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NEWS AND VIEWS

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Collective and harmonized high throughput barcoding of insular arthropod biodiversity: Toward a Genomic Observatories Network for islands

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Abstract

Current understanding of ecological and evolutionary processes underlying island biodiversity is heavily shaped by empirical data from plants and birds, although arthropods comprise the overwhelming majority of known animal species, and as such can provide key insights into processes governing biodiversity. Novel high throughput sequencing (HTS) approaches are now emerging as powerful tools to overcome limitations in the availability of arthropod biodiversity data, and hence provide insights into these processes. Here, we explored how these tools might be most effectively exploited for comprehensive and comparable inventory and monitoring of insular arthropod biodiversity. We first reviewed the strengths, limitations and potential synergies among existing approaches of high throughput barcode sequencing. We considered how this could be complemented with deep learning approaches applied to image analysis to study arthropod biodiversity. We then explored how these approaches could be implemented within the framework of an island Genomic Observatories Network (iGON) for the advancement of fundamental and applied understanding of island biodiversity. To this end, we identified seven island biology themes at the interface of ecology, evolution and conservation biology, within which collective and harmonized efforts in HTS arthropod inventory could yield significant advances in island biodiversity research.

KEYWORDS
arthropods, biodiversity conservation, island community ecology, island evolution, multiplex barcoding, wocDNA metabarcoding

1 | INTRODUCTION

Islands have long been a focus for evolutionary and ecological understanding (Warren et al., 2015), largely due to their limited geographic extent, long-term isolation, often replicated nature, simplified biota relative to continental settings, high levels of endemism, and diverse ecological settings. At the same time, their flora and fauna are increasingly at risk from global change for some of the very same reasons that have attracted scientific interest. Depauperate communities that have evolved in isolation may be more susceptible to invasive species (Bellard et al., 2017; Borges et al., 2020; Spatz et al., 2017). Within the context of ongoing climate change, island biodiversity requires specific attention because of its increased vulnerability for multiple reasons (see e.g., Manes et al., 2021; Veron, Mouchet, et al., 2019). When climate change is combined with other impacts of increasing human population size and economic development, such as habitat modification and degradation, the challenge for managing and conserving insular biodiversity presents itself as being immediate and large-scale (Russell & Kueffer, 2019). It is not only the loss of species and their interactions that is particularly relevant on islands, but also the loss of unique evolutionary history (phylogenetic and functional diversity), reflecting the loss of unique adaptations to the environment (Sayol et al., 2021; Soares et al., 2022).

Given the above, there are pure and applied scientific reasons for scaling up our understanding of island biodiversity. Scientifically, there is still much to be gained from the investigation of insular biotas (Patiño et al., 2017; Warren et al., 2015; Whittaker et al., 2017), but many questions remain open due to limited arthropod data (Table 1). Our current understanding of ecological and evolutionary processes within islands, and most of the proposed island biodiversity patterns, rules and models, largely derive from empirical data on plants and birds (Matthews, Rigal, et al., 2019; Matthews, Sadler, et al., 2019; Valente et al., 2020; Veron, Haevermans, et al., 2019; Veron, Mouchet, et al., 2019). While arthropods played a key role in the early developments of island biology theory (MacArthur & Wilson, 1963, 1967; Wilson, 1959, 1961), and typically represent the vast majority of insular biodiversity, arthropod data pertaining to range size and co-occurrence remain under-represented in existing data sets. This can be explained by the difficulty of obtaining such data, due to the massive taxonomic diversity of arthropods and often limited taxonomic expertise. It is recognized that arthropods play a fundamental role in ecosystem processes and services (Dangles & Casas, 2019), and the potential negative impacts of introduced species are also well appreciated, with an estimated annual cost of more than 20 billion US$ (Diagne et al., 2021) associated with introduced invertebrate species. However, understanding of the contribution of arthropod species to ecosystem resilience, and their

TABLE 1 A nonexhaustive list of open questions in island biodiversity research for which HTS arthropod inventory could yield significant advances.

1. Global patterns and drivers of island arthropod biodiversity	*How does arthropod species richness respond to island area, age, elevation and isolation?*
	To what extent are island arthropod assemblages species poor and/or disharmonic?
	What biogeographic processes drive island species-area relationships (SARs)?
	Is there a general island SAR across all arthropod fractions, or do they vary?
	How do arthropod SARs differ among oceanic, continental-shelf, continental fragment and habitat islands?
2. Island community assembly of arthropod biodiversity	*What are the relative roles of stochastic and niche-based processes in driving arthropod community structure within insular systems?*
	What is the role of niche conservatism for ecological assembly across insular environmental gradients?
	How do island area, elevation and isolation influence community composition and dynamics?
	What metrics (species richness, functional group composition, phylogenetic diversity, interaction network properties, SADs, etc.*) characterize communities of different ages, disturbance regimes,* etc.*?*
	What factors contribute to the resilience of insular arthropod communities to perturbation?
	How can we best incorporate population genetic and/or phylogenetic data to advance island biogeography models?
3. Drivers of island arthropod speciation	*What are the relative roles of ecological and geographical drivers for diversification among arthropods within individual oceanic islands?*
	What species traits underpin diversification within arthropod island faunas?
4. Arthropod species abundances, endemicity and rarity within islands	*How and why do species abundances change as communities assemble?*
	What are the linkages between species rarity (geographical, habitat specificity and/or local population size) and endemicity in islands?
5. Biotic interactions of insular arthropods	*What role do biotic interactions play in island community assembly?*
	How do the interaction network properties impact island ecosystem function and vulnerability to disturbance?
6. Spatial and temporal monitoring to understand declines in and threats to insular arthropods	*How, if at all, do island arthropod biotas differ from continental biotas in their response to global change?*
	Which islands and island habitats are more susceptible to arthropod biodiversity loss?
	Which island arthropod taxa are most at risk from global change and what species-traits are associated with risk?
7. Invasive arthropod species detection, identification and implications for island biodiversity	*What is the magnitude of arthropod species introduction and invasion within islands?*
	What are the primary sources and mechanisms of arthropod introduction in islands?
	What are the dynamics of species naturalization on islands?
	How and why do natural habitats vary in their resilience against invasive species?

vulnerabilities, remain strongly data-limited (Cardoso et al., 2011; Cardoso & Leather, 2019; Harvey et al., 2020).

A recent initiative calling for the integration of arthropods within the monitoring of insular forest biodiversity also highlights the potentially prohibitive workload for this, even for a limited subset of arthropod biodiversity (Borges et al., 2018). The broad characterization of arthropod communities is a universal challenge, largely caused by logistical constraints associated with both the sorting of large volumes of arthropod material, and its classification to species. However, addressing these challenges through the application of genome-based sampling and taxonomic assignment is an area of intense activity (Arribas, Andújar, Bidartondo, et al., 2021; Arribas, Andújar, Salces-Castellano, et al., 2021; Kennedy et al., 2020; Piper et al., 2019), currently only paralleled by recent advances in the application of machine learning for the identification of taxa from image processing (Ärje et al., 2020; Valan et al., 2019; Wührl et al., 2022). Both DNA-based and image-based automated identification have the potential to exponentially accelerate arthropod diversity biomonitoring in the near future (Høye et al., 2021; Wührl et al., 2022). It is now timely to consider how these developments might be integrated to advance the understanding, management and conservation of insular biotas (Figure 1, Table 1).

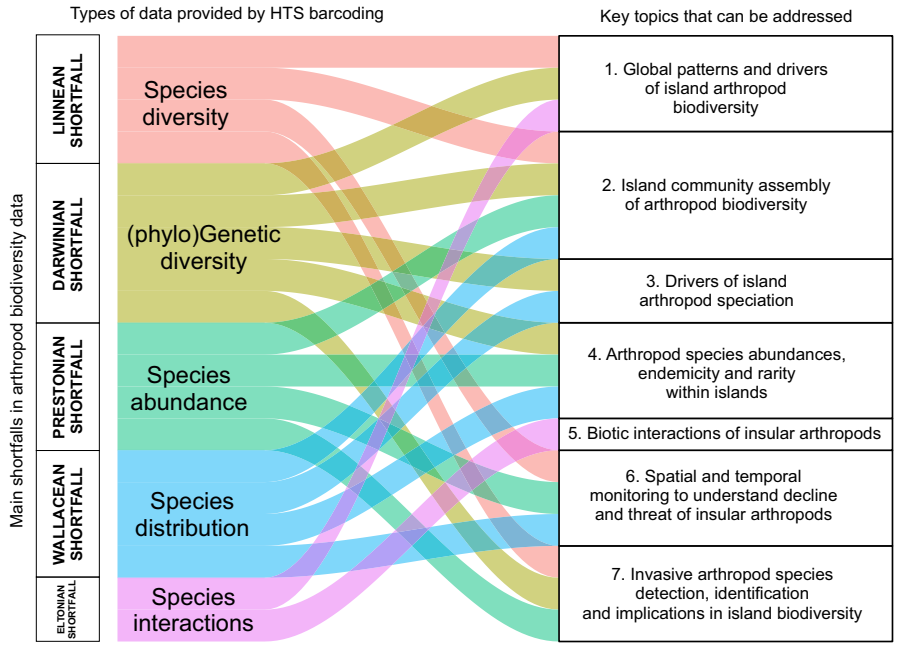

FIGURE 1 Schematic representation of the types of data provided by HTS barcoding, and their correspondence with key shortfalls for arthropod biodiversity data, and research areas within which collective and harmonized efforts in HTS arthropod inventory could yield significant advances in island biodiversity research.

Here, we focus on the arthropod fraction of terrestrial invertebrate biodiversity to provide a collective opinion of how we might most effectively exploit new technologies and techniques to inventory and monitor insular arthropod biodiversity. This should provide a baseline for the harmonization of future research work on insular arthropod diversity.

2 | HIGH THROUGHPUT BARCODE SEQUENCING OF ARTHROPODS AT SCALE

Arthropods offer high potential for structured sampling to obtain data-rich site-based community data, through the use of multiple complementary sampling methods (Montgomery et al., 2021). For nearly all sampling methods, sorting of samples and classification to species are substantial challenges, and thus a limitation to understanding the composition of arthropod communities at scale. For many groups, regional taxonomic knowledge is incomplete and, even for those groups that benefit from a robust taxonomic framework, sorting and species assignment is still hampered by the lack of highly trained personnel. Molecular barcode-based sequencing tools have already helped to overcome the challenges of taxonomic assignment and facilitate new species discovery and monitoring (deWaard et al., 2019; Hebert et al., 2003; Ronquist et al., 2020), and there are broader benefits for the characterization of diverse arthropod communities using high throughput sequencing (HTS) barcoding (Hajibabaei et al., 2016). HTS can be employed at the scale of individual specimens or bulk community samples (see Kennedy et al. (2020) and sections below), and both can greatly reduce existing limitations for identifying and understanding biodiversity patterns and processes across entire arthropod assemblages on islands. Additionally, even in the absence of a local reference library, taxonomic assignment is aided by the nearly 10 million arthropod specimens with barcode sequences within the BOLD repository when HTS metabarcoding is coupled with the use of the universal mitochondrial DNA (mtDNA) barcode region (Andújar et al., 2018).

2.1 | Multiplex barcoding and whole organism community metabarcoding

While classical barcode sequencing involves the individualisation of both the PCR and sequencing reactions, HTS platforms now offer the opportunity to pool thousands of amplicons from individual specimens via tagged amplicon sequencing (Creedy et al., 2020; de Kerdrel et al., 2020; Hebert et al., 2018; Shokralla et al., 2014; Srivathsan et al., 2019, 2021). This can be scaled up to 10,000 multiplexed individuals within a single MinION flow cell (Srivathsan et al., 2019, 2021) or several hundred thousand for one lane of NovaSeq 6000 when a reduced length "mini barcode" is used (Yeo et al., 2020). HTS multiplex barcoding provides a direct link between DNA sequences and the individuals from which they were amplified. This has several advantages. It allows for the sorting of physical specimens into putative species and resolving taxonomic disagreements between barcodes and other data (Wang et al., 2018), which can involve few species, but large numbers of specimens in some samples (Hartop et al., 2022). Disagreements occur when the associated barcode sequences are unusual (e.g., unexpectedly high sequence divergence within species or low divergence between species) or species delimitation approaches with different algorithms return conflicting results (Meier et al., 2021). Fortunately, Hartop et al. (2022) show that the morphological study of as few as 5% of all specimens can resolve such disagreements. Individual barcoding also allows one to return to the DNA extract, should there be interest in further exploring the nuclear genome, diet content or microbiome of specific specimens (Kennedy et al., 2020). Another

very obvious advantage is that abundance estimates can be directly obtained from the DNA sequence data.

In contrast to multiplex barcoding, whole organism community DNA (wocDNA) metabarcoding (Andújar et al., 2018; Creedy et al., 2022; Yu et al., 2012) involves a single DNA extraction for multiple individuals from multiple species, that is subsequently PCR amplified and sequenced, typically using the Illumina platform. This reduces the individualized processing of specimens, which is particularly relevant for hyperdiverse (and minute specimen) arthropod assemblages (Arribas et al., 2016; Creedy et al., 2019) and/or high numbers of community samples (e.g., for long-term or broad-scale approaches). However, there are a number of ways in which the information content of wocDNA metabarcode data is different from multiplex barcode data, either requiring additional data processing or placing limits on inferences that can be derived. An important feature of wocDNA metabarcode sequence output is the difficulty to discern spurious sequences (PCR and DNA sequencing artefacts, contamination, nuclear copies, or different combinations of these) from real (but low abundance) sequences in the community sample. With appropriate laboratory protocols, design and bioinformatic processing, contamination issues and PCR and DNA sequencing artefacts can be substantially reduced (Alberdi et al., 2018; Creedy et al., 2022). It has also recently become possible to effectively remove nuclear copies of mtDNA sequences, providing for haplotype-level resolution from wocDNA metabarcode data (Andújar et al., 2021). Within wocDNA metabarcode data, there is no correspondence between sequences and the individual from which they are derived. While biodiversity patterns can still be explored without taxonomic assignment, species-level taxonomic assignment is generally a desirable feature, and in this case, can be only achieved with taxonomically assigned barcode reference sequences. Even without species-specific reference libraries, arthropod sequence assignment to some taxonomic level can be achieved using public repositories (e.g., GenBank or BOLD). Finally, the extrapolation of abundance data from metabarcode sequence output is complicated, but several promising approaches for deriving abundance data from standardized samples have been developed (Ji et al., 2020; Krehenwinkel et al., 2017; Lim et al., 2022; Luo et al., 2022).

The choice of HTS barcoding approach to catalogue arthropod biodiversity will be dependent on financial resources and the specific objectives to be addressed. In principle, multiplex barcoding and metabarcoding complement each other in that the data obtained from the latter are more readily interpreted when a DNA barcode library is available. Typically, wocDNA voucher sequences are obtained by selecting voucher material from wocDNA samples that broadly represent morphological diversity within the sample (Arribas et al., 2016; Noguerales et al., 2022). Such metabarcode vouchering may thus be considered unnecessary when a well-parameterized reference library is simultaneously obtained with multiplex barcoded vouchers. Another important benefit of extensive reference barcode databases is that they provide a direct connection between biodiversity metrics and indices, and the species they represent, which is likely to be of particular relevance and importance for environmental managers. Individualized and validated barcode sequences are also of particular relevance for the bioinformatic processing of metabarcode reads to remove nuclear copies (Andújar et al., 2021), a known source of artefactual taxonomic inflation (Arjona et al., 2022).

2.2 | Robotics, artificial intelligence and the integration of image analysis and barcode sequencing

Exciting advances are being made in the areas of robotics and image analysis for arthropods. Species identification via image analysis is currently based on convolutional neural networks (CNNs), a specific tool in the field of deep learning (DL), where complex image patterns are classified taking advantage of training sets (Valan et al., 2019, 2021). However, the training of CNNs requires large sets of training images whereby each image has to be labelled with reliable taxonomic information. Perhaps not surprisingly, such data sets are available for bees and butterflies (Buschbacher et al., 2020), but are largely missing for the bulk of arthropods collected by standardized trapping. The challenge is to generate these data sets, and this is where a combination of robotic specimen handling and HTS multiplex barcoding can help. Recently, Wührl et al. (2022) presented a first-generation robot for this purpose. It images each specimen before it is moved into the well of a 96-well microplate for HTS barcoding. After barcoding, the images can be assigned to molecular operational taxonomic units (mOTUs) and convolutional neural networks can be trained once a sufficiently large number of assigned images become available. This approach potentially opens the door for a transition away from multiplex barcode sequencing of all individuals toward taxonomic assignment by image recognition, as images with barcode sequences contribute to training images for machine learning. The level of taxonomic assignment will likely depend on the number of training images available, and the ease with which species can be distinguished (see Wührl et al., 2022, for a discussion of challenges). Image-based specimen identification could, nevertheless, be used as an external validation of molecular-based diversity estimations at, for example, genus level. Similarly, image analyses can yield information on sample biomass and abundance (Ärje et al., 2020; Schneider et al., 2022; Wührl et al., 2022).

3 | GENOMIC OBSERVATORIES: A FRAMEWORK FOR HARMONIZED HIGH THROUGHOUT BARCODE SEQUENCING OF ISLAND ARTHROPODS

The biodiversity, ecology, and evolution of island arthropod communities can be studied at unprecedented scales and resolution through the individual or joint application of (i) wocDNA metabarcoding, (ii) barcode reference libraries, (iii) multiplex barcoding and (iv) image analyses. Harmonization across the first three approaches can also provide for a common data currency, facilitating comparisons and

synthetic analyses across independent studies. By incorporating the universally accepted arthropod barcode region of the mitochondrial cytochrome oxidase subunit I (COI) gene into wocDNA metabarcoding (Andújar et al., 2018; Elbrecht et al., 2019), the COI barcode region can act as a directly comparable species tag across any given study, transcending potential taxonomic assignment errors within individual studies. The Genomic Observatory concept, within which HTS serves as a core tool for biodiversity assessment (Arribas, Andújar, Bidartondo, et al., 2021), provides a solid foundation for implementing genome-based inventory and monitoring of insular arthropod biodiversity.

Harmonized HTS data generation and bioinformatic workflows for general arthropod inventory and assessment are emerging (Arribas et al., 2022; Creedy et al., 2022; Srivathsan et al., 2021). However, more development is needed for an inclusive range of sampling protocols that can capture important arthropod fractions of biodiversity on islands (see Montgomery et al., 2021 for a review). For terrestrial fractions of arthropod biodiversity, these can be developed as submodules within the recently proposed framework of Arribas et al. (2022), taking advantage of their proposed downstream submodules for the processing and sequencing of samples.

In addition to the need for harmonized data generation protocols, there are other generic obstacles for Genomic Observatories that need to be addressed for an efficient island Genomic Observatories Network. One important challenge is to ensure that, together with barcode reference sequences, morphological voucher images and metabarcode data conform to Findable, Accessible, Interoperable and Reusable (FAIR) Data Principles (Wilkinson et al., 2016), such that new wocDNA metabarcode and multiplex barcoding data sets can be cross-referenced to previous work. In the same way that cross-referencing sequence reads to barcode sequence repositories can assign taxonomy and clarify species origins, additional cross-referencing to a metabarcode sequence repository would facilitate understanding the structure of community similarity over a range of spatial scales. The GEOME (Genomic Observatories Metadatabase; Deck et al., 2017; Riginos et al., 2020) initiative offers a very useful platform, facilitating FAIR data archival practices. GEOME also facilitates DNA data sharing through the deposition of raw genetic data to the Sequence Read Archive (SRA, www.ncbi.nlm.nih.gov/sra), while maintaining persistent links to standard-compliant metadata held in the GEOME database. Achieving seamless cross-referencing among de novo wocDNA metabarcode sequences, multiplex barcoding sequences and repositories of both barcode sequences and wocDNA metabarcode sequences has the potential to dramatically extend the scope and reach of such data.

4 | ISLAND GENOMIC OBSERVATORIES—A NETWORK FOR ISLAND ARTHROPOD CONSERVATION AND BROADER BIODIVERSITY UNDERSTANDING

With strategic implementation, an island Genomic Observatories Network (iGON) has the potential to advance understanding in three areas, the first and more fundamental of which is that of knowledge acquisition and transfer for conservation and sustainable management. Arthropods dominate the native and endemic fractions of island biodiversity, while also representing substantial invasive species risk, but are data deficient compared to vertebrates and plants. HTS barcoding can greatly contribute to knowledge deficits concerning species inventory, species distributions, the geographic structuring of genetic variation within species, and the factors that explain this structure (Arjona et al., 2022). With specific regard to islands, the generation of HTS barcode data within an iGON opens the door to improved investigation of fundamental island biogeographic theory using arthropods (Andújar et al., 2022; Armstrong et al., 2022; Lim et al., 2022). Finally, island communities can be leveraged to address the recognized need for integration across the disciplines of macroecology and macroevolution, where synthesizing data, tools and perspectives is required (McGill et al., 2019). The often simplified and replicated nature of island ecosystems, together with increasingly available technology to characterize the arthropod fractions of their biodiversity, provides a profitable arena for such integration.

To explore the potential of an iGON for the advancement of fundamental and applied biodiversity understanding, we use two recent reviews as a guiding framework, focused on open questions in island biology (Patiño et al., 2017) and the unification of macroecology and macroevolution (McGill et al., 2019). Within this framework, we identify key themes within which collective and harmonized efforts in HTS arthropod inventory (either in isolation or in concert with other approaches) could yield significant advances in island biodiversity research (see Figure 1, Table 1). Some of these themes include questions related to basic properties of species diversity of island arthropods, compared to more studied vertebrate groups, while others pertain to fundamental research areas that have been constrained by access to data.

4.1 | Global patterns and drivers of island arthropod biodiversity

Studies of global-scale patterns and drivers of island biodiversity rely on the existence of island species inventories (Borges et al., 2018). Arthropod species lists for islands have been leveraged for comparative analyses to infer the processes that shape variation in species richness (Chown et al., 1998; Santos et al., 2011; Triantis et al., 2015). However, many arthropod species are still not formally described (commonly referred to as the Linnean shortfall, Lomolino, 2004), strongly hampering inferences of richness, diversity and endemism (Cicconardi et al., 2013; Emerson et al., 2011; Legros et al., 2020), and hence, conservation efforts (Cardoso et al., 2011). Structured HTS inventories of arthropod communities across islands hold great potential to overcome this shortfall by providing a way forward. HTS barcoding allows for the species diversity of communities to be quantified independently of the proportion of undescribed species present. Species that lack a barcode reference sequence and/or undescribed species will initially be assigned to the level of a molecular Operational Taxonomic Unit (mOTU) which can

serve as a species-proxy in many analyses. Only when local barcode reference libraries for already described species become complete will it be possible to identify which mOTUs represent undescribed species. Such undescribed species should be subject to formal taxonomic classification, that may potentially be aided by sequenced voucher material in the case of multiplex barcoding. Complete barcode reference libraries are thus an important pillar for revealing undescribed species and facilitating their description.

HTS barcoding also opens the door for inclusive inventories that include immature life history stages, and extend to the typically small and cryptic taxa fractions of arthropod diversity that are associated with high levels of undescribed species, the so called "dark taxa" (Hartop et al., 2022; Hausmann et al., 2020). As proof of concept, Yeo et al. (2021) implemented multiplex barcoding to inventory the tropical arthropod fauna of Singapore across six different forests and a freshwater swamp. They generated 140,000 barcoded specimens belonging to c. 8500 species and identified an overlooked hotspot of insect diversity within the mangrove habitat. Similarly, Arjona et al. (2022) applied wocDNA metabarcoding to characterize the coleopteran fauna sampled from soils within an island cloud forest, highlighting the power of HTS for both detecting unrecorded species and species discovery. They additionally demonstrated the value of barcode reference libraries, even if incomplete, for efficient bioinformatic processing to achieve reliable haplotype data (Andújar et al., 2021) and, in doing so, provided strong evidence for taxonomic inflation in the absence of such processing. Complete island arthropod inventories (i.e., from exhaustive sampling and encompassing undescribed species) that are comparable across different insular systems (by direct comparison of DNA barcodes) can be used to address fundamental topics within island biology, for which understanding is still limited. These include: (i) the relationships among island area, geological age, elevation and isolation and arthropod species richness; (ii) the biogeographic processes driving island species-area relationships (SARs), and (iii) how arthropod SARs vary among different arthropod fractions and among different island contexts, including oceanic, continental-shelf, continental fragment and habitat islands.

WocDNA metabarcoding can be applied to generate vast amounts of site-based data, and if combined with multiplex barcoding, barcoded vouchers can be retained for specific taxonomic reference. Such HTS barcoding data opens the door for the phylogenetic placement of potentially all sampled species when combined with appropriate backbone trees (Balaban et al., 2018). With the development of mitochondrial metagenomics (Crampton-Platt et al., 2016), backbone trees can now be generated with good resolution for major arthropod lineages (Arribas et al., 2020; Tang et al., 2019). Thus, by returning to multiplex barcode DNA extracts or strategically sampling vouchers from wocDNA samples prior to bulk DNA extraction, such backbone trees for an island fauna can be obtained. Assemblage level phylogenetic trees then provide the needed framework to ask, for example, how taxonomic and phylogenetic diversity vary across gradients of interest, within islands, among islands, and between islands and ecologically comparable continental areas.

4.2 | Island community assembly of arthropod biodiversity

Understanding how biological communities form, and why they differ spatially and temporally, is a key objective in ecology. The integration of phylogeny into the analysis of community ecology has provided new dimensions for comparing and contrasting communities, within which insular environments have proven to be useful sampling frameworks (Emerson & Gillespie, 2008; Shaw & Gillespie, 2016). Island systems can yield significant arthropod structuring and turnover over relatively limited spatial scales and across entire assemblages (Salces-Castellano et al., 2021). Such limited spatial dimensions allow for fine-scale but geographically representative community-level sampling to characterize the community assembly process. When executed across multiple islands and coupled with remote sensing data, there is much potential for an improved understanding of the factors that shape such patterns (Bush et al., 2017).

Community-scale investigation to describe patterns and infer processes for island biodiversity requires multiple site-based characterisations of communities, which is a clear bottleneck in the case of the arthropod biodiversity. Existing studies in this area have been limited to specific arthropod lineages, such as beetles or spiders, for which conventional taxonomical and molecular processing is time-consuming (Malumbres-Olarte et al., 2021; Salces-Castellano et al., 2020). HTS barcoding provides an opportunity to increase both the taxonomic and geographic scale of arthropod community sampling. When combined with distribution data across gradients (e.g., elevation, disturbance, island age) or trait data (e.g., dispersal ability, body size), the opportunities for macroevolutionary and macroecological unification become tangible. As a proof of concept, Lim et al. (2022) applied wocDNA metabarcoding to characterize complete arthropod communities across elevational gradients within the island of Hawaii. They revealed that climatic niche conservatism is an important factor shaping ecological assembly across elevation, thus implicating topographic complexity as an important driver of diversification. Similarly, wocDNA metabarcoding approaches to characterize soil arthropod assemblages on the islands of Tenerife and Cyprus have revealed strong habitat filtering and dispersal limitations as drivers of community assembly within islands (Andújar et al., 2022; Noguerales et al., 2022).

Islands, particularly remote islands, offer much potential for integrating intraspecific-scale analyses together with phylogenetic sampling for the investigation of community assembly. Speciation represents an important contribution to both the origin and evolution of community structure on remote islands (Shaw & Gillespie, 2016), thus providing opportunities to link diversification patterns within species to patterns of speciation at higher levels. Community-level intraspecific sampling on islands has seen less implementation, and it is here that HTS barcoding can play an important role. As well as recording species presence, HTS barcoding provides a measure of haplotype variation within and across communities, thus addressing the traditional Darwinian shortfall (defined as the lack of knowledge

regarding the evolution of lineages, species, and traits; Diniz-Filho et al., 2013) for arthropod island faunas. Thus, alpha and beta diversity can be analysed for hyperdiverse arthropod communities from genetic to different levels of taxonomic hierarchy to understand how community-level processes drive macroecological and macroevolutionary patterns. Processes that can be characterized include the relative importance of stochasticity, isolation by distance, and habitat or host-associated differentiation (Andújar et al., 2022; Noguerales et al., 2022; Arribas, Andújar, Salces-Castellano, et al., 2021). Additionally, the extent to which species diversity and genetic diversity covary can be derived from such data (Vellend, 2010; Vellend et al., 2014). Overcast et al. (2019) have recently described a mechanistic model of community assembly that can generate linked patterns of abundance and genetic diversity under an assumption of joint ecological and evolutionary neutrality, allowing for the estimation of community abundance structure using only intraspecific genetic variation. As proof of concept, this study demonstrated that the abundance structure of spiders on the island of Reunion could be accurately estimated from intraspecific variation from barcode data (Emerson et al., 2017). Further theoretical developments will be needed to fully exploit the potential of genetic community-level data for unifying macroevolution and microevolution, together with macroecology and microecology, and thus further advance island biogeography theory.

4.3 | Drivers of island arthropod speciation

Traditional approaches to speciation research typically analyse a limited number of species in great detail, necessitating accurate estimation of population and phylogenetic histories, and the limitations of single-locus markers for such purposes are well recognized (Bazin et al., 2006; Toussaint et al., 2015). However, it has been shown that, across multispecies comparisons, potentially idiosyncratic single marker signals within a subset of arthropod species may be outweighed by common community level signatures (Salces-Castellano et al., 2020; Scalercio et al., 2020). As the histories of individual species complexes may themselves be idiosyncratic, having noisy data across hundreds or even thousands of species may, in some cases, be more revealing of general patterns and processes in a region than deeper sequencing of a more limited number. With the ability to now obtain reliable haplotype-level data from metabarcode sequence output (Andújar et al., 2021), it is possible to implement both multiplex barcode and wocDNA metabarcoding to explore the patterns and drivers of diversification and speciation across arthropod assemblages. Andújar et al. (2022) demonstrate the implementation of such a metaphylogeographic approach with wocDNA barcoding to understand the relative roles of ecological and geographical drivers for diversification among soil arthropods within a single oceanic island. Extending such an approach across multiple islands within archipelagos can provide baseline data on the relative importance of ecological and geographical speciation within many as yet largely unstudied fractions of arthropod diversity. When contrasted with existing data for plants, vertebrates, and more easily studied arthropod groups, a fuller understanding of: (i) dispersal dynamics within and among islands; (ii) the role of environment in structuring genetic variation within species, and (iii) their implications for speciation, will emerge. Recent work also demonstrates how a single locus community-level approach can inform about the relative importance of specific traits for diversification within islands (Salces-Castellano, Andújar, et al., 2021). In conjunction with barcode reference libraries with trait data (e.g., body size, dispersal ability, niche) multiplex barcoding and wocDNA metabarcoding can be used to scale up both geographic and taxonomic sampling to identify functional traits associated with arthropod diversification within and across island systems.

4.4 | Arthropod species abundances, endemicity and rarity within islands

The Prestonian shortfall is defined as the lack of knowledge about the abundance of species and their population dynamics in space and time (Cardoso et al., 2011). This shortfall is extremely pronounced in the case of arthropods (Cardoso & Leather, 2019), likely associated with the high diversity and complexity of both individual population trends and species interactions of local arthropod communities. HTS barcoding, particularly multiplex barcoding, has much potential to address this shortfall. Generating abundance estimates through HTS barcoding for insular arthropod communities is a potentially rich source of information for empirical testing of island biogeographic theory. This is particularly relevant for questions regarding arthropod species abundance distribution within islands (Borda-De-Água et al., 2017), and questions at the intersection of species abundances patterns and the processes of speciation and extinction. Such abundance data can now be directly generated for complete arthropod assemblages, even in the absence of formal species description, using multiplex barcoding (Srivathsan et al., 2021). PCR-free metagenomic approaches can also provide abundance estimates (Ji et al., 2020). In addition to this, the integration of image analysis, together with either multiplex barcoding, or wocDNA metabarcoding, can further remove limitations of scale. Beyond specific interest in island biogeographic process, it has also been pointed out that sampling across islands can provide for a more general understanding of how and why species abundances change through community assembly (Warren et al., 2015). The neutral spatially explicit model (NSIM; Rosindell & Harmon, 2013) predicts patterns as islands approach equilibrium conditions, in the classic sense of the equilibrium theory of island biogeography (ETIB; MacArthur & Wilson, 1967), reflected in immigration rates, extinction rates and species abundance distributions (SADs).

Within islands, HTS barcoding also harbours the potential to overcome the Wallacean shortfall for arthropod faunas, which is defined as the lack of knowledge regarding the geographical distributions of species (Hortal et al., 2015; Lomolino, 2004). Arjona et al. (2022) provide a clear example of this, revealing substantial

improvements to beetle species distribution data from wocDNA metabarcoding. Geographical distribution data for insular arthropod faunas, together with genetic and abundance data at the community-level (also derivable with the HTS barcoding tools) offer an ideal setting to explore linkages between species rarity (geographical, habitat specificity and/or local population size) and endemicity (Fernández-Palacios, Kreft, et al., 2021; Fernández-Palacios, Otto, et al., 2021; Ribeiro et al., 2005).

4.5 | Biotic interactions of insular arthropods

Islands are providing important advances in the application of ecological network approaches for the understanding of ecosystem function, and vulnerability to disturbance (Traveset et al., 2016). The time-consuming task of arthropod sorting and identification that is needed to quantify plant-arthropod or arthropod-arthropod associations is a bottleneck for addressing the Eltonian shortfall for arthropods, defined as the lack of knowledge of interactions among species or among groups of species (Hortal et al., 2015). However, progress toward addressing this shortfall can be scaled up with the application of HTS barcoding. WocDNA metabarcode data can be used to estimate ecological/trophic networks through co-occurrence analysis (Bohan et al., 2017). Sampling strategies that yield few arthropod individuals per sampled plant would be most efficiently coupled with multiplex barcoding. However, larger arthropod samples, such as aggregating arthropod samples by plant species (Rego et al., 2019; Ribeiro et al., 2005), can be coupled to wocDNA metabarcoding. Recently, environmental DNA metabarcoding from plant material offers promise as an additional tool to recover arthropod-plant interactions (Krehenwinkel et al., 2022; Thomsen & Sigsgaard, 2019). Barcode reference sequences for taxonomic assignment will be desirable, but even in their absence, ecological networks can still be established with higher-level taxonomic assignment. For example, recent work using metabarcoding across the geological chronosequence provided by the Hawaiian archipelago revealed a trend of increasing specialization with community age (Graham et al., 2022).

One largely unresolved challenge for understanding the biotic interactions of many arthropod species is the different biology of the life history stages. The problem is exacerbated by the fact that most arthropod sampling methods favour adults, although the larvae of many species may be important for biotic interactions. An in-depth understanding of the interaction thus often requires multiplex barcoding of adults and larvae in order to establish barcode matches between adult and larval stages (Yeo et al., 2018).

Moving from association data to trophic interactions can be integrated within a multiplex barcoding framework, and may be particularly useful to improve predictions within the trophic theory of island biogeography (Gravel et al., 2011; Holt, 2009). Gut or digestive system metabarcoding from appropriate individual DNA extractions (e.g., whole organism) can be used to characterize both herbivore (Kitson et al., 2016) and predator diet (Cuff et al., 2021; Kennedy et al., 2019). This can be more challenging in predators due to the issue of coamplification of predator DNA (see Kennedy et al., 2020, for review), although this obstacle can be overcome via careful primer design (Krehenwinkel et al., 2019). Advances in the characterization of arthropod microbiomes offer new dimensions to investigate the dynamics of both ecological success (e.g., invasive species) and vulnerability (e.g., range-restricted endemic species), while also investigating the temporal and spatial dynamics of microbiome evolution (Leo et al., 2021). For example, independent but geographically coincident patterns of island colonization and speciation, such as those conforming to the progression rule (Shaw & Gillespie, 2016), can be used to understand potential generalities of microbiome evolution, associated with a history of founder event speciation. As a proof of concept, Armstrong et al. (2022) have explored how the associated microbial communities within a lineage of spiders have changed with colonization across a chronosequence of volcanoes in Hawaii.

4.6 | Spatial and temporal monitoring to understand declines in and threats to insular arthropods

Evidence is accumulating globally that terrestrial insect abundance and biomass are in decline across multiple regions, habitats and taxa (Hallmann et al., 2017; Wagner et al., 2021), although the historical scarcity of highly-standardized long-term arthropod monitoring programmes leaves uncertainty of the nature, scope, and taxonomic and geographic variation of the problem. The establishment of such programmes has been limited by the time and specialized expertise required to process samples across whole arthropod communities. It is difficult to evaluate which of the potential drivers of long-term declines are most responsible, and thus most important to address, without extensive data with minimal biases (Cardoso & Leather, 2019; van Klink et al., 2022). Thus, HTS combined with methods to measure abundance provide a route to the practical and comparable long-term monitoring of communities globally.

Islands should be particular priorities for monitoring given their relative biodiversity value, high human impact, and utility as harbingers of more general global change (Fernández-Palacios, Kreft, et al., 2021; Fernández-Palacios, Otto, et al., 2021). However, they are underrepresented in global initiatives for biodiversity monitoring and biodiversity indicator frameworks, prompting calls for coordinated surveying and monitoring of island biotas (Borges et al., 2018). Two facets of island biota provide cause for concern in the context of potential decline in abundance and biomass. First, general decreases in arthropod abundance are likely to exacerbate extinction risk at the level of individual species, due to already geographically limited range sizes (Manes et al., 2021; Veron, Mouchet, et al., 2019). Second, island biotas are inherently at risk from species invasion and decreased local abundance of native species could increase this threat (Bellard et al., 2017; Borges et al., 2020; Russell & Kueffer, 2019). Understanding island arthropod decline in the (broadly common) absence of historical data (but see e.g., Colom

et al., 2021; Theng et al., 2020) can, to some extent, be addressed by sampling across gradients for suspected drivers of decline, such as climate (Ferreira et al., 2016) and disturbance (Cardoso et al., 2013). Given the critical focus on abundance and biomass, multiplex barcoding can be used, and total abundance partitioned to individual species for the identification of more nuanced abundance changes across species. Alternatively, PCR free metagenomic approaches allow estimating the abundance of different arthropod species (Ji et al., 2020), and wocDNA metabarcoding has been demonstrated to reveal relative abundances of species, when coupled with specimen counts (Lim et al., 2022). Although still in early development, CNNs and DL (see above) hold promise for photographing and archiving samples prior to wocDNA metabarcoding, for future abundance estimation (Arribas et al., 2022).

The high throughput and efficiency of HTS barcoding approaches represent a viable long-term solution for monitoring and documenting change within island arthropod communities and, in the context of an iGON, these can be integrated within existing frameworks (Borges et al., 2018). Suggestions for a coordinated approach to inventory and temporal monitoring, through spatially extensive inventory with a subset of sites subject to temporal sampling (Arribas, Andújar, Bidartondo, et al., 2021), can provide needed baseline data for conservation planning. Range size is frequently used in conservation planning, within which species with small ranges and often declining abundances are given higher priority. Indeed, range restriction and population trends are integral to the International Union for Conservation of Nature (IUCN) criteria to identify and classify species threatened with global extinction. While downstream bottlenecks of the red-listing process are now being addressed by semi-automated systems (Cazalis et al., 2022), upstream the common data deficiency for arthropods within islands limits effective red listing by the IUCN. Strategically designed spatial and temporal HTS barcode sampling networks can provide species records at scales appropriate for both IUCN needs, and the needs of local conservation and management agencies and stakeholders. Such scales go as far as the microhabitat level, as threat might be influenced by it. As an example, classical sampling of Madeiran spiders suggests ground-associated species are at greater risk of local extinction than those from canopy microhabitats (Cardoso et al., 2017; Crespo et al., 2021). This parallels more general inferences for greater climate change impacts for forest floor arthropod species compared to canopy species in Puerto Rico (Lister & Garcia, 2018). More involved implementations of stratigraphically structured sampling and HTS barcoding with abundance data (i.e., multiplex barcoding or wocDNA barcoding with artificial intelligence for image recognition) also has the potential to simultaneously contribute local species records, basic niche information (stratigraphic distribution), and local abundance.

4.7 | Invasive arthropod species detection, identification and implications for island biodiversity

Non-native arthropod species within insular environments represent a fundamental dimension of the ongoing biodiversity crisis (Borges et al., 2020). The typically depauperate biotas of islands contribute to increased sensitivity to invasive species when compared with continental areas (Bellard et al., 2017), and it is generally understood that early warning and rapid response to new arrivals is necessary to head off establishment and spread, highlighting a need for robust and rapid island monitoring (Borges et al., 2018). A strong argument for the continued effort toward global arthropod barcoding reference databases is the added value these can provide for HTS-based approaches for the biosurveillance of nonindigenous species. Traditional detection methods are expensive, prone to time lags, and require specialized expertise, creating a need for rapid and accurate biosurveillance tools, tailored to the needs of particular biogeographic regions (Westfall et al., 2020). As reference barcode sequences accumulate globally for both recognized and potential arthropod pest species, HTS barcoding for biosurveillance becomes a more powerful alternative to traditional approaches. Even in the absence of reference sequences for taxonomic assignment, genetic signatures can be leveraged for the inference of probable non-native species. Using insects and spiders on the island of Moorea, Andersen et al. (2019) have demonstrated a novel approach to categorize species as being either likely native or likely non-native, based solely on measures of nucleotide diversity. When coupled with spatially structured and temporally replicated haplotype-level wocDNA metabarcoding, novel appearance and increasing site occupancy data could also potentially be leveraged to infer novel non-native species and range expansions. The advent of high-throughput multiplex HTS barcoding also allows for testing the resilience of natural habitats against invasive species. Baloğlu et al. (2018) showed that the rich chironomid midge fauna (c. 300 spp.) of a very small remnant of a swamp forest (90 ha) was resilient against invasion by c. 50 species of "reservoir" chironomid midge species from three adjacent man-made reservoirs: only eight species accounting for c. 3% of the 14,000 barcoded specimens were shared.

Well-inventoried island systems can be used to test fundamental invasive species theory (Schaefer et al., 2011) and, when coupled with temporal sampling, the dynamics of introduced arthropod species abundances can be used to guide management strategy (Matthews, Sadler, et al., 2019). The often relatively simplified nature of island ecosystems provides opportunities for both island-wide and community-level sampling to contribute to a more general understanding of the properties and dynamics of introduced and invasive species (Borges et al., 2020). Schaefer et al. (2011) sampled the entire Azorean flora for a phylogenetic understanding of evolutionary relatedness as a predictor of invasion potential. In concert with mitogenome backbone trees (see Section 1), similar opportunities arise for arthropod fractions of island biodiversity with HTS barcode data. Indeed, if combined with DNA sequence-based frameworks to assign likelihood for native or non-native species status, such as that of Andersen et al. (2019), spatially explicit HTS barcode data can address the uncertainty of species status for more robust inferences. Detailed sampling of arthropods to quantity functional trait structure in the Azores has revealed that, in agricultural landscapes, non-native species may contribute positively to the maintenance of some ecosystem functions (Ferrante et al., 2022; Rigal et al., 2018).

Barcode reference libraries with relevant trait data, together with HTS barcoding of arthropods across comparable natural and agricultural gradients in other islands, provide a cost effective and logistically feasible pathway to assess the broader generality of these findings.

5 | CONCLUSIONS

Advances in high throughput DNA barcoding, together with progress in the field of automated image-based identification, are providing new ways to generate fundamental biodiversity data for arthropods. These exciting developments can be leveraged to address key data shortfalls for arthropods that have important implications for both conservation and management, and answering key questions in ecology and evolution. We have focused on islands, due to their biological importance and conservation concern, to assess how such developments can be integrated to advance the understanding, management and conservation of their biotas. Taken together, there is a strong rationale for global, coordinated and funded island Genomic Observatories, to complement other forms of space and ground-based Earth observation. These "biodiversity weather stations" could help monitor and understand climate and degradation-driven biodiversity trends, track the global spread of invasive species in real time, and be harbingers for changes that will ultimately manifest in continental systems. We conclude that high throughput barcoding can be applied to address multiple dimensions of existing data shortfalls for insular arthropods, and that ongoing developments in the area of image-based identification will likely lead to even higher efficiency. The DNA barcode provides a universal currency for measuring and comparing arthropod biodiversity and, if implemented within the framework of an island Genomic Observatories Network, can connect island biodiversity research at a global scale.

AUTHOR CONTRIBUTIONS

Carmelo Andújar, Paula Arribas and Brent Emerson organized and coordinated the working group. All authors contributed ideas and discussion to this Opinion article. Brent Emerson led the writing, together with Paula Arribas and Carmelo Andújar, with contributions from all authors.

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CONFLICT OF INTEREST

There are no conficts of interest associated with this work.

DATA AVAILABILITY STATEMENT

No data were analysed.

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