil studies relevant to agriculture. Instead, we direct readers to the following reviews for more discussion on this topic (Levy-Booth et al., 2007; Rolf, 2005; Taberlet et al., 2018). Below, we discuss recent studies where the benefits and limitations of eDNA in agricultural systems are highlighted.

3.1. Pest and pathogen surveillance - cropping systems

Cultivated landscapes provide favourable conditions for the evolution, selection and spread of plant pests and pathogens (Brown and Hovmøll, 2002; Smith and Guégan, 2010). In the presence of a susceptible host and appropriate environmental conditions these pathogens and pests can threaten crop and pasture production, with global yields estimated to be reduced by 20–40 % annually (see Flood, 2010) in the absence of effective control. Crop disease burdens escalate with farming intensity and are predicted to increase as crop yields double to achieve food security by 2050, with the suite of disease-causing pathogens predicted to expand dramatically (Amari et al., 2021; Chaloner et al., 2021). As a consequence, the viability of current farming systems may be threatened by the emergence of new plant pests and pathogens and/or changes in the virulence and distribution of known pests and pathogens, especially if new innovations and technologies are not harnessed to identify and monitor their emergence (Jones, 2009; Osunkoya et al., 2021; Wintermantel and Hladky, 2010). Two salient examples are seen in the global spread of wheat blast fungus (*Magnaporthe oryzae*) and Ramularia leaf spot in barley (*Ramularia* sp.). Both pathogenic fungi are difficult to detect/culture and have quickly spread across international boundaries, where in some farms annual yield losses are being reported of up to 70 % (barely infected with *Ramularia* sp.; see Havis et al., 2015) and 100 % (wheat infected with *M. oryzae*; see

Table 1

Forty-five studies found from SCOPUS. Search terms for SCOPUS included; ('eDNA' OR 'environmental') AND 'DNA' AND ('barcode' OR 'barcoding' OR 'metabarcoding' OR 'metabarcoding') AND ('agriculture' OR 'agricultural' OR 'horticulture' OR 'horticultural'). Only studies that used the term 'eDNA' or 'environmental DNA' for the purposes of taxonomic identification were included, as well as studies that used bulk sampling combined with an eDNA workflow. Metagenomic and total soil DNA papers were not included as they were outside of the scope of this review. The literature search was conducted up to 6th January 2022 and generated 107 results, all results were checked manually to determine if they were relevant to applications of eDNA for agricultural practices.

Reference	Country	System	Substrate	Barcoding	Target taxa
Ashfaq et al. (2016)	Canada	Review	–	–	–
Wang et al. (2013)	China	Review	–	–	–
Littlefair et al. (2016)	England	Review	–	–	–
Tordoni et al. (2021)	Italy	Various locations in two Italian regions	Air	Metabarcoding	Fungi
Karlsson et al. (2020)	Sweden	Various locations in two Swedish regions	Air	Metabarcoding	Bacteria and fungi
Redondo et al. (2020)	Sweden	Wheat fields	Air	Metabarcoding	Fungi
Rasmussen et al. (2021)	Germany	Vineyard	Bulk-insect samples	Metabarcoding	Insects
Zenker et al. (2020)	Brazil	Agricultural fields	Bulk-insect samples	Metabarcoding	Insects
Song and Huang (2016)	China	Farmland	Bulk-insect samples	Metabarcoding	Insects
Boetzi et al. (2021)	Germany	Flowering fields and calcareous grasslands	Bulk-insect samples	Metabarcoding	Insects
Edwards et al. (2014)	Malaysia	Oil palm plantations	Bulk-insect samples	Metabarcoding	Insects
Dopheide et al. (2020)	New Zealand	Perennial cropland	Bulk-insect samples	Metabarcoding	Various Metazoa
Chang et al. (2018)	China	Island habitat for long-distance migrating pest moth	Moths	Metabarcoding	Plants
Macgregor et al. (2019)	England	Farmland	Moths	Metabarcoding	Plants
Emeyeonu et al. (2018)	Australia	Laboratory	Flour, seed mixes and air	Species-specific	<i>Zea mays</i> and <i>Vigna unguiculata</i>
Latz et al. (2021)	Denmark	Greenhouse and field trial	Leaf, root, seed, and air	Metabarcoding	Fungi
Milazzo et al. (2021)	Australia	Barley fields	Leaf	Metabarcoding	Fungi
Barroso-Bergadà et al. (2021)	France	Vineyard	Leaf	Metabarcoding	Fungi
Loit et al. (2019)	Estonia	Laboratory	Leaf and tuber	Metabarcoding	Fungi
Smessaert et al. (2019)	Belgium	Apple and pear orchards	Nectar	Metabarcoding	Bacteria
Danner et al. (2017)	Germany	Agricultural landscapes	Pollen	Metabarcoding	Plants
Smart et al. (2017)	USA	Agricultural landscapes	Pollen	Metabarcoding	Plants
Michelot-Antalik et al. (2021)	France	Dairy Farms	Pollen	Metabarcoding	Plants
Sternhagen et al. (2020)	Costa Rica	Coffee fields	Root	Metabarcoding	Fungi
Mezzasalma et al. (2017)	Italy	Vineyards	Grapes	Metabarcoding	Bacteria and yeast
Zhou et al. (2020)	China	Rice Field	Seeds and roots	Metabarcoding	Bacteria
Makiola et al. (2019)	New Zealand	Perennial cropland	Soil, root and leaf	Metabarcoding	Bacteria, fungi and oomycetes
Caldwell et al. (2015)	Brazil	Coffee fields	Soil	Metabarcoding	Archaea and bacteria
Jiang et al. (2014)	China	Various crops	Soil	Metabarcoding	Archaea and bacteria
Wang et al. (2020)	China	Cropland soils	Soil	Metabarcoding	Bacteria and eukaryotes
Frøslev et al. (2021)	Denmark	Agricultural fields	Soil	Metabarcoding	Bacteria, fungi and eukaryotes
Meyer et al. (2019)	Gabon	Manioc and banana plantations	Soil	Metabarcoding	Bacteria
Navarro-Noya et al. (2021)	Mexico	Maize fields	Soil	Metabarcoding	Fungi
Todd et al. (2020)	New Zealand	Apple and kiwifruit orchards	Soil	Metabarcoding	Insects
Epelde et al. (2020)	Spain	Cultivated vegetable orchards	Soil	Metabarcoding	Fungi
Srivastava et al. (2021)	India	Field trial	Compost	Metabarcoding	Bacteria
Valentin et al. (2020)	USA	Various trees, shrubs and understorey vegetation	Spray aggregate and rollers from tree bark and leaf surfaces	Species-specific	<i>Lycorma delicatula</i>
Allen et al. (2021)	USA	Vineyards	Leaf and stem surfaces	Species-specific	<i>Lycorma delicatula</i>
Gamage et al. (2020)	Sri Lanka	Agricultural or rice fields	Water	Species-specific + Metabarcoding	<i>Leptospira</i> sp. and bacteria
Valentin et al. (2018)	USA	Apple Orchards	Water	Species-specific	<i>Halyomorpha halys</i>
Valentin et al. (2021)	USA	Laboratory	Fruit and leaf surfaces	Species-specific	<i>Halyomorpha halys</i>
Utzeri et al. (2018)	Various - Europe	Various orchards	Honey	Metabarcoding	Hemiptera species
Crisol-Martínez et al. (2016)	Australia	Macadamia orchards	Faecal	Metabarcoding	Insects
Aizpurua et al. (2017)	Various - Europe	Caves within agricultural landscape	Faecal	Metabarcoding	Insects
Tournayre et al. (2021)	France	Caves within agricultural landscape	Faecal	Metabarcoding	Insects

Ceresini et al., 2019). eDNA-based identifications from agricultural substrates (i.e. leaf material, soil or air) offers a powerful and rapid method for pathogen detection (Fig. 1). Tordoni et al. (2021) sampled fungal spores from air and were able to identify three times more fungal taxa with eDNA metabarcoding than from manual identifications, indicating that this technique is already helping detect and identify plant pathogens that may otherwise remain undiscovered within cultivated landscapes (Michael et al., 2020). Similarly, Redondo et al. (2020) measured spatio-temporal

variation of airborne fungal spores within forest-agricultural mosaic landscapes using passive and active air samplers combined with eDNA metabarcoding. The results showed that the composition of fungal spore communities were consistently dominated by two potential agricultural pathogens, *Alternaria* spp. and *Ustilago* spp. With similar monitoring on smaller geographic scales, agricultural practitioners could use spatially focused fungicide applications, spraying only in areas where pathogen presence has actually been confirmed, maximising their effective lifespan and

improving the return on investment. Further, by reducing and/or targeting fungicide usage, the risk of environmental damage may be minimised compared to more widespread application strategies (Sowunmi et al., 2019). We envisage that a comparable eDNA-based monitoring protocol could also have utility for biosecurity monitoring purposes, for example eDNA sampling (air, water-wash, crop surfaces, etc.) could be adopted at points of border control, complementing current techniques to help identify plant pests and pathogens and reduce instances of cross-border outbreaks (Boykin et al., 2019). These eDNA techniques are still emerging for agricultural systems, although their greater adoption holds promise to enhance current detection methods for plant pathogens such as *M. oryzae* and *Ramularia* sp., as well as helping to develop adaptive management solutions.

Spatially focused eDNA surveys can help detect emerging pests and pathogens with timely fine-scale geographical detections which allow for targeted sampling and decisions on control measures. Herbivorous pest insects typically feed on a defined range of host species or specialised groups of plants (Imms, 1947). The techniques traditionally used for identifying these potentially damaging species include; direct observation, microscopy work, rearing of pest insects, and feeding trials (Hamilton et al., 2005; Symondson, 2002; Vu et al., 2018). These traditional methods rely on detailed taxonomic expertise, and also require significant time commitments (Kudoh et al., 2020; Symondson, 2002). For instance, feeding trials can last up to 20 days, not including data analysis, and depending on the target species (Clay et al., 1985; Dunse et al., 2010). Such extended time-periods will delay both detections and the subsequent targeted pesticide response, potentially resulting in major infestations and outbreaks (Kudoh et al., 2020; Simberloff et al., 2013; Valentin et al., 2018). Further, some traditional techniques such as direct observation by taxonomic specialists are simply not feasible given the extremely short generation times of some pest insects (i.e. aphids) and large scales that need to be surveyed in agriculture systems (Edwards et al., 2014; Rouland-Lefevre, 2010; Simberloff et al., 2013). This implies that practitioners are often left to adopt generalised/prophylactic pesticide applications, which are expensive, environmentally damaging and can increase the potential for pesticide resistance (Leskey et al., 2012; Morales, 2006; Rouland-Lefevre, 2010). As such, there exists a need to rapidly and accurately detect emerging plant pests within food production systems.

Barcoding and metabarcoding herbivorous insect DNA from plant material (i.e. leaves & fruit) or bulk insect traps (i.e. Vane traps & funnel traps) can be an effective means to rapidly assess the presence of pest and beneficial insects on crop and orchard species at large scales (Thomsen and Sigsgaard, 2019; Valentin et al., 2018; Young et al., 2021). Insects leave traces of DNA when they feed and/or excrete on, plant tissue, and this has allowed researchers to retrieve genetic insect identifications for flower-visitors, plant parasites, as well as insect prey (Bittleston et al., 2016; Derocles et al., 2015; Kudoh et al., 2020). Such eDNA methods have also proven useful for the detection of pest taxa from plant material in croplands, viticulture and orchards. By using a species-specific assay and targeting rinse water collected after the harvested apples were cleaned, a cost-effective eDNA detection method for the highly invasive and destructive pest species (brown marmorated stink bug, *Halymorpha halys*) proved more efficient than traditional methods of pheromone traps and black lights (Valentin et al., 2016, 2018). Such accurate detection methods are not only important for treating crops post-harvest, but could also be extended to early pre-harvest detections, allowing for targeted pesticide applications before crops are widely damaged (Leskey et al., 2012; Sánchez-Bayo and Wyckhuys, 2019; Valentin et al., 2018). Further, eDNA-based surveys could help detect co-occurring beneficial insects (i.e. native bees) to assess recovery following broad-spectrum insecticide applications, this approach could determine both the length of time it takes for the pest and beneficial species to return, thereby informing future spraying timings and strategies. Insect traps may also be considered as a complementary means to assess pest emergence which, if combined with traditional identification, can allow for abundance measures as well as molecular verification.

3.2. Pest and pathogen surveillance - livestock

Of globally emerging pathogens, 75 % are estimated to be zoonotic (infect multiple host species including domesticated animals and humans) and twice as likely to be associated with emerging diseases as non-zoonotic pathogens (Taylor et al., 2001). Zoonotic pathogens in livestock can threaten animal welfare by increasing animal stress, inducing abortions, as well as decreasing overall herd productivity (Mohamed, 2020; Narrod et al., 2012; Saadiid et al., 2020). Such pathogens can also pose direct (i.e. human transmission) and indirect risks (i.e. economic losses) to human health (Alemayehu et al., 2021; Dorjsuren et al., 2020; Mohamed, 2020). Detecting and managing zoonotic pathogens remains challenging in many countries around the world, especially in emerging economies (FAO, 2020; Gebreyes et al., 2014; Paternoster et al., 2020; Thomas et al., 2020). For food production systems in developed economies, preventative measures such as surveillance are now a major focus (Narrod et al., 2012; Smith et al., 2017). Effective surveillance leading to early detection helps to circumvent mass livestock slaughter and quarantine necessary to prevent further spread of disease (Sobrinho and Domino, 2001). Current surveillance methods for zoonotic pathogens include the collection of excretory products or blood, the detection of antibodies (either directly from the animals or from a mouse model), Polymerase Chain reaction (PCR) based detection of species-specific pathogens, or pathogen identification via microscopy (Abdel-Moein and Saeed, 2016; Delpietro et al., 2001; Rathinasamy et al., 2021; Sulaiman et al., 2003; Vasco et al., 2016). These techniques are sufficient for individual zoonotic species identification; however, a greater resolution may be needed given that bacterial, fungal, and viral infections are often made up of complex mutualistic interactions among multiple species (Roossinck, 2015; Roossinck and Bazán, 2017). For this, screening samples using eDNA metabarcoding based on primers with a broader multi-taxonomic detection spectrum could offer support for current surveillance methods.

The ideal mechanism for zoonotic pathogen surveillance is to use standardised individual based sampling, where blood, tissue, faecal, or swab samples are taken from individual animals and tested for an array of pathogens (Brunner, 2020). However, such tests are simply not feasible in either the live export trade or the domestic market, where the large number of samples required makes this financially unfeasible. For instance, the live export trade in Australia alone for 2019–2020 saw 1.3 million cattle and 1 million sheep exported (LiveCorp, 2020). Instead, eDNA analysis of pooled samples from animal consignments is providing a cost-effective alternative, to detect both common and rare zoonotic pathogens with relatively few non-invasive samples (Brunner, 2020; Trujillo-González et al., 2019). Indeed, the early use of eDNA-based tools provided health measures for individual animals by analysing diversity of prokaryotes and fungi from ruminal digesta (Fouts et al., 2012). Since then, eDNA measures have been extended (e.g. to detect zoonotic *Leptospirosis* causing bacteria (*Leptospira*) with universal and species-specific assays in agricultural irrigation water and determine which vertebrate animals act as reservoir hosts, concluding that cattle (*Bos indicus*) and water buffalo (*Bubalus bubalis*) showed a high correlation with the pathogenic bacteria; Gamage et al., 2020). If broadly adopted, eDNA-based monitoring for zoonotic pests and pathogens could provide detections for individual farms and at border control points. In theory, by pooling faecal, urine, or swab samples and using multiple assays, scientists would be able to detect a range of zoonotic pathogens, something not currently possible for large animal consignments (i.e. detection of SARS-Cov2 from sewerage; see Tran et al., 2021) (Brunner, 2020; Carroll et al., 2018). Further research is needed to test and develop this concept, and to establish the optimal baseline number of samples from different substrates (i.e. faecal, urine, or swab) which can be pooled and still provide accurate detections. With this knowledge, eDNA detections could help diagnose emerging zoonotic pests and pathogens with accurate and timely assessments, allowing for preventative measures that benefit both animal welfare and herd productivity.

3.3. Soil health - soil microbiome, macrofauna, mesofauna, and the rhizobiome

Unlike most other agricultural monitoring efforts, DNA analyses have been the standard tool used to identify soil microorganisms for over two decades (Fig. 4) (Hugenholtz and Pace, 1996; Rolf, 2005). Primarily because many soil microorganisms are difficult to cultivate and identify with traditional methods (i.e. only 0.1–1 % of bacteria are culturable using traditional cultivation methods; Rolf, 2005). The DNA methods used to identify soil microorganisms are analogous to those used for eDNA and metagenomic studies, although these terms have been inconsistently applied in the soil literature (Taberlet et al., 2018). Here, we focus on soil studies in food production systems that use the term eDNA and measure taxonomic diversity of the soil microbiome (archaea, bacteria, fungi, and eukaryotes) (Figs. 3, 4 & Table 1).

Soil microbiome biological and functional diversity are intrinsically linked with plant health and productivity (Barrios, 2007; Delgado-Baquerizo et al., 2017). Biologically diverse soils help suppress soil-borne pests and diseases through predation, competition, and parasitism that in turn benefit crop growth (Barrios, 2007; Susilo et al., 2004). Agricultural intensification practices (i.e. tillage regimes, grazing, and weed management) can however reduce the complexity of these soil food webs, driving parallel reductions in pest and disease-causing pathogen suppression qualities (Adhikari et al., 2016; de Graaff et al., 2019; Tsiafouli et al., 2014). Practices which maintain and enhance soil biodiversity have therefore been identified as important elements of sustainable agriculture and global food security (FAO, 2020; Sarkar et al., 2020). Here, eDNA has enabled the classification of the major biotic components of soil microbiomes in agricultural systems, including archaea, bacteria, fungi and eukaryotes (Frøslev et al., 2021; Makiola et al., 2019; Wang et al., 2020). For example, Frøslev et al. (2021) collected bulk soil samples and amplified eDNA from bacteria, fungi and eukaryotes to determine if the tillage regimes associated with different agricultural practices changed soil biota composition and richness. Less intensive tillage regimes were found to only lead to minor compositional differences in soil microbiota, leading the authors to conclude that although reduced tillage can benefit soil diversity (see Brennan et al., 2006), this may not be the most appropriate strategy in all farming contexts. With greater adoption, eDNA-based monitoring of soil microbiome diversity could be a useful tool to identify soil biodiversity associated with different food production systems, which may ultimately help benefit crop productivity (de Graaff et al., 2019). Although currently there still remains a need to establish baselines for eDNA detections in soil (i.e. length of time eDNA is detected in soil; see Guerrieri et al., 2021). Integration of these baselines will help develop eDNA datasets which include temporal ranges for detections in various soil substrates (i.e. relative abundance of added *Escherichia coli* eDNA decreased by 98 % after 30 days in control clay-loam soils; see Morrissey et al., 2015). Together, the detailed eDNA community identifications and temporal ranges for the taxa detected could provide a useful tool for agricultural practitioners to help monitor their own soil biodiversity.

Microorganisms only form part of the total biodiversity present in soil, their larger invertebrate counterparts, soil mesofauna (> 40 µm) and macrofauna (> 1 cm) also significantly contribute to soil health, although these taxa are relatively unexplored in agricultural eDNA monitoring (7 % of all studies) (Blouin et al., 2013; Menta and Remelli, 2020; Orgiazzi et al., 2015). Current monitoring of soil meso- and macrofauna relies predominantly on morphological identification based on taxonomic keys (George et al., 2017; Gerlach et al., 2013), in contrast, eDNA-based detections offer a standardised high-throughput alternative to classify soil invertebrate diversity (Lanzén et al., 2017; Taberlet et al., 2012a; Todd et al., 2020). An early example is the use of taxa-specific assays to identify extracellular earthworm DNA from soil enabling classification of species assemblages (Bienert et al., 2012). Compared to the time consuming manual detections and morphological identifications typically used, eDNA surveys allowed for the complete description of earthworm communities collected from <50 g of soil (Bartlett et al., 2006; Bienert et al., 2012; Čoja et al., 2008). More recently, eDNA biomonitoring has been trialled to detect

differences in mesofauna communities associated with different horticultural crops. Here, universal and species-specific assays were compared with traditional monitoring in kiwifruit (*Actinidia* sp.) and apple (*Malus domestica*) orchards. Species-specific assays (100 % detection rate) and morphological analysis (40–100 % detection rate) performed significantly better than the universal assay (2.5 % detection rate) (Todd et al., 2020). These findings indicate that future meso- and macrofauna surveys may require universal assays which account for DNA degradation (see van der Heyde et al., 2020), or alternatively, morphological identifications can be combined with species-specific assays to survey both known and unknown diversity to increase the accuracy of eDNA biomonitoring. Further development of eDNA-based tools to detect soil invertebrate diversity will require testing in diverse agricultural and horticultural systems across broad and narrow geographic ranges to establish detection limits and verify assay specificity.

The complex microbial associations between plants and their immediate soil environment, the rhizobiome, are an essential component of plant health (Dessaux et al., 2016). These interactions not only help to maintain crop vigour, they also contribute to nutrition and reduce crop stress levels in some instances (Meena et al., 2017; Olanrewaju et al., 2018; Pandey et al., 2016). Thus, classifying the species composition of rhizobiomes associated with different agricultural and horticultural species has gained significant attention over the last decade (Berendsen et al., 2012; Castellano-Hinojosa and Strauss, 2021; Visioli et al., 2015). Although to date, monitoring rhizobiome diversity to inform management strategies for food production systems has remained relatively unexplored (Aloo et al., 2020; Caldwell et al., 2015). Recent studies have emerged demonstrating the potential of eDNA to identify these rhizospheres within agricultural ecosystems, with implications for developing new management strategies (Table 1). For instance, Sternhagen et al. (2020) used eDNA metabarcoding to show that the diversity of rhizosphere fungi associated with coffee plants (*Coffea* sp.) was lower in conventionally managed fields compared to organic fields. While, Epelde et al. (2020) highlighted that inoculation of lettuce (*Lactuca sativa*) with naturally occurring arbuscular mycorrhizal fungi increased yield without influencing the composition of co-occurring soil fungi. More eDNA studies are now needed to measure rhizosphere diversity across a greater diversity of crop species in different farming contexts (i.e. different soil types, fertiliser inputs, etc.). This information is crucial in developing practices that enhance either overall diversity or the presence of specific beneficial taxa (Dessaux et al., 2016; Pandey et al., 2016; Schmidt et al., 2020), ultimately increasing crop productivity.

3.4. Pollination - monitoring flower visitors

Wild pollinator numbers have more than halved in some areas of Europe and managed pollinators - typically the European honey bee (*Apis mellifera*) - are starting to mirror these losses with colony collapse reaching 30 % annually both in European nations and North America (Biesmeijer et al., 2006; Gray et al., 2020; Steinhauer et al., 2021). In China, the demand for managed pollinators in 2018 was three times the stock available, a problem predicted to worsen for an ecosystem service valued at US\$106 billion in 2010 (Mashilingi et al., 2021). Such pollinator declines are driven by a combination of habitat destruction, agro-chemicals, invasive species, climate change and disease, all of which place further pressure on future food security (Mbow and Rosenzweig, 2019; Potts et al., 2010, 2016; Sammartaro et al., 2000). An accurate assessment of the health of plant-pollinator networks within cultivated food systems is a crucial first step to prevent further losses (IPBES, 2019; Ricketts et al., 2008; Tylianakis et al., 2010; Van Zandt et al., 2020). Regrettably however, pollinator monitoring is insufficient in many areas because observing flower visitors and identifying pollen grains are time-consuming practices that require specialist taxonomic expertise which are becoming increasingly rare (Bell et al., 2016; Bosch et al., 2009; Howlett et al., 2018; Van Zandt et al., 2020). eDNA biomonitoring has the potential to greatly increase the capacity to study flower-visitor interactions through accurate analyses of large sample

numbers, less need for taxonomic expertise, and an ability to detect rare plant-insect interactions (Evans and Kitson, 2020; Pornon et al., 2017; Thomsen and Sigsgaard, 2019). Thomsen and Sigsgaard (2019) were the first to use this approach for biomonitoring in a diverse grassland ecosystem in Denmark. They used two assays to identify 135 arthropod species from >60 families, representing insect pollinators, parasitoids, and predators. This successful broad-scale community assessment based on a non-invasive approach supports the concept of using eDNA to identify flower-visiting insects (Evans and Kitson, 2020). This is especially true for the identification of unmanaged pollinators, which are often less well-known, but, regarded as equally important pollinators for many crop species.

Unmanaged non-bee pollinating taxa have typically been omitted from crop pollination studies (Rader et al., 2016). Consequently, little is currently known about the services they provide or how they are impacted by anthropogenic stressors (Biesmeijer et al., 2006; Garibaldi et al., 2013; Potts et al., 2010; Rader et al., 2016). In an agricultural context, this means that pollination services are often increased only through greater hive numbers, rather than by encouraging native pollinators (Pardo and Borges, 2020; Potts et al., 2010; Rader et al., 2016). eDNA-based monitoring offers a means to help bridge this knowledge gap (Evans and Kitson, 2020). For example, eDNA metabarcoding data obtained from pollen collected by moth species has helped classify the often unobserved nocturnal pollen transport networks within a farmland site (see Macgregor et al., 2019). Metabarcoding analyses increased the number of known pollen types per moth species and resulted in the assembly of more complex flower-visitor networks than could be achieved by traditional microscopy techniques. Similarly, eDNA-based surveys have helped classify a broader range of host plant species and foraging resources for an economically damaging pest species, the turnip moth (*Agrotis segetum*), than had previously reported (see Chang et al., 2018). The use of eDNA to monitor pollinators and flower-visitors is still in its infancy for agriculture and horticulture, although the field is rich with open questions that could be answered with this technology. For example, vertical and horizontal stratification of unmanaged flower-visitors can significantly impact fruit production as a consequence of competition and predation (Cook and Power, 1996; Wyatt, 1983). Despite this, fine-scale variation is rarely measured during agricultural pollinator monitoring (Frimpong et al., 2011; but see Krishnan et al., 2014). Use of eDNA-based monitoring for flower samples collected at different horizontal and vertical stratification levels could help identify if variation exists for flower-visitor cohorts within cultivated tree canopies. This merits investigation because such information could be used to help develop new management practices, such as reducing canopy density, which may encourage more pollinator visitations (managed and unmanaged) and potentially increase yield.

4. Limitations, and how to overcome them

eDNA biomonitoring is already demonstrating potential to classify the biodiversity associated with plant, animal and soil health (i.e. classifying meso- and macrofauna diversity in orchard soils; Todd et al., 2020), and to aid in the early detection of invasive pests and pathogens (i.e. detecting Hemiptera pest species from honey; Utzeri et al., 2018) before large-scale outbreaks occur. Such information may enable improved accuracy of evidence-based decision making to inform orchard, farm and vineyard management practices. Despite these prospects, a number of potential pitfalls are associated with the collection, amplification and interpretation of data from environmental samples collected from agricultural systems (Ruppert et al., 2019; Taberlet et al., 2012b). The technical challenges of eDNA-based surveys include; contamination (Olds et al., 2016), false positives (Ficetola et al., 2015, 2016), false negatives (Ficetola et al., 2015), incomplete databases (Jackman et al., 2021), and degraded DNA (Deagle et al., 2006; Goldberg et al., 2018), each of which has been reviewed extensively. Below, we focus on some of the limitations that may currently prevent an efficient implementation of eDNA technology as a

biomonitoring tool in agricultural systems, and a discussion of the possible solutions currently available or on the horizon.

4.1. DNA deposition and degradation

A better understanding is needed of the mechanisms by which DNA is released into the environment, and how its persistence is affected by various factors in order to take full advantage of eDNA-based biomonitoring technology. These factors include time, chemistry of the local environment (i.e. soil, gut contents, water), UV levels, temperature and microbial presence (Dejean et al., 2011; Levy-Booth et al., 2007; Nielsen et al., 2007). Fast DNA degradation has the potential to create false negative results (i.e. an apparent absence of taxa that are actually present) which can confound biodiversity assessments and lead to incorrect interpretations of community assemblages (Foote et al., 2012; Harrison et al., 2019; Thomsen and Sigsgaard, 2019). For instance, Todd et al. (2020) attempted to analyse soil eDNA collected from two orchards using universal metabarcoding primers which amplified the entire COI gene (710 bp, Folmer primers; Folmer et al., 1994). Likely due to the deterioration of eDNA in the soil environment, this relatively large DNA fragment could not be PCR-amplified (see Jo et al., 2021), meaning that the diversity of ecologically important taxa captured from the metabarcoding results was significantly lower when compared to the results from species-specific PCR assays and manual surveys. Valentin et al. (2021) reported similar results on leaf surfaces with 3 μ L of *Halyomorpha halys* eDNA added. Here, simulated rainfall events were found to reduce detection rates by 75–100 %, while exposure to high UV levels meant that extracellular *H. halys* eDNA could not be detected after four days of full-sun treatment. Amelioration of such issues requires the use of assays which target a range of amplicon sizes to account for DNA degradation (e.g., Haile et al., 2009), or some adaptation of a shotgun sequencing approach where even very short DNA fragments can be sequenced. Further, if a specific taxon is of interest, then species-specific assays should be used for detections rather than relying on universal assays that may have low affinity for certain taxa and also amplify non-target DNA (Saccò et al., 2022). As well as tailoring assay design, establishing detection thresholds for target taxa can also aid in authenticating the taxon identifications generated from eDNA biomonitoring.

Detection thresholds established with pilot studies are occasionally used to determine how long eDNA remains detectable and what sized fragments amplify successfully after exposure to locally relevant factors (i.e. low and high UV levels) (Mächler et al., 2016; Poudel et al., 2019). For eDNA-based tools in agriculture, such information helps provide a temporal range for the detected species or community of interest. For instance, eDNA is unstable in high moisture, high temperature, tilled soils where universal bacterial primers were unable to amplify added DNA (> 99 %) within 7 days because the fragments had degraded beyond the point of amplification for the chosen assay (Sirois and Buckley, 2019). With such information available, long term soil biomonitoring for agricultural regions with higher rates of DNA decay (i.e. tropical countries) could account for more degradation (and increased chances for false negatives) by sampling more frequently and using assays that target shorter DNA fragments (van der Heyde et al., 2020). Goldberg et al. (2018) has recommended that optimised eDNA sampling to account for degradation and dispersion requires data on eDNA production, the space covered by the taxon of interest, and the removal rate of DNA from the system under study (i.e. DNA degradation due to acidic conditions). Similar principles could be applied to eDNA-based monitoring in food production systems to increase the spatial sampling density when DNA degradation is significant or when a conservative approach is needed to capture a rare taxon. Furthermore, as modern agricultural production systems typically include high levels of mechanisation, there are opportunities to design high coverage and high frequency sampling methods that utilise or complement existing machinery and infrastructure. Together these approaches could enable greater accuracy and reproducibility of species detections for orchards, farms, and vineyards.

4.2. Assay development and biased amplification

To date, the assays used to target biological organisms within agricultural systems have generally provided broad-community, rather than taxon-specific monitoring (13 % of studies) (Table 1). Assay development is restricted when the target taxa are largely undescribed, known as the Linnean shortfall (Lomolino, 2004). Such shortfalls are common in both microorganisms (i.e. only 3–8 % of all fungi described; Hawksworth and Lücking, 2017) and macroorganisms (i.e. only 20 % of all insects described; Stork, 2018). In the context of agricultural communities, microorganisms, unmanaged pollinators, and pests composed largely of unknown species may be missed if the assays used for such classification are too narrow, leading to incomplete community descriptions (Evans and Kitson, 2020). Instead, combinations of assays are needed to target the full variety of taxa present within these ecosystems. This approach is referred to as the ‘needle vs haystack’, where the ‘haystack’ metabarcoding (using universal assays) generates sequences from a broad range of taxa to assess complete diversity (generally at the genus or family level) for environmental samples (i.e. using fungal Internal Transcribed Spacer region 2 fragment to target airborne fungal spores; Tordoni et al., 2021). Although it should be noted that universal assays are not a ‘silver bullet’ and can show taxonomic biases (i.e. COI, a universal primer used for insects, has been shown to amplify only 62 % of invertebrates; Horton et al., 2017) and therefore must be thoroughly tested (in silico, in vitro, and in vivo) prior to monitoring (Saccò et al., 2022). While, the ‘needle’ (using taxon-specific markers) approach generates sequences specific to individual species or group contained in the ‘haystack’, i.e. use of species-specific assay that targets the marmorated stink bug (*H. halys*) from fruit wash water; see Valentin et al., 2018) (Saccò et al., 2022). This taxon-specific approach is, however, particularly prone to the knowledge gaps associated with Linnean shortfalls. Meaning that researchers may wish to use both the ‘haystack’ and the ‘needle’ to investigate a community of interest; specific taxonomic groups are targeted using universal assays that simultaneously capture the many unknown taxa present in environmental samples. The unknown organisms can then subsequently be described using traditional methods and targeted using the species-specific assays if they are of relevance to the orchard, field, or vineyard being surveyed (i.e. emerging pathogen or pollinator).

Biased amplification of specific sequences and the complete failure of other sequences to amplify can prevent effective detection of target species and communities from environmental samples. Although metabarcoding has the potential to detect multiple taxa from complex samples, the universal assays used for such broad assessments can often under-represent or entirely miss particular taxa (Clarke et al., 2014). In part, this issue arises when the homologous regions targeted and amplified by universal assays are not equally conserved across all taxonomic groups. The resulting sequence variation (i.e. base mismatches) can lead to the biased amplification of certain taxa or prevent amplification entirely (i.e. no bee taxa sequences amplified from vineyard insect traps despite visual confirmation of bees in the traps; Rasmussen et al., 2021) (Bellemain et al., 2010; Rodgers et al., 2017). These incomplete community descriptions can, if not corrected by manual verification, then misinform management decisions for agricultural practitioners (i.e. unnecessarily increasing bee colony numbers; Ritten et al., 2018). The choice of which universal assay to use is therefore dependent on the presence and suitability of a conserved target locus as well as the availability of target reference sequences (Saccò et al., 2022). With the target locus chosen, the following should be considered for the design and validation stage of metabarcoding assays: i) desktop-based in silico validation - collect reference sequences and identify sympatric, and confounding taxa, then design an assay specific to the taxa of interest using tailored design software (i.e. Primer3 or Primer Premier); ii) lab-based in-vitro validation - synthetic or organic DNA for the taxa of interest at low concentrations to confirm high PCR sensitivity; and iii) field-based in-situ validation - consideration of assays with locally relevant degradation and inhibition found in environmental samples (Harrison et al., 2019; Langlois et al., 2021; Saccò et al., 2022). Taking into account these

considerations, assays can be developed which minimise the potential for biased amplification and generate reliable detections for informed management decisions.

4.3. Incomplete databases

Inferring taxonomic nomenclature using eDNA for agricultural ecosystems ideally requires the members from the community of interest to have assigned taxonomic ranks, voucher specimens identified and sequence data available (Saccò et al., 2022). The two most widely used databases which contain this information are GenBank and the Barcode of Life Data System (Meiklejohn et al., 2019). Although given the Linnean shortfall and that new species are continually being discovered, direct or even closely related sequence data may not be available in the current databases for the organisms under study (Saccò et al., 2022). Indeed, Aizpurua et al. (2017), when monitoring pest insect species in agricultural landscapes using eDNA, were unable to assign species-level identifications to 53 % of the samples collected. This limited the conclusions that could be made about shifts in dietary niche of pest-feeding bats in agricultural landscapes across Europe. For eDNA-based monitoring more broadly, the absence of pest and pathogen sequences could lead to false negatives and potentially fail to identify emerging pest/pathogen outbreaks (Jones, 2009; Valentin et al., 2016). Unfortunately, sequences available on public databases may still be subject to issues such as: incorrect taxonomy, sequence coverage variation (i.e. species barcoded for only one loci), or sequence data without species level taxonomic rank assignment (Saccò et al., 2022). Overcoming these knowledge gaps and inherent database issues can require in silico verification, the creation of custom databases, or the use of degenerate secondary assays.

Reference databases need to be assessed with in silico studies to determine if the taxa of interest (if known) have been sequenced for the chosen barcode loci (Bylemans et al., 2018). This desktop search helps identify if the taxa of interest are well represented in online databases or require the creation of a custom Barcode Reference Library (BRL) (Ruppert et al., 2019; Taberlet et al., 2012b). Custom BRLs are traditionally created by Sanger sequencing target barcode loci from voucher specimens, these custom barcodes are then incorporated into the chosen bioinformatic pipeline (i.e. OBITools, Barque or QIIME 2; see Mathon et al., 2021) with Basic Local Alignment Search Tool (BLAST) to provide taxonomic identifications (Kress et al., 2015). Although a limitation to this approach is the significant expense and time commitment required in diverse agricultural ecosystems where large numbers of unknown taxa have to be sequenced. An innovative alternative is to use genome skimming to produce custom BRLs from many vouchered specimens (Nevill et al., 2020). If voucher specimens are not available however, or low-cost alternatives are needed, in silico studies and emerging GAPeDNA databases can provide an overview of genetic completeness for a given taxon (see Marques et al., 2021). With this information, a lower resolution secondary assay can be used to generate Family or Order level taxonomic assignments from eDNA samples (i.e. Leese et al., 2021). In the case of Aizpurua et al. (2017), the authors overcame the need to make a local reference database with a secondary low resolution assay to cross-reference species assignments and determine which taxa were missed. Verification may also be possible with traditional methods (i.e. Macgregor et al., 2019; Todd et al., 2020). With these approaches, eDNA-based monitoring for food production systems can generate community data without sequence data necessarily being available for all of the taxa present.

4.4. Abundance data

Multi-species reads generated from eDNA samples cannot currently be used to estimate taxonomic abundance or population size for complex environmental samples (Fonseca, 2018; Ruppert et al., 2019). Each PCR reaction in the metabarcoding workflow is unique (i.e. differences in chemistry, primer mismatch, see Cha and Thilly, 1993), meaning Operational Taxonomic Unit (OTU) reads cannot currently be compared

quantitatively (Fonseca, 2018). Instead, the data generated from eDNA monitoring provides presence/absence measures for specific taxa and semi-quantitative results (i.e. weak versus strong interactions) (Ficetola et al., 2008; Pornon et al., 2016, 2017). These data can be used to infer relative abundance and commonality for the taxa of interest (i.e. universal fungi assay used to determine relative abundance of natural arbuscular mycorrhizal fungi in managed and unmanaged soils; Epelde et al., 2020). However, some have argued that quantitative counts for populations and taxonomic abundance still remain the gold standard (Blanchet et al., 2020). New statistical methods are still being developed for eDNA presence/absence data to help derive ecologically meaningful conclusions, these include; occupancy models to account for imperfect detections of specific taxa (Dorazio and Erickson, 2017; Doser et al., 2022), multiview modelling for relative abundance estimation (Williamson et al., 2021), generalised dissimilarity modelling of zeta diversity (Latombe et al., 2017), and joint species distribution modelling for inference of biotic interactions and conditional prediction (Poggiato et al., 2021). Although, as far as we are aware, none of these new statistical methods have been used in the eDNA studies for agriculture found in this review.

Integration of cross-validation techniques as well as alternative technologies to quantify DNA copy numbers may help to increase the robustness of eDNA surveys and generate abundance data. The first, and most relatively straight forward approach is to incorporate traditional surveys (i.e. visual observation) with eDNA surveys, thereby maximising the taxonomic breadth afforded by eDNA while also obtaining abundance data to inform on the strength of ecological interactions (Kelly et al., 2017; Schmidt et al., 2013). Alternatively, researchers may wish to use multiple species-specific assays combined with droplet digital PCR (ddPCR) (Capo et al., 2021). This approach can be used to quantify the number of DNA sequences and estimate population abundance for the taxa of interest, although recent studies have shown considerable unexplained variation in these estimates (Capo et al., 2021; Mauvisseau et al., 2019). A third solution may be to add one or multiple generic internal standards (ISDs) (i.e. synthetically designed DNA molecules; see Harrison et al., 2020) to all samples prior to qPCR in known absolute abundance (i.e. number of moles of a DNA molecule) (Ushio et al., 2018). Through comparison to the ISD, the relative abundance of target eDNA can be converted into DNA copy numbers (see Harrison et al., 2020; Ushio et al., 2018), potentially allowing for more accurate population abundance estimates for the target taxa. We envisage a combined methodology, where eDNA could be used with universal assays to detect organisms of interest, which could then be counted using either traditional surveys, estimated using multiple species-specific assays with ddPCR or estimated by spiking in ISDs to samples prior to qPCR to estimate population sizes, allowing managers to determine the most appropriate management strategy for the taxa of interest in their orchard, farm or vineyard.

5. Future prospects

Applications of eDNA biomonitoring for agriculture are already aiding in the detection of pest and pathogenic species, as well as the classification of soil microbial biodiversity. More recent applications have emerged with biomonitoring of flower-visitors and soil meso- and macrofauna. The field of eDNA biomonitoring for food production systems is burgeoning, with new innovations and areas for future research (Fig. 2). The topics of research listed below are nascent; however, their continued development holds exciting potential for eDNA-based monitoring to enable more sustainable cultivated food systems and aid global food security.

5.1. Air eDNA

Isolation of eDNA from air is a novel survey method capable of detecting and characterising taxa from airborne particles (Folloni et al., 2012; Johnson et al., 2019a). Initial air eDNA studies targeted airborne pollen (Kraaijeveld et al., 2015; Longhi et al., 2009) and spores (Pashley et al., 2012; Williams et al., 2001) using aerobiological tape and vacuum

pumps. Since then, eDNA has been used to characterise trace amounts of airborne DNA from microbes, plants, fungi, and animals in a variety of systems (Clare et al., 2021; Johnson et al., 2019; Tong et al., 2017; Tordoni et al., 2021). These detections may otherwise remain unknown given that some taxa cannot easily be identified from conventional monitoring or cultivating methods (Folloni et al., 2012; Tong et al., 2017; Tordoni et al., 2021). Although studies targeting air eDNA still remain relatively rare in both the eDNA literature more broadly and agriculture (Clare et al., 2021; Johnson et al., 2019). Namely, eDNA captured from the air accounted for only 7 % of substrates targeted in agricultural studies (Fig. 3 & Table 1). These studies and those undertaken in other human-modified ecosystems do however provide a blueprint for future research to identify airborne DNA in the context of food production systems. For instance, Tong et al. (2017) illustrated that eDNA from archaea, bacteria, fungi and viruses could be collected from active air samplers indoors. This technique could be used to identify airborne microorganisms associated with zoonotic diseases within indoor livestock facilities, such as poultry markets, where disease-causing pathogens circulate but adequate surveillance remains an issue (Lu et al., 2021). Using eDNA to capture signals of emerging pathogens could provide an early warning system to identify the presence of pathogens and potentially isolate infected animals before widespread transmission occurs. Such techniques may also apply to cropping systems, where air eDNA could be used for timely detection of economically damaging weed species. Airborne plant material (vegetative fragments, pollen, etc.) can be captured and targeted with eDNA-based surveys to provide taxonomic classifications for local plants, without them necessarily being in flower (Johnson et al., 2019b). In crop fields, air sampling could provide a fine-scale presence/absence measure of weed species which are often difficult to detect in low numbers (Emenyeonu et al., 2018). Such a resource may help inform managers where infestations are emerging and support targeted herbicide applications. Although for now, more studies are needed to determine the basic characteristics of air eDNA (i.e. fragment sizes and taxonomic identity) as well as the abiotic conditions which influence DNA molecule persistence in the atmosphere (Clare et al., 2021; Johnson et al., 2019). Thus, one of the primary questions for cultivated ecosystems is can air eDNA reliably provide taxonomic detections in farms, orchards and vineyards across a variety of different climates, which may have implications for how much eDNA can accumulate and persist in air (i.e. comparison of air eDNA composition in tropical and temperate farmlands).

5.2. Organic sentinel monitoring

Biological organisms harnessed as sampling units for the intermediary organisms that they interact with (organic sentinels) could provide an unparalleled ability to measure microcosms which make up agricultural systems (Bromenshenk et al., 1985, 2015; Gregorič et al., 2022; Halliday et al., 2007). Two examples which are relevant to food security include eDNA classifications obtained from within managed beehives and using trace amounts of DNA to detect plant pests and diseases (Sammataro et al., 2000; Tremblay et al., 2019; Utzeri et al., 2019). Managed bee species are currently the most important animal pollinators for cultivated plant species, and safeguarding their services is considered essential for food security (IPBES, 2019; Lautenbach et al., 2012). When foraging for pollen, bees incidentally collect pathogens that can subsequently be transmitted to the hive (i.e. chalkbrood disease caused by *Ascosphaera apis*) (Goulson and Hughes, 2015; Pereira et al., 2019). These pathogens are associated with conditions that range from declines in sexual reproductively to increased mortality rates, and can ultimately serve to reduce pollination services in surrounding crop species (Genersch et al., 2010; Lach et al., 2015; Pereira et al., 2019; Sammataro et al., 2000). Pathogen classifications using eDNA could help address this issue, potentially allowing for detections that may otherwise be difficult to achieve at the scale of food production systems.

At least 39 viruses and some fungal pathogens use pollen grains as an intermediary between host plants (Card et al., 2007). By collecting pollen, and foraging between flowering agricultural species, honeybees can

inadvertently act as a vector for these plant pathogens, which can reduce yield and quality of produce (Card et al., 2007; Dodd et al., 1990; Tremblay et al., 2019). Given that the interactions between bees, and the plants that they pollinate can have such a significant influence on plant productivity, and that they exhibit predictable and consistent behaviour, their use as organic sentinels merits investigation (Bromenshenk et al., 1985, 2015). By placing sterilised filter paper at the entrance of a beehive, where the paper would come into direct contact with the bees themselves, as well as the pollen on their bodies, researchers could amplify the trace amounts of parasite and pathogen eDNA collected during foraging in crop fields (Tremblay et al., 2019; Utzeri et al., 2019). With this approach, eDNA-based tools could provide early detections for both significant bee pathogens present in the hive and potentially plant diseases in the fields that the bees are servicing.

5.3. DNA sequencing in the field

Taking eDNA biomonitoring out of the laboratory and into farms, orchards and vineyards offers a rapid means to monitor organisms, while simultaneously reducing processing costs (Boykin et al., 2019; Loeza-Quintana et al., 2020). Significant expenses are associated with high-throughput lab-based sequencing platforms, especially with the input of skilled technicians required for successful data generation (Skinner et al., 2020; Thomas et al., 2019). Not only are laboratory costs expensive, but the processing times for eDNA samples can also take weeks or sometimes even months depending on the number of samples and assays, often requiring refrigeration and taking samples back to the lab, potentially delaying opportunities for rapid detections (Loeza-Quintana et al., 2020; Nguyen et al., 2018). In agriculture, real-time monitoring is often critical for timely and informed management decisions, especially when monitoring disease-causing pathogens and pest outbreaks (Badial et al., 2018; Boykin et al., 2019; Valentin et al., 2018). Portable PCR machines (i.e. Field-portable quantitative PCR (qPCR)) and sequencers (i.e. Oxford MinION) were initially used as a human-point of care tool for disease diagnostics (Marx, 2015; Nguyen et al., 2018; Quick et al., 2016). Now these portable technologies are being utilised as a diagnostic tool for invasive species and pathogens with implications for food production. Badial et al. (2018) were the first authors to successfully detect crop pathogens from infected plant tissue and insect vectors using the portable Oxford MinION sequencer. In contrast to the standard immune assays and multiplex PCR used to detect plant pathogens, the Oxford MinION could detect a larger number of possible target pathogens in less than two hours. This technology has been trialled on small-scale cassava farms in sub-saharan Africa, where researchers were able to generate on-the-spot pest and disease diagnostics within one day (Boykin et al., 2019). Similarly, field-portable qPCR tools used in combination with species-specific primers, have been used to streamline a workflow that traditionally required three days on the lab bench into <60 min (Thomas et al., 2019). The information generated from these rapid tests could be used to help identify specific pathogens at fine spatial scales, thereby enabling targeted pesticide applications while also reducing expenditure and minimising environmental harm (Badial et al., 2018). In the future, this technology could be extended to rapidly assess other taxa of economic value (i.e. wild pollinators, soil biodiversity, etc.) within food production systems when linked with appropriate sampling techniques (i.e. sampling air, honey or soil). Used in combination with improved bioinformatic pipelines (i.e. PEMA; see Pafilis et al., 2020, and eDNAFlow; see Mousavi-Derazmahalleh et al., 2021), portable PCR and sequencing technologies hold great potential for eDNA in food production systems, although much work is required to establish the protocols and limitations of these technologies.

5.4. Equitable eDNA monitoring - LAMP assays

eDNA-based monitoring requires precision equipment as well as ultra-clean laboratories (Ficetola et al., 2016; Yoccoz et al., 2012). Unfortunately, these equipment and facilities are typically underrepresented in developing

countries where food security concerns are often greatest (FAO, 2020; Hamdi et al., 2021; Mbow and Rosenzweig, 2019). Likely this is also the reason for the low number of eDNA studies found in emerging economies (Fig. 3). Low-cost equivalents for eDNA biomonitoring are therefore needed for the countries in greatest need of this technology, but who may lack the necessary infrastructure (Ibaba and Gubba, 2020). Loop-mediated isothermal amplification (LAMP) assays may provide one such alternative by allowing for the identification of individual species without the need for laboratories, PCR machines, or high-throughput sequencers (Ahuja et al., 2021; Davis et al., 2020; Notomi et al., 2000). Using only species-specific assays, DNA polymerase, a water bath/heating block, as well as a stain or dye, researchers have been able to identify the presence/absence of species of interest from eDNA samples (Davis et al., 2020; Notomi et al., 2000; Quyen et al., 2019). To date, LAMP assays have been used to detect a wide variety of plant and animal pathogens predominately in natural settings (Ahuja et al., 2021; Deng et al., 2019; Panno et al., 2020). While more recently, the technique has successfully been used within an agricultural context to measure the presence of an intermediary host species (*Galba truncatula*) for two trematodes (parasitic flatworm); *Fasciola hepatica* and *F. gigantica*, both of which cause the potentially fatal Fascioliasis disease in livestock (Davis et al., 2020; Deng et al., 2019). Although in the developmental stage, the potential to use LAMP assays in combination with multiple species-specific markers (one marker per reaction) could provide a low-cost counterpart for conventional eDNA-based monitoring in agricultural ecosystems. If successfully implemented, this technology could aid in the timely detection of known plant and animal pathogens, hopefully helping prevent pest and disease outbreaks for food production systems in both developed and emerging economies.

6. Conclusion

Given the extensive use of eDNA in natural systems, biomonitoring using eDNA in agricultural systems is underutilised despite it being a potentially powerful tool to measure a wide variety of microcosms (Fig. 5). Applications of this technology in food production systems are still in their infancy, with the exception of the soil sciences (Fig. 4), and the field remains wide open for future eDNA applications for both cultivated plants and domesticated animals (Figs. 2 & 3). Here, we have highlighted the growing number of studies that are now identifying specific species, monitoring communities, and rapidly detecting pests and pathogens in agriculture (Fig. 4). We acknowledge that there are limitations to using eDNA for species identifications and detections within food production systems, and that as a consequence, applications of eDNA will not be equally effective in all settings and that current traditional and other molecular methods will still be the best practice in such cases (i.e. Todd et al., 2020). However, we argue that with further research into the locally relevant conditions for eDNA degradation, adequate pilot studies, and the development of local reference libraries, eDNA-based tools will offer a strong complement for current monitoring methods, and merits further integration into agricultural systems. In the future, eDNA is likely to include; unmeasured microcosms, sequencing in the field, as well as the wide-spread uptake of cost effective equivalent techniques. With such expansions, eDNA will offer a powerful tool to help maintain and increase food production with the ultimate goal of helping achieve more widespread food security for food production systems in developed and emerging economies alike.

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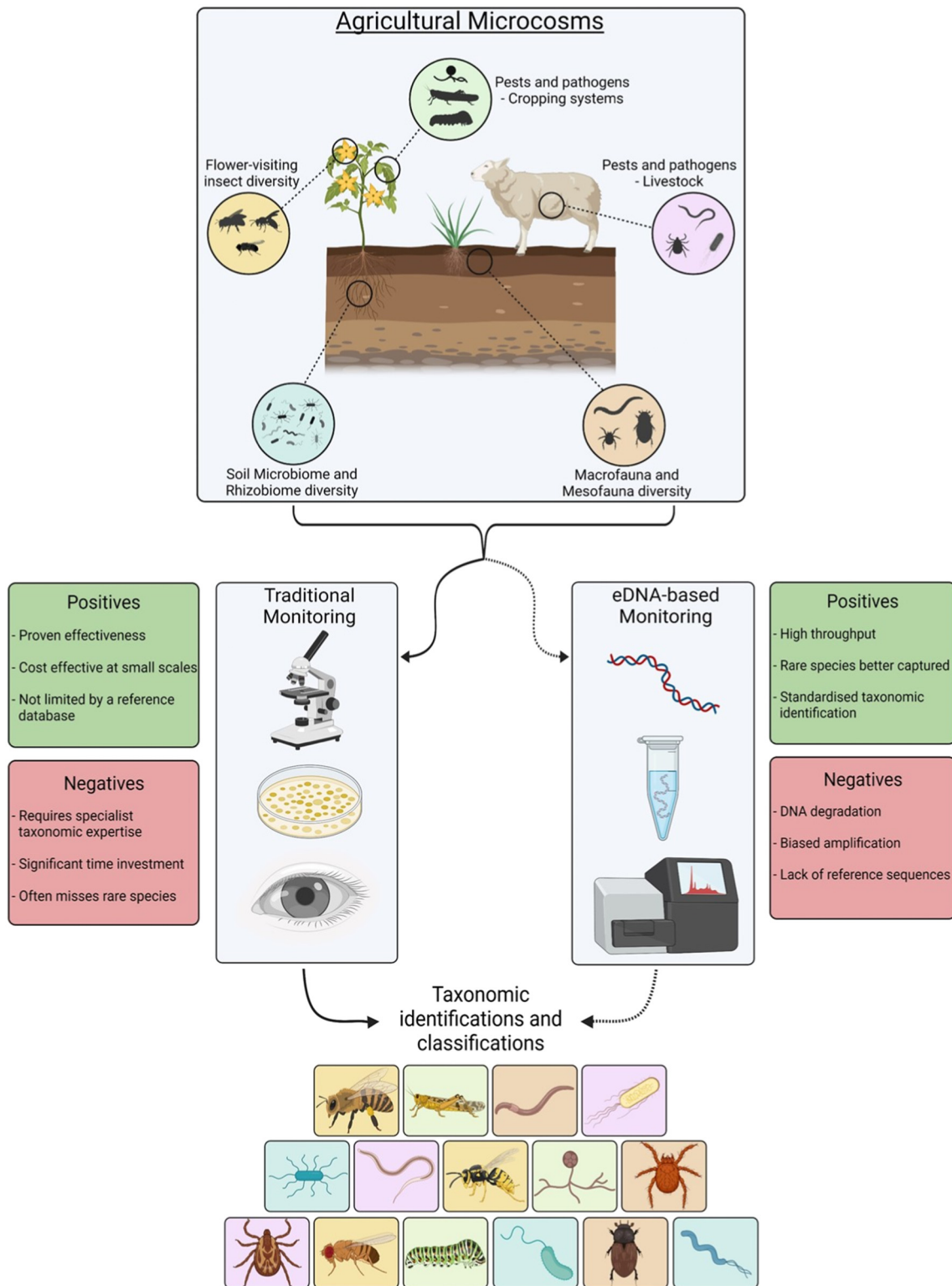


Fig. 5. Current and emerging monitoring techniques for agricultural microcosms. Substrates presented are currently being monitored using both traditional and eDNA-based monitoring to detect mutualistic (i.e. pollinators) and antagonistic species (i.e. pathogens). The potential to further incorporate eDNA-based monitoring (dashed line) to support current methods (solid line) would greatly aid in taxonomic identifications and hopefully improve monitoring for food production systems. Both techniques are presented with some of the major pros and cons which have been identified here, and in other studies (Kelly et al., 2017; Pornon et al., 2017; Rasmussen et al., 2021; Todd et al., 2020). Graphic created using BioRender.

CRediT authorship contribution statement

Joshua H. Kestel: Conceptualization, Methodology, Visualization, Writing – original draft. **David L. Field:** Writing – original draft, Writing – review

& editing. **Philip W. Bateman:** Conceptualization, Methodology, Writing – original draft. **Nicole E. White:** Writing – original draft, Writing – review & editing. **Morten E. Allentoft:** Writing – review & editing. **Anna Hopkins:** Writing – review & editing. **Mark Gibberd:** Writing – review & editing.

Paul Nevill: Conceptualization, Writing – original draft, Methodology, Writing – review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Glossary

Amplicon: The gene region and size chosen to be amplified. Amplicon size choice is based on how conserved the chosen gene region is for the taxa of interest, as well as the deterioration of the sample; degraded samples are often targeted for shorter amplicons, while extant samples can be targeted for longer amplicons.

Assay: The combination of primers used to achieve either species-specific or multi-species identifications.

DNA reference database: Compiled DNA sequences for the barcode region of choice for identified specimens.

Environmental DNA: Any extracellular DNA isolated and characterised from biological substrates including; soil, scats (faeces), plant material and water.

eDNA monitoring: Monitoring using trace amounts of degraded DNA fragments from biological substrates to provide either single (barcoding) or multi-species identifications (metabarcoding).

Food security: The physical, social and economic access to safe and nutritious food.

Metabarcoding: Amplification, sequencing and alignment of multi-species identifications from an environmental sample.

High-Throughput Sequencing (HTS) technologies: Massively parallel or deep sequencing platforms able to generate reads from millions of DNA fragments simultaneously.

OTU: A molecular Operational Taxonomic Unit (OTU) assigned to an organism or group of organisms based on sequence similarity to a reference sequence (generally over 97 %).

Pathogen: An organism capable of causing host damage and disease.

Pest: An organism that damages, destroys or transmits/causes disease which harm species or alter the structure and functioning of natural or anthropogenic ecosystems.

Primer: Species-specific or universal primers are used which amplify conserved regions present at the level of phylum, order, family, or genus. For a universal primer, a standardised locus with highly conserved priming sites is amplified from the target DNA; the resulting amplicons contain sufficient variability to assign taxonomic identifications. While for a species-specific primer, a gene region is chosen which is divergent from other closely-related species and able to provide species differentiation.