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REVIEW ARTICLE

Advances in insect biomonitoring for agriculture and forestry

Metabarcoding advances agricultural invertebrate biomonitoring by enhancing resolution, increasing throughput and facilitating network inference

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Abstract

1. Biomonitoring of agriculturally important insects is increasingly vital given our need to understand: (a) the severity of impacts by pests and pathogens on crop yield and health and (b) the impact of environmental change and land management on insects, in line with sustainable development and global conservation targets.
2. Traditional entomological traps remain an important part of the biomonitoring toolbox, but sample processing is laborious and introduces latency, and accuracy can be variable. The integration of molecular techniques such as environmental DNA and DNA metabarcoding into insect biomonitoring has gained increasing attention, but the advantages of doing so, the kind of data this can generate, and how easily and effectively molecular analyses can be integrated with the diverse types of entomological traps currently used remains relatively unclear.
3. In this review, we examine how combining DNA metabarcoding with a range of conventional and unconventional entomological sampling techniques can advance biomonitoring in a way that is useful to researchers and practitioners. We highlight some of the key challenges and how to mitigate them, using examples of its integration with different sampling methods from the literature (e.g., interception, pitfall and sticky traps) to demonstrate efficacy and suitability.
4. We discuss how metabarcoding data can be used to infer ecological networks, emphasizing the importance of this as a framework for understanding species interactions and ecosystem functioning for more effective and descriptive biomonitoring.
5. Finally, future advances in biomonitoring are highlighted, alongside recommendations of best practice for researchers both new to and experienced in invertebrate biomonitoring with metabarcoding.

KEYWORDS
agroecosystems, entomology, environmental DNA, high-throughput sequencing, insects, molecular ecology, surveys, trapping

INTRODUCTION

Assessing the condition of biodiversity in agroecosystems is a global priority. It is vital to tackle the parallel issues of biodiversity decline and food insecurity, which are amongst the greatest challenges of the 21st century (Fischer et al., 2017). Invertebrate functional groups and their contributions to food production are crucial to monitoring; an example of this is the pollinator investigation by the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Service (IPBES, 2016). Investigations like those of the IPBES are carried out to inform policies (Dicks et al., 2016), particularly to meet biodiversity targets, such as Target 10 of the Kunming-Montreal Global Biodiversity Framework (Convention on Biological Diversity, 2022), which aims for sustainably managed areas of agriculture, aquaculture, fisheries and forestry to contribute to secure and resilient food production systems. In a European context, Hochkirch et al. (2023) highlight that 24% of invertebrates are at risk of extinction, with proposed mitigations including changes to agricultural practices and associated habitat loss. Incentivised agricultural land interventions are crucial for meeting these targets, for example, the UK Environmental Land Management Schemes (ELMs), developed to encourage interventions to promote invertebrate biodiversity, and, consequently, ecosystem services (Department for Environment, Food, & Rural Affairs, 2023). Ensuring that the desired outcomes of these initiatives are achieved requires measurable evidence, for which assessment of agricultural interventions through biomonitoring is imperative (Biodiversa+, 2023; Boetzl et al., 2021; Høye et al., 2023).

Invertebrate biomonitoring is a key part of ecological research, agricultural and forest management, and biodiversity conservation. Reasons include measuring and assessing biodiversity, tracking invasive species (Piper et al., 2019), investigating impacts of environmental change (Fernandes et al., 2019) and, perhaps most commonly, detecting and managing pests and beneficial insects in agriculture and forestry (Breeze et al., 2021; Cardim Ferreira Lima et al., 2020; O'Connor et al., 2019). The many conventional sampling methods used for biomonitoring (e.g., pan, malaise and pitfall traps) can be grouped based broadly on the strata of target organisms or by units/measure of detection (i.e., species abundance or activity density; Figure 1). Taxonomic biases are associated with each trap type (Ritter et al., 2019), with no single method able to examine entire communities objectively

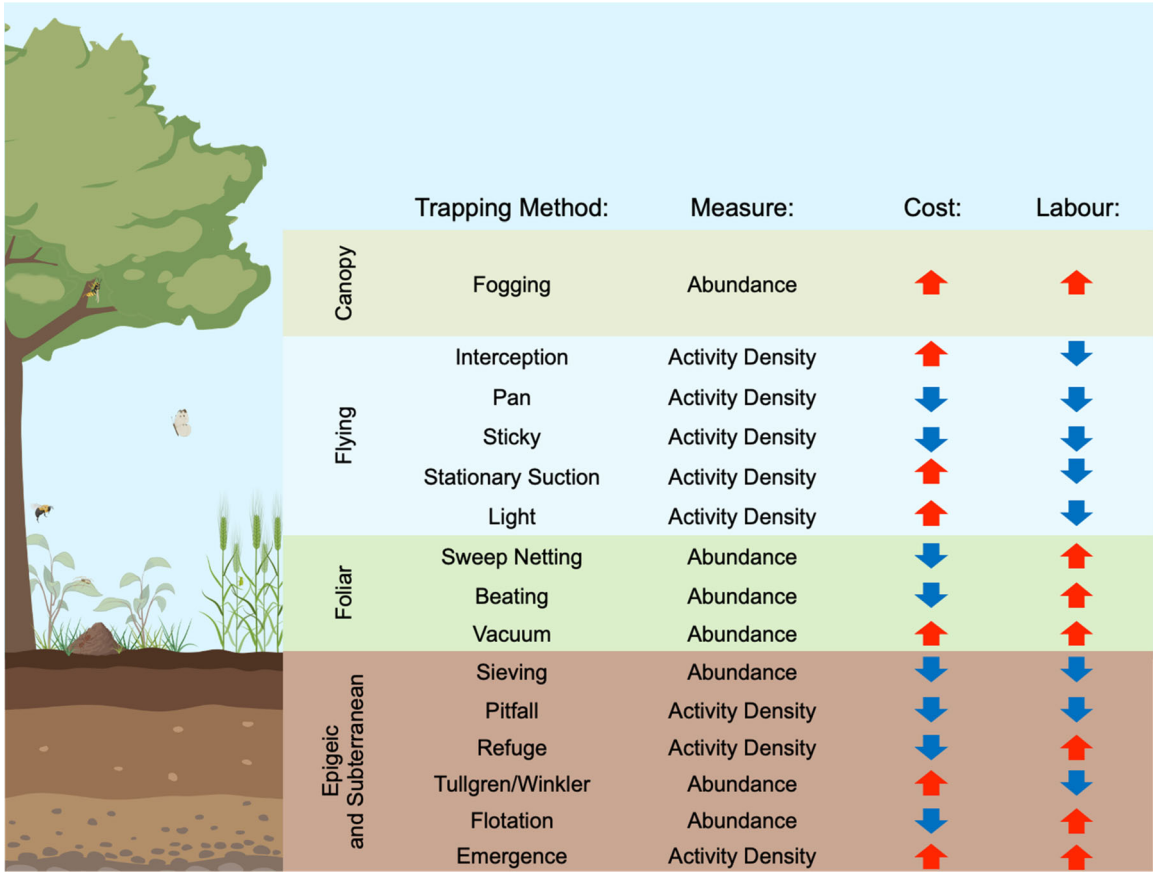

FIGURE 1 Conventional arthropod sampling methods and factors that differentiate them, including the type of measure, relative initial capital cost and labour requirements (time and effort taken to complete sampling) with morphological identification. Species abundance measures assume the samples captured are representative of the communities present in a defined area, usually achievable with active sampling methods like sweep netting (McCravy, 2018; Tonkyn, 1980). Whereas activity density measures are representative of the species active in a defined area, therefore disproportionately representing the most active species, usually determined with traps such as pitfall traps (Gardiner et al., 2010; Greenslade, 1964). This is based on a modified version of Table 1 in McCravy (2018). Created with BioRender.com.

(Figure 1). Similarly, bias is introduced for sexually dimorphic and/or polymorphic species (e.g., the flightless female and winged male winter moth, *Operophtera brumata*; Wheater et al., 2020). Due to the design of traps and/or behaviours exploited to capture invertebrates (e.g., white, yellow and blue colours used as an attractant for different groups of pollinators in a pan and sticky traps; Leather, 2005; Vrdoljak & Samways, 2012; Moreira et al., 2016), these biases are unavoidable, yet widely understood and considered in experimental design to ensure suitable data is collected for the study aims and hypotheses (Sutherland, 2006). The intricacies and methodological considerations of different entomological sampling methods in isolation are reviewed comprehensively elsewhere (see Leather, 2005; Sutherland, 2006). The different invertebrates collected with each method affect species abundance estimates and understanding of ecosystem function, varying further between environments and contexts.

The understanding of ecosystem function that biomonitoring can generate informs decision-making and policy for increasing food production whilst mitigating biodiversity loss. As it stands, however, global assessments for vertebrates tend to be more developed than they are for invertebrates, evidenced by the IUCN Red List (The IUCN Red List of Threatened Species, 2023). Whilst progress is being made for invertebrates, the resolution and scale required for effective monitoring of invertebrate populations across a broad range of contexts requires a throughput intractable with traditional techniques. This presents the question: can invertebrate surveys be improved, and, if so, how?

Insect biomonitoring has traditionally relied on morphological identification of species collected in traps, which is laborious and sometimes lacks taxonomic resolution (Figure 1; Piper et al., 2019; Serrana et al., 2019; Strutzenberger et al., 2023). Advances in molecular techniques provide new approaches to invertebrate sampling, processing and identification, which overcome some of the aforementioned problems, supplementing or expediting traditional methods. These include rapid diagnostic methods, which determine the presence or quantity of specific organisms, such as quantitative Polymerase Chain Reaction (qPCR; Obrepalska-Steplowska et al., 2008; Solà et al., 2017), droplet digital PCR (Zink et al., 2017, 2022), loop-mediated isothermal amplification (Blacket et al., 2020; Blaser et al., 2018) and some emerging CRISPR-Cas-based methods (Durán-Vinet et al., 2023). Whilst these methods are a valuable part of the biomonitoring toolbox and are the optimal method in many cases (Rennstam Rubbmark et al., 2019), they are, however, targeted and, therefore, neglect unexpected taxa and require individual assays for each target organism. Sequencing-based methods can provide data on a broader range of organisms. DNA barcoding has been used to identify individual organisms for decades from short identifying DNA sequences (hence 'barcode'; Hebert et al., 2003) and has generated reference data against which subsequent DNA sequences can be identified. With the advent of high-throughput sequencing (HTS), metabarcoding, the parallel sequencing of many DNA barcodes, has increased the scale of this and facilitated the analysis and identification of mixed samples (Chua et al., 2023). Indeed, metagenomics, PCR-free HTS of all DNA fragments without selecting specific markers, may also advance biomonitoring (Arribas et al., 2020; Chua et al., 2021; Schmidt et al., 2022); however, this review will strictly discuss metabarcoding given its greater accessibility to a range of end-users.

Metabarcoding is the process where strands of nucleic acids are isolated and simultaneously copied (i.e., amplified), read (i.e., sequenced) and assigned to taxa by comparison against existing reference data (Taberlet et al., 2018). Nucleic acids can be sourced from individual organisms, whole communities or the environment (e.g., soil, water and air; Valentini et al., 2016; Kirse et al., 2021; Bohmann & Lynggaard, 2023), the latter termed environmental DNA/RNA (eDNA/eRNA; Yu et al., 2012). Metabarcoding has predominantly been applied to eDNA samples from aquatic environments for the identification of arthropod species, with equal, if not better, accuracy and efficiency than morphological identification (Elbrecht, Vamos, et al., 2017). However, the increasing application of metabarcoding in terrestrial ecological studies is also demonstrably effective for monitoring invertebrates (Dopheide et al., 2019; Elbrecht et al., 2019; Holdaway et al., 2017).

With the rapid development of terrestrial invertebrate biomonitoring using metabarcoding, it is important to evaluate current progress and evolving best practices. An up-to-date synthesis of the benefits of integrating metabarcoding with traditional monitoring methods and ways to mitigate the challenges involved is required. This review compares traditional survey methods employed to monitor terrestrial invertebrates and evaluates the effectiveness of combining each with metabarcoding. First, the benefits of applying metabarcoding to invertebrate sampling methods and ways to mitigate limitations will be discussed, supported by examples from the literature. Following this, the potential for inferring or resolving ecological networks via metabarcoding will be discussed, with reference to the ways in which this can inform policy and assess progress toward biodiversity targets. This provides an accessible resource for new and seasoned users of molecular methods for the biomonitoring of terrestrial invertebrates with the aim of catalysing the increased adoption of metabarcoding for enhanced biomonitoring.

THE BENEFITS OF BIOMONITORING WITH METABARCODING

Traditional morphological identification requires trained insect taxonomists, time and effort (Table 1; Cook et al., 2010; Yu et al., 2012; McCravy, 2018); this results in many studies lacking taxonomic resolution and/or breadth. Targeted biomonitoring schemes, such as the Rothamsted Insect Survey (RIS) aphid monitoring, would benefit from the identification of potentially ecologically important bycatch, yet this is not possible with morphological identification due to finite resources (Petsopoulos et al., 2021). Trained taxonomists are also an increasingly rare resource, termed the 'taxonomic impediment' (Taylor, 1983), with the European Commission finding taxonomic expertise in Europe to be threatened for 41.4% of insect orders (Hochkirch et al., 2022). Hochkirch et al. (2022) also identify a strong age bias

TABLE 1 Comparison of invertebrate morphological identification and metabarcoding (a modified version of tab. 1 by Piper et al. (2019)).

Identification method	Taxonomic expertise	Identify specific taxa	Identify broad range of taxa	Throughput level	Time per identification
Morphological					
Microscopic examination	High	High	High	Low	Moderate
Molecular					
Metabarcoding	Low	High	High	Very high	Low

Note: The classifications rely on several assumptions, such as a high level of taxonomic expertise and low human error rate for morphological identification, and high reference database coverage with a low database error rate for molecular identification.

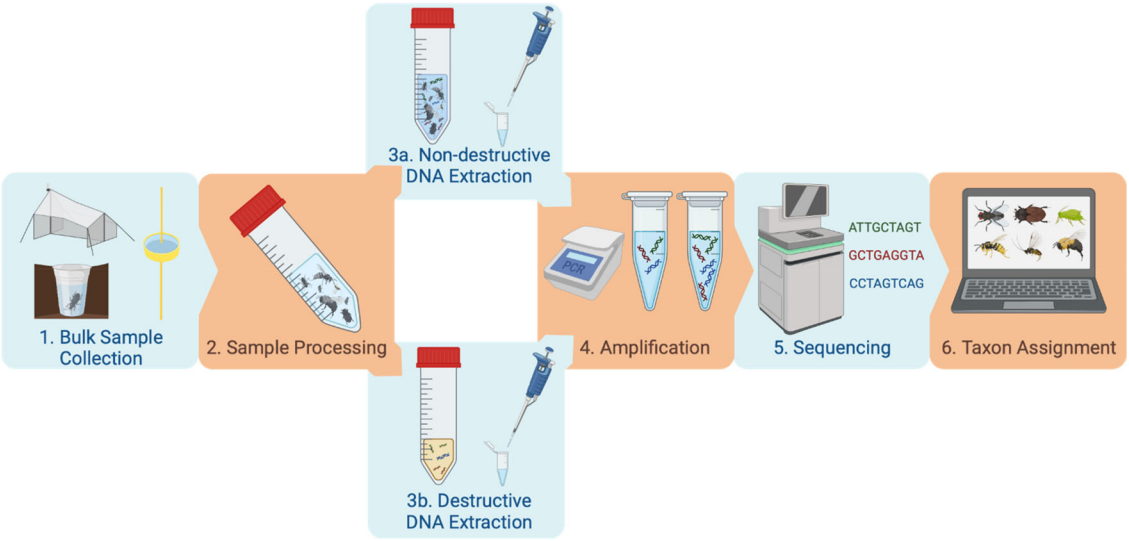

FIGURE 2 The metabarcoding process from sample collection to taxonomic assignment, highlighting two different approaches for DNA extraction (3a. Non-destructive, using a lysis buffer, and 3b. Destructive, which involves grinding samples). Created with BioRender.com.

amongst taxonomists, where ~77% of taxonomists are over the age of 40, with poor recruitment of younger taxonomists due to inadequate training opportunities. This presents a challenge for the future of biomonitoring with morphological identification. However, novel technologies such as metabarcoding may provide solutions to supplement this expertise for the continuity and enhancement of biomonitoring.

The benefits of metabarcoding for invertebrate biomonitoring can largely be summarised as (1) increased taxonomic resolution, (2) increased taxonomic coverage (including the potential for species-interactions) and (3) increased cost and time efficiency. The relative importance of each of these depends on the specific context in which they are applied, the focal taxa of the study and the equipment and facilities available to realise each of the benefits fully. The greatest benefit of metabarcoding, and perhaps the largest incentive for its adoption, is the potential to achieve greater taxonomic resolution and coverage compared with morphological identification (Table 1; Holdaway et al., 2017; Piper et al., 2019). It also offers the advantage of identifying whole communities from many samples in parallel by utilising HTS (Figure 2), saving time and money (Table 1; Yu et al., 2012; Evans et al., 2016; see fig. 6 in Macgregor et al., 2019; Evans & Kitson, 2020; Cuff, Windsor, et al., 2022). For non-target bycatch unanalysed due to a lack of time and resources (Petsopoulos et al., 2024), metabarcoding can unlock these valuable data to understand and address long-term insect declines. Furthermore, metabarcoding methods are conserved regardless of geographic location, justifying the upscaling of biomonitoring with metabarcoding, whereas morphological identification relies on taxonomists having knowledge of local species for different geographic locations—though taxonomic assignment will vary geographically due to disproportional reference database coverage and resolution, which is discussed later in the review as a limitation. Global and even local variation between populations may cause mismatches with reference data, but metabarcoding equally has the potential to resolve intraspecific differences (e.g., in ring species; Song et al., 2016), depending on the genetic marker used.

Invertebrates that have polymorphic life stages or variable phenotypes, for example, polymorphic worker ants in the genus *Melophorus* (Meier et al., 2016), make morphological identification challenging for inexperienced taxonomists. Metabarcoding can overcome this issue with the selection of appropriate PCR primers (Fernandes et al., 2019), as the standard barcoding regions used (e.g., cytochrome oxidase subunit 1 [COI]) can reliably differentiate species independent of polymorphisms. Similarly, in diagnostic applications (e.g., detecting

the occurrence of pest invertebrates), specimens can be collected in immature stages that are morphologically indistinguishable from other species. Traditionally, these would have been reared to an identifiable stage (Ruiter et al., 2013), which is not compatible with many sampling methods that result in the mortality of specimens, for example, sticky traps or pan traps. By avoiding this issue, metabarcoding takes less time for identification, allowing more rapid intervention in response to biomonitoring outcomes. Additionally, unlike morphological identification where damage to diagnostic features impedes identification (Hodgetts et al., 2016), specimens do not need to be intact or in good condition to identify them via metabarcoding.

Aside from capturing whole specimens, methods are being developed to apply metabarcoding for alternative sources of eDNA that avoid disturbing invertebrate populations altogether; for example, detecting species from airborne eDNA (Clare et al., 2022; Pumkaeo et al., 2021; Roger et al., 2022), or eDNA in rain and on foliage (Allen et al., 2023; Valentin et al., 2020; Weber et al., 2023; Yoneya et al., 2022). This overcomes the need to kill specimens during conventional entomological trapping, which occurs for morphological identification and bulk sample metabarcoding, and alleviates the problem of biomonitoring where rare species or sensitive populations are known to occur (Chua et al., 2023).

Mitigating the limitations of metabarcoding for effective biomonitoring

Metabarcoding evidently has the potential to enhance biomonitoring efforts, providing benefits that complement traditional morphological identification. As with most emerging techniques though, there are challenges and limitations that need to be considered and mitigated when implementing metabarcoding to attain high-quality data.

Destructive approaches for DNA extraction typical to metabarcoding require the homogenisation of invertebrates and are not compatible with retaining voucher specimens (similarly, eDNA is limited by a lack of voucher specimens). This was previously a barrier to applying DNA-based analyses for samples that needed to be retained for posterity (e.g., long-term monitoring schemes and museum collections). However, non-destructive approaches are emerging, in which DNA is extracted from specimens while leaving the exoskeleton and other morphological features intact (Figure 2; Carew et al., 2018; Nielsen et al., 2019; Ritter et al., 2019; Batovska et al., 2021; Petsopoulos et al., 2021). These methods facilitate the extraction of valuable abundance data, otherwise absent from metabarcoding alone (Lamb et al., 2019), and validation with parallel morphological examination (Martoni, Smith, Piper, Lye, et al., 2023; Martoni, Smith, Piper, Nancarrow, et al., 2023). This offers a sound alternative to using read counts to infer relative species abundance, which is often inaccurate due to primer-template mismatches (Piñol et al., 2015), polymerase binding efficiency differences between taxa (Creedy et al., 2019) attributed to different guanine-cytosine (GC) contents (Nichols et al., 2018), and the dynamic interactive effects of biomass and degradation times on the quantity of DNA present in the sample (Deagle et al., 2019). In bulk samples, larger specimens tend to release more DNA than smaller ones (Liu, Clarke, et al., 2020), which can arise in instances such as differences between species sizes, life stages, or damaged specimens. Whilst impacting the ability to infer abundance from read counts, this can also lead to the DNA from larger invertebrates dominating sequencing outputs (Elbrecht & Leese, 2015); pooling invertebrates of similar sizes can mitigate this (deWaard et al., 2019; Köthe et al., 2023).

Taxonomic biases can be introduced throughout the metabarcoding workflow, for example, through differential primer binding and amplification efficiencies between taxa during PCR (Elbrecht & Leese, 2015), the extent of which differ between primers. Primer biases can ultimately under- or over-represent certain taxa, which is particularly problematic in studies for which the target taxa are unknown. Similarly, species in high abundance can prevent rare species from being detected during sequencing (Iwaszkiewicz-Eggebrecht et al., 2023); this could be problematic in the instance of insect swarms, for example. Intentionally biased PCR primers can be utilised to reduce the prevalence of overabundant species amplification (Cuff, Kitson, et al., 2022; Lafage et al., 2020), as can CRISPR-Cas (Gu et al., 2016; Ramani & Shendure, 2016) and hybridisation-capture approaches (Aylward et al., 2018; Seeber et al., 2019). Alternatively, using multiple primer pairs can provide overlapping yet complementary detections to mitigate individual primer biases and even overabundant species amplification (Cuff, Kitson, et al., 2022; Cuff, Windsor, et al., 2022).

DNA degradation presents another significant challenge for metabarcoding: the more intact DNA is, the better the chances of successfully detecting it. Degradation occurs naturally over time in the environment, in traps and even in storage, but can be exacerbated by factors like UV light (Gomes et al., 2009) and temperature (Ballari & Martin, 2013; Kagzi et al., 2023). Suboptimal storage of samples can lead to a greater rate of DNA degradation. With bulk sample traps, the preservative used can determine the subsequent recovery of DNA. Liu, Clarke, et al. (2020) recommend >95% ethanol and provide further advice on storage to prevent DNA degradation.

Due to PCR sensitivity, another major problem is contamination, which often leads to false positives (Drake et al., 2022; Kwok & Higuchi, 1989). For example, contamination of pollinators with DNA from other insects being transported between flowers on the pollinators (Thomsen & Sigsgaard, 2019) can lead to false identification of a pollination event between an uninvolved insect and the flower. Furthermore, contamination of pre-PCR samples in the laboratory can arise, particularly through DNA introduced from PCR products. If primers bind more efficiently to the contaminant DNA than the target DNA in the sample, this can be even more challenging (Taberlet et al., 2018). There are ways to reduce such contamination through good laboratory practices such as physically separating pre-PCR and post-PCR workspaces (Taberlet et al., 2018). Alongside environmental/laboratory contamination, cross-contamination of samples, sequencing errors, tag-jumping and misassignment of sequences can generate 'false positives' (i.e., data that arise erroneously; Zinger et al., 2019; Drake et al., 2022). Including negative and positive controls in PCRs is generally good practice, helping to detect false positives, and also

useful for setting thresholds to remove them (Ando et al., 2020). Minimum sequence copy thresholds are used to remove low copy number sequences usually attributed to contamination, the values of which are usually informed by evidence from experimental controls (Drake et al., 2022). This can, however, introduce false negatives (i.e., the absence of data) given the low copy number associated with some legitimate detections (Littleford-Colquhoun et al., 2022). Increasingly accurate evidence-based strategies for data curation are, however, emerging, with great potential to increase the accuracy of metabarcoding data (González et al., 2023).

The coverage and resolution of reference databases also have implications for assigning taxonomy to DNA sequences (Kestel et al., 2022; Thomsen & Sigsgaard, 2019; Watts et al., 2019). The most common approach for assigning taxonomy in metabarcoding studies is a best-hit classification, which assigns reads to the taxon with the most similar sequence in the reference database (Piper et al., 2019); for species missing from databases, however, this leads to classification at a coarser level, or can even lead to incorrect assignment and, therefore, false positives (Piper et al., 2019). Furthermore, since databases are continuously being updated, metabarcoding results generated from different years lack direct comparability, particularly with the best-hit approach to datasets (Taberlet et al., 2018). The impacts of these vary depending on geographic location: more emphasis has been given to genome sequencing in the Global North (Leandro et al., 2024), with Hotaling et al. (2021) finding it contributes 77% of all genome assemblies. There are many organizations and projects working to increase database coverage, however, by sequencing genomes across as many taxa as possible; for example, the Darwin Tree of Life project (The Darwin Tree of Life Project Consortium et al., 2022). Tools such as GAPeDNA, a web interface highlighting gaps in genetic databases for a given taxon, can inform resource allocation for increasing reference database completeness (Marques et al., 2021).

A lack of standardization impedes comparison between studies. Results can diverge depending on the protocol used for DNA extraction, PCR reagents and conditions, and sequencing protocols (Bohmann et al., 2022; Taberlet et al., 2018). The variety of commercially available kits adds further inconsistency between studies (Liu, Clarke, et al., 2020). A modular universal DNA extraction toolkit has been developed (Sellers et al., 2018), but when bias can be introduced at each step of the metabarcoding process, does one size fit all? With the development of multiple competing approaches, such as the BOMB Bio nucleic acid extractions (Oberacker et al., 2019), standardization is inadvertently reduced amongst metabarcoding methods. Arribas et al. (2022) have provided guidelines and recommendations for a harmonization of methods between terrestrial invertebrate metabarcoding studies in attempts to facilitate better comparison between whole-organism community DNA studies. Their modular approach enables flexibility within the guidelines, accounting for future advances, whilst also advocating for appropriate reporting of data and metadata to integrate datasets in further analyses.

It is imperative to consider these limitations when planning a study which utilises metabarcoding; however, implementing the appropriate steps to account for these will be greatly beneficial. Fortunately, in the context of terrestrial invertebrate biomonitoring with metabarcoding, existing trapping approaches need not change, as many studies have successfully combined traditional methods with metabarcoding to produce comprehensive investigations on terrestrial invertebrates.

Examples of metabarcoding-based biomonitoring with traditional entomological sampling methods

Interception traps

Interception traps (e.g., window flight traps and Malaise traps) have been combined with metabarcoding in many cases already. For example, Remmel et al. (2024) compared metabarcoding with morphological identification for malaise trap samples, finding 76.2% of species identified with metabarcoding, with an overlap of 54.8% of species detected by each method. The authors found species at low biomass and abundance were more likely to be missed, even after a two-fraction size sorting; similarly, Moreira et al. (2016) found size sorting by order to only increase the yield of high score BINs by 30%, prompting suggestions to consider sorting invertebrates only if there is enough time and resource to do so. However, storing samples and DNA allows researchers to revisit samples with updated methods after new ways to mitigate limitations are developed, such as addressing biomass biases. Remmel et al. (2024) recommend applying metabarcoding for long-term biomonitoring for traps, which are species-rich.

Studies have also combined malaise traps with metabarcoding to assess changes in species richness in conservation areas (Köthe et al., 2023), species diversity in differently managed forests (Wildermuth et al., 2023), biodiversity in restored environments (Lynggaard et al., 2020) and temporal changes in invertebrates across agricultural (Hausmann et al., 2022) and forest landscapes (Barsoum et al., 2019; Kirse et al., 2021), and to create species inventories (Li et al., 2023). Due to the design of the trap, specimens are immediately stored in a suitable preservative, such as a high-purity ethanol (deWaard et al., 2019; Kirse et al., 2021; Swenson et al., 2022), requiring no modifications.

This method has also secondarily detected plant species being used by invertebrates by metabarcoding plant eDNA in the killing agent (Köthe et al., 2023; Swenson et al., 2022). To eliminate contamination from airborne plant DNA in the working area during sample processing, Swenson et al. (2022) deployed a Petri dish with a thin layer of Vaseline to capture plant pollen, which was also analysed by metabarcoding. These methods may be complementary to field plant surveys and provide insight into the species being utilised by invertebrates. Furthermore, this could streamline invertebrate and plant surveys when limited by time, resources, and/or expertise.

Netting

Nets are a common tool for entomological surveys, and different types of net have been used in combination with metabarcoding to

investigate insect-plant trophic interactions (Foster et al., 2020) and biomonitoring (Li et al., 2023; Pentinsaari et al., 2020; Svenningsen et al., 2021). Furthermore, in a study by Svenningsen et al. (2021), nets attached to the roof of cars were used to sample flying insects in Denmark. Metabarcoding detected spatial patterns of species richness for 15 insect orders. This was compared against a long-term flying insect survey that used morphological identification (the Swedish Malaise Trap Project) and found a similar taxonomic composition overall. Foster et al. (2020) collected bulk insect samples directly from spotted knapweed plants via sweep netting to assess the impact of knapweed on invertebrate communities. Details on practices to reduce contamination between samples collected using the same net are lacking, which is an important consideration for metabarcoding studies (Harwood, 2008). There are multiple studies that either omit this information or do not consider cross-contamination (e.g., Foster et al., 2020; Li et al., 2023). We recommend that studies implement measures such as decontaminating nets between sampling or using different nets for each sample—this is true for any equipment reused between samples.

Soil and leaf litter sampling

The combination of soil core sampling and metabarcoding can reveal differences in biodiversity between environments and conditions, as demonstrated by Hermans et al. (2022) and Ferrín et al. (2024). However, metabarcoding soil core samples struggled to detect temporal changes in species richness (Carini et al., 2016). The sensitivity of metabarcoding to preserved DNA in the soil might obscure the detection of temporal patterns, thereby indicating a more suitable approach to be metabarcoding arthropods extracted from soil samples with a Berlese-Tullgren funnel, for example, as demonstrated by Basset et al. (2022). These studies highlight the importance of choosing a sampling method to fit the research question, distinguishing eDNA in soil, water and air from whole specimen insect DNA (Yu et al., 2012), though the two sources are sometimes grouped together as eDNA (Taberlet et al., 2018).

Primer choice for PCR was highlighted as a challenge for soil eDNA studies for invertebrates by Brunetti et al. (2024). The 18S rRNA primers had broader taxonomic coverage for soil taxa and were less prone to bacterial contamination. However, the COI gene has higher variability and more reference sequences for these primers, making identification of earthworms and insects, for example, better for lower level classification. Neither marker identified any isopods in the study. Increasing reference database coverage will undoubtably address problems with soil eDNA studies, as identified Brunetti et al. (2024).

Invertebrates extracted from leaf litter samples with Winkler bags (substrate in mesh bags suspended over bottles containing a killing agent, in a sealed bag) can also be used for metabarcoding, as demonstrated by Beng et al. (2016), who investigated the effect of land use on arthropod community composition. A flotation-Berlese-flotation (FBF) protocol was used with metabarcoding by Arribas et al. (2016) to identify soil mesofauna with reduced contamination from bacteria and PCR inhibitors. Furthermore, this modified technique is proposed to minimise mortality while maximising species detection. The FBF protocol also allows >20 L of soil to be used for a more representative analysis of communities compared with ~200 g collected for typical soil metabarcoding studies (Arribas et al., 2016).

Pitfall traps

Pitfall traps are easily combined with metabarcoding, much like many of the other fluid-based traps. Dietary metabarcoding has been used to determine the trophic interactions of trapped invertebrates (Huszarik et al., 2023), but much like similar methods, cross-contamination within the trap results in many false positive detections (Athey et al., 2017), requiring surface sterilization (e.g., with bleach) to reduce these instances (Miller-ter Kuile et al., 2021). Bulk sample metabarcoding has, however, been applied very successfully; for example, to monitor and assess ecosystem restoration (Fernandes et al., 2019; Van Der Heyde et al., 2022), and beetle responses to human disturbances in forests (Liu, Baker, et al., 2020). Ethylene glycol is often used as a killing agent in studies combining metabarcoding and pitfall traps (Hohbein & Conway, 2018), with subsequent washing of samples prior to molecular analysis (e.g., with ethanol or water; Fernandes et al., 2019; Van Der Heyde et al., 2022).

Pan traps

Metabarcoding of bulk samples from pan traps is relatively underrepresented in the literature. However, they have been combined to build DNA barcode inventories (Pentinsaari et al., 2020) and compare biodiversity between habitats (Wang et al., 2019). Pan traps are sometimes deployed for the capture of specific taxa, but often collect a lot of bycatch, which can provide a wealth of information for broader biomonitoring (Petsopoulos et al., 2021). Wang et al. (2019) metabarcoded the bycatch of sampling which focused on bees. They were able to produce evidence to show the benefit of restoring native forests on arthropod diversity, over other monoculture plantations, in China's Grain for Green Program.

Fogging

Collecting bulk samples by fogging invertebrates in tree canopies can provide large volumes of samples for biomonitoring. Creedy et al. (2019) used this method to measure species richness in tropical rainforest canopies, deeming metabarcoding to be accurate and comprehensive for global ecosystem studies. The authors found size differences between invertebrates did not greatly affect species recovery during metabarcoding, contrary to other studies (Elbrecht, Peinert, & Leese, 2017); however, this will be greatly affected by the proportion of large to small invertebrates in the sample.

Light traps

Typically, conventional light traps involve the capture and release of specimens. However, combining them with metabarcoding requires the killing and processing of the invertebrates caught (Basset et al., 2020; Li et al., 2023); one exemplary exception to this is unconventionally collecting dead arthropods from home light fixtures (Elbrecht et al., 2021). Basset et al. (2020) included light traps in their study to assess the diversity of ants, springtails and termites, and, whilst this method was less effective than malaise traps and soil samples (not typically deployed for soil/litter taxa), it captured distinct species of these taxa unrepresented by soil samples. Li et al. (2023) also used light trapping with metabarcoding to identify insect communities distinct from those caught by sweep netting and malaise traps. Similarly, when using light traps, Mata, Ferreira, et al. (2021) found metabarcoding identified almost four times the number of Lepidoptera species originally identified using morphology despite some poor discrimination with the marker used and reference database errors/omissions, which is attributed to the ability of metabarcoding to identify even highly damaged specimens. Strutzenberger et al. (2023) found singleton species in light traps less likely to be detected in metabarcoding, due to biomass differences; this, however, can be mitigated with size sorting.

Vacuum/suction sampling

While purpose-built vacuum samplers (e.g., 'D-Vac'; Dietrick, 1961) and modified leaf-blowers/vacuums are frequently deployed in invertebrate sampling studies (Cherrill, 2015; Hossain et al., 1999), this method is yet to be combined with metabarcoding for species identification to our knowledge. However, molecular methods have been applied to successfully identify eDNA collected with atypical vacuums for entomological studies, for the purpose of detecting parasitoid DNA from a pest snail species (Campbell et al., 2022) and pest beetle DNA (Trujillo-González et al., 2022). On the other hand, bulk samples collected by stationary suction traps have been identified with metabarcoding. Martoni, Smith, Piper, Lye, et al. (2023) deployed an iMap-PESTS Sentinel model 4 smart suction trap to investigate the presence of pest Asian citrus psyllids in Australian citrus orchards. Whilst the pest psyllids were not detected, new records for a native psyllid species not previously known from the region were. Another study applied the same methods to investigate the presence of pest aphid species in grain crops (Martoni, Smith, Piper, Nancarrow, et al., 2023). Petsopoulos et al. (2024) applied metabarcoding to archived aphid samples of the RIS collected from 2003 to 2018 with 12 m tall suction traps, finding recovery of over 76% of genera. Identification with metabarcoding was less successful to species (54%); however, sample storage was suboptimal for metabarcoding, which would impact the success of identification. Furthermore, airborne invertebrate eDNA collected with suction samplers has been metabarcoded, showing applications for the emerging method of 'airDNA' in biomonitoring efforts (Roger et al., 2022).

Sticky traps

To our knowledge, bulk sample community metabarcoding has not yet been used for sticky traps, potentially due to prolonged exposure to conditions that degrade DNA, such as sunlight (UV; Gomes et al., 2009), and high temperatures (Ballari & Martin, 2013; Butterwort et al., 2022; Kagzi et al., 2023); although, metabarcoding has successfully detected the diet of sticky trapped coccinellids (Ammann et al., 2020). The removal of invertebrates from the adhesive can be challenging, with solvents like Histo-clear oil inhibiting the PCR process (Maxwell et al., 2011). A study by Butterwort et al. (2022) tested this, however, and found non-significant inhibition of PCR with different concentrations of this solvent. Barcoding has been applied to sticky trap insects, demonstrating effective identification of thrips (Marullo et al., 2020), as well as a single-species detection with real-time PCR for a method extracting DNA from sticky trap bulk samples (Butterwort et al., 2022).

Invertebrate interaction data derived from metabarcoding for ecological networks

Typically, biomonitoring focuses solely on richness-based measures of diversity which, whilst important, neglect the interactions between organisms that underpin ecosystem processes and functioning (Cuff et al., 2023). These interactions form interconnected 'webs': ecological networks. Whereas species richness can remain stable after a series of extinctions balanced by immigration, interactions are likely to change much more markedly as the dynamic ecologies, life histories and behaviours of organisms also respond (Hillebrand et al., 2018). By studying and comparing networks, the impacts of human activities such as land management and other perturbations on interactions and their emergent ecosystem services can be studied quantitatively with greater clarity (Evans et al., 2013; Memmott et al., 2007; Tylianakis et al., 2007). Ecological networks contextualise interspecific interactions and identify underlying structures of communities, and ecosystem function and stability (Montoya et al., 2006). Recent decades have seen significant advances in the theoretical understanding, construction, analysis and application of complex species interaction networks (see Fontaine et al., 2011; Kéfi et al., 2012 for reviews).

The evidence that ecological networks describe the impacts of environmental management on ecosystem function and service provision in agroecosystems means they can be used to measure progress toward targets for food security and biodiversity, such as Target 10 of the Kunming-Montreal Global Biodiversity Framework (Convention on Biological Diversity, 2022). Achieving these targets relies on the success of interventions such as the ELMs developed by the UK government to improve carbon sequestration, water retention and biodiversity in agri-environments (Department for Environment, Food, & Rural Affairs, 2023). By simultaneously examining a suite of mutualistic and antagonistic interactions (e.g., plant-pollinator and plant-herbivore, respectively), specific ELM actions such as off-crop management (e.g., field margins and hedgerows) can be measured. On

the one hand, such management interventions can in some cases have insignificant impacts on some ecosystem services (i.e., biocontrol) whilst benefiting others (i.e., pollination; Albrecht et al., 2020). On the other hand, wildflower strips (a widely used agri-environment scheme) can benefit disservice providers (e.g., wireworms) rather than their target pollinators (Feng et al., 2019). Ecological network approaches can guide land management practices to optimise the trade-offs in ecosystem services/disservices (Windsor et al., 2021). Constructing and analysing farm-scale (and beyond) ecological networks using DNA metabarcoding is the state of the art and has the potential to generate more informative metrics for assessing the impacts of land management on biodiversity to provide evidence and inform policy (Derocles et al., 2018; Evans et al., 2016; Evans & Kitson, 2020; Miller et al., 2021).

Networks are traditionally constructed from observed interactions (e.g., insect flower-visitation and host-parasitoids), but metabarcoding can significantly improve resolution and sampling completeness (Evans & Kitson, 2020; Krehenwinkel et al., 2024). For example, metabarcoding can better identify host-parasitoid interactions (Kitson et al., 2019), trophic interactions (Cuff et al., 2021), scatophagy (Sigsgaard et al., 2021), disease vectoring (Miller et al., 2021) and a range of plant–animal interactions, such as herbivory and flower visitation (Banerjee et al., 2022; Kestel et al., 2024; Newton et al., 2023; Thomsen & Sigsgaard, 2019; Weber et al., 2023) by analysing the DNA present in or on individual organisms. The ability to detect interactions without direct observation is particularly powerful for cryptic interactions that occur rarely, or outside typical observation time frames (e.g., at night; Cuff, Windsor, et al., 2022; Macgregor et al., 2019; Quintero et al., 2022). Applying this to biomonitoring in agroecosystems can advance our understanding of ecosystem service (e.g., biocontrol, pollination) and disservice (e.g., crop herbivory) provision (Cuff, Tercel, et al., 2022; Lowe et al., 2022; Mata, Da Silva, et al., 2021; Rader et al., 2016).

The integration of metabarcoding with traditional monitoring samples (i.e., bulk samples of mixed invertebrate communities) is unlikely to yield reliable interaction data directly though. Whilst interactions can be detected from individuals collected via bulk sampling (e.g., from the gut contents of collected invertebrates; Lynggaard et al., 2019), it is difficult to determine both interacting partners confidently. Extracting the necessary interaction data from the species lists typically associated with biomonitoring presents a challenge, but is not impossible (Cuff et al., 2023; Petsopoulos et al., 2021). There are numerous ways in which ecologists can produce the interaction data necessary to construct ecological networks from species lists. Most simply, likely interactions can be derived from those already reported in the literature; this can be expedited using text mining, which builds large datasets from the literature via machine learning (Tamaddoni-Nezhad et al., 2013).

When unobserved or otherwise unknown, interactions can be inferred using a range of approaches, some of which, such as deep learning, are actively being developed (Barraquand et al., 2021; Hampton et al., 2013; Volkov et al., 2009). Network inference has most commonly been achieved using co-occurrence analyses, which determine when species co-occur more or less than expected by chance, often based on null models. When species co-occur more often than expected, it could be inferred that these species interact (Blanchet et al., 2020). Since metabarcoding generates species lists from which co-occurrences can be elucidated, it can be used to infer networks in this manner. Caution must, however, be taken with this approach as interactions can be falsely inferred due to co-occurrence not necessarily denoting interactions and sometimes instead relating to shared habitats or resources (see Blanchet et al., 2020). Alternative increasingly accurate network inference methods are also emerging which use patterns in count data whilst accounting for environmental effects and distinguishing direct from indirect interactions (Momal et al., 2020), such as Bayesian networks (Milns et al., 2010) and trait matching (Pereira et al., 2023); this is well discussed by Blanchet et al. (2020) and reviewed by Cuff et al. (2023). Moreover, by using data collected in space and time from biomonitoring projects, an outstanding opportunity exists to compare inference methods, for example, based on MaxEnt (Volkov et al., 2009) and Matrix Autoregression approaches (see Barraquand et al., 2021; Hampton et al., 2013) supplemented with trait and phylogenies/taxonomic information (Ovaskainen et al., 2017). Although still largely theoretical, portions of the inferred networks generated using metabarcoding could be validated against invertebrate networks that are well described within agro-ecosystems, such as plant-pollinator and host-parasitoid interactions. Furthermore, a wider benefit of incorporating molecular data is that ecology networks can be phylogenetically structured, allowing previously intractable questions in ecology and evolution to be addressed (Raimundo et al., 2018).

Future advances

Biomonitoring is rapidly advancing with the emergence of technologies that facilitate cost-effective and high-throughput methods like metabarcoding but also approaches such as automated image analysis via AI, bioacoustics and radar (Besson et al., 2022; Cuff et al., 2023; van Klink et al., 2022). Whilst these share common goals (i.e., effective and streamlined biomonitoring), they provide data types and benefits complementary to those offered by metabarcoding, rationalizing their parallel application. Of these examples, automated imaging is the most relevant to pre-collected bulk samples. Tools like BIODISCOVER, an automated image-based identifying device (Ärje et al., 2020), could theoretically be used on samples destined for metabarcoding, which could provide cross-validation of both methods and complementary taxonomic resolution. This will, however, require additional handling time, money and data storage. The species abundance and biomass data theoretically provided by imaging approaches, when integrated with the high-resolution identification of metabarcoding (alongside the identification of cryptic species and parasitism) could present a significant advance for biomonitoring data. This data merging through parallel application of emerging technologies is likely to present the greatest advance for biomonitoring (Besson et al., 2022; van Klink et al., 2022; Windsor, 2023).

Although best practices will be dependent on study goals, capabilities, and sampling methods, we recommend some best practices

common to all studies based on the literature to ensure the quality of future invertebrate biomonitoring with metabarcoding. Sampling methods do have some overlapping attributes that can inform which approaches are appropriate for the research capabilities (Table 2). It is key to consider and state decontamination practices used for entomological equipment in studies, for better reproducibility. Equally, sample integrity is important, which can be impacted by sample collection (for pan and sticky traps, e.g., which are exposed to DNA-degrading environmental conditions) and storage. Selecting PCR primers that match the invertebrates sampled is important to ensure optimal data recovery and identification; being mindful of the taxa caught by each approach can help inform this.

We posit that standardization will be an urgent priority for the future of metabarcoding, particularly in the context of biomonitoring. For metabarcoding to become a standard part of the biomonitoring toolbox globally, increased comparability between applications is required, only possible through standardization of protocols and data processing. Without this, results cannot be reliably compared, and biomonitoring will be regionally and contextually siloed. This is particularly vital if the resultant data are to be integrated into setting and monitoring progress toward global biodiversity targets. Applying metabarcoding to biomonitoring and assessing biodiversity gains through land use interventions such as the UK ELMs will provide the resolution, coverage and throughput of species detections necessary to monitor the impact of such schemes (Boetzl et al., 2021). The time and cost efficiency metabarcoding offers exemplify the suitability of this technique for returning meaningful data to inform global policy.

CONCLUSIONS

Metabarcoding has the potential to revolutionise invertebrate biomonitoring by increasing the resolution, throughput and efficiency of current monitoring efforts based on bulk invertebrate sampling and identification. The breadth and depth of species identification possible through metabarcoding can upscale and enhance biodiversity studies to an unprecedented extent, especially when integrated with other emerging technologies and approaches. The efficacy of this advance will, however, depend on the coverage and resolution of reference databases, the standardisation of practices and robust validation of its application to a range of contexts and sample types. Limitations of the method, such as the inability to determine species abundance accurately and the lack of interaction data available directly from bulk samples mean that it will not be a panacea, but certainly an effective addition to the biomonitoring toolbox.

Many studies have demonstrated the ease with which conventional traps or collection methods can be combined with metabarcoding for biomonitoring across applications, including measuring the impact of environmental change, generating species inventories and assessing restoration practices. However, comprehensively understanding the implications of integrating metabarcoding with different collection methods is imperative for providing context to the invertebrate assemblages collected by each method. Similarly, considering the source of DNA (e.g., target organisms and environmental) can help explain the patterns detected via metabarcoding. Inferring ecological networks from these data to refine biomonitoring assessments is a particularly promising but challenging advance with great promise for

TABLE 2 Points of consideration for each sampling method; 'Y' = 'yes' and 'N' = 'no'.

		Considerations			
Strata	Sampling method	Liquid killing agent can act as preservative	Samples exposed to degrading environmental conditions (e.g., heat and UV)	Invertebrates already killed by trap	Equipment requires decontamination between samples
Canopy	Fogging	N	N	Y	Y
Flying	Interception	Y	Y	Y	Y
	Pan	Y	Y	Y	Y
	Sticky[a]	N	Y	Y	N
	Stationary Suction	N	Y	N	Y
	Light	N	N	N	Y
Foliar	Sweep Netting	N	N	N	Y
	Beating	N	N	N	Y
	Vacuum	N	N	N	Y
Epigeic and Subterranean	Sieving	N	N	N	Y
	Pitfall	Y	N	Y	Y
	Refuge	N	N	N	Y
	Tullgren/Winkler	Y	N	Y	Y
	Flotation	N	N	N	Y
	Emergence	N	N	N	Y

[a]Sticky traps require solvent removal to free invertebrates from glue—consider any PCR inhibition from the solvent used, as noted in the 'Sticky Traps' section.

the future of invertebrate biomonitoring. Caution must, however, be taken to mitigate contamination and other sources of false or missing detections. With appropriate care and sufficient prior validation, metabarcoding is likely to present a paradigm shift for global invertebrate biomonitoring.

AUTHOR CONTRIBUTIONS

Ben S. J. Hawthorne: Conceptualization; funding acquisition; investigation; project administration; visualization; writing – original draft; writing – review and editing. **Jordan P. Cuff:** Conceptualization; funding acquisition; supervision; writing – review and editing. **Larissa E. Collins:** Conceptualization; funding acquisition; supervision; writing – review and editing. **Darren M. Evans:** Conceptualization; funding acquisition; project administration; supervision; writing – review and editing.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data sharing is not applicable to this article as no new data were created or analysed in this study.

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