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PERSPECTIVE

The future of zoological taxonomy is integrative, not minimalist

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Roughly 18,000 species are described annually as new to science, while estimated extinction rates are comparable to or even exceeding these new discoveries. Considering the estimates of up to 15 million extant eukaryotic species on Earth, of which only about 2 million have been described so far, there has been a recent 'boom' of new potential approaches to more quickly discover and describe the millions of unknown species. This deficit is particularly noted in hyperdiverse taxa, as the current rate of species discovery is considered too slow. Recently, a 'minimalist' alpha taxonomic approach was proposed, relying solely on DNA barcoding and a habitus photograph, in a claimed effort to expedite the naming of new species to combat the so-called taxonomic impediment. In this paper, we point to limitations of minimalist taxonomy, present arguments in favour of the integrative approach, and finally explore a number of potential solutions to combat the taxonomic impediment in hyperdiverse taxa without sacrificing utility and quality for apparent speed and quantity.

Key words: automated morphological classification, biodiversity, citation mandate, eDNA, hyperdiverse taxa, integrative taxonomy, museomics, species description, systematics, taxonomic impediment

Introduction

It is estimated that there are up to 15 million extant eukaryotic species on Earth, of which only about 2 million have been discovered and described so far (Mora et al., 2011; Zamani et al., 2021). This puts taxonomists in a race against time to discover and describe the vast unknown portion of Earth's biodiversity before it is lost as a result of the Anthropocene mass extinction. Each year about 18,000 species are described as new to science, with the annual species loss similar to, or even higher than, the rate of new species discoveries (Zamani et al., 2021), excluding the annual number of new synonyms which could be quite significant (e.g., around 20% of names in insects; Stork, 1997). While naming new species is important, it is but one of the goals taxonomists are tasked with, the others being to circumscribe, properly describe and classify new taxa alongside their relatives (Seberg et al., 2003), as well as to curate existing names. Whereas naming follows enforced convention, species delimitation and their systematic relationships are scientific hypotheses rather than facts (Pante et al., 2015). As such, these practices need to be formulated in a way that clarifies species' differences from other previously described species via a clear *diagnosis* (i.e., unique traits or combinations of traits), as well as a suite of shared traits representing the ancestor-descendant lines that connect all life (ICZN, 1999; Pante et al., 2015). This process can be time consuming, and new approaches are needed to quickly discover and

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accurately describe millions of currently unknown species in a timelier manner.

Since the foundational paper by Hebert et al. (2003) introducing a standardised fragment of mitochondrial cytochrome oxidase I (COI; i.e., a molecular 'barcode') as a means of *identifying* known animal species, DNA barcoding has served a major role in biological sciences. In particular, DNA markers, especially DNA barcodes, have been a boon to species *discovery* when complemented with morphological studies and additional molecular and ecological data, made possible by having DNA barcodes of previously described species (e.g., Vieites et al., 2009). Its utility in systematics is widely recognised, and since its inception, DNA barcoding has been seen as a useful, albeit imperfect, tool in integrative taxonomy (e.g., Dayrat, 2005; DeSalle et al., 2005; Wheeler et al., 2004). A recent move towards a 'minimalist' alpha taxonomic approach relies solely on a consensus DNA barcode and a habitus photograph (Meierotto et al., 2019; Sharkey et al., 2021b). This effort to expedite the *naming* of new wasp species to combat the so-called taxonomic impediment represents a problematic inflexion in the applications of DNA barcoding, contrary to principles professed by its own proponents when this discussion first emerged in the early 2000s. In several DNA barcoding proponents' own words, "the discovery of previously undescribed species is augmented when information on morphological and ecological characters are fused with DNA barcodes" (Hebert & Barrett, 2005). Also, "we emphasize that DNA barcoding seeks merely to aid in *delimiting* species – to highlight genetically distinct groups exhibiting levels of sequence divergence suggestive of species status. By contrast, DNA barcodes – by themselves – are never sufficient to *describe* new species" (Hebert & Gregory, 2005). Finally, "it is important to note that it [DNA barcoding] does not seek to replace the Linnaean system of classification, and thus differs fundamentally from proposals to create a new taxonomic system based solely on DNA" (Gregory, 2005). "Hence, we urge strong collaborations between barcoders and taxonomists" (Hebert & Barrett, 2005).

This recent shift towards a DNA barcoding-based minimalist taxonomy materialises early concerns that it would try to replace an integrative taxonomy and classification system, as expressed by dozens of taxonomists and systematists (e.g., Carvalho et al., 2007; Ebach & Holdrege, 2005; Lipscomb et al., 2003; Moritz & Cicero, 2004; Seberg et al., 2003; Will et al., 2005) and has received substantial criticism recently (Ahrens et al., 2021; Engel et al., 2021; Meier et al., 2022; Zamani et al., 2021, 2022). While we note the inconsistency above for historical context, our goal here is to highlight why DNA taxonomy, and DNA barcoding in particular, is fraught with failure in resolving the taxonomic impediment of any group, particularly of hyperdiverse taxa. In turn, we present arguments in favour of the more robust integrative approach to taxonomy and systematics, and further explore potential solutions to the taxonomic impediment in hyperdiverse taxa, without sacrificing utility and quality of taxonomic descriptions for perceived speed and quantity.

Why (not) move toward a minimalist barcoding-based taxonomy?

Minimalist taxonomy's reliance on a single mitochondrial barcode is at the crux of the problem. It has been known for decades that mitochondrial phylogenies frequently depart from the species tree for several reasons, such as introgression, incomplete lineage sorting, and infection with reproduction-manipulating endosymbionts in the case of arthropods and filarial nematodes (Funk & Omland, 2003). Even if consistent with the evolutionary history of a species, a mitochondrial barcode might be uninformative for delineating species, particularly in rapidly speciating, hyperdiverse groups (Wiemers & Fiedler, 2007). Thus, it comes without surprise that barcoding approaches that incorporate the multispecies coalescent into the analysis of multilocus sequence data have been proposed (Dowton et al., 2014), even if these more robust statistical methods tend to over-split species in widespread taxa, especially if geographical sampling is inadequate (e.g., Chambers & Hillis, 2020; Mason et al., 2020). Because mitochondrial DNA has clear and long-known evolutionary blind spots, DNA barcoding as the sole source of information for species *delineation* and *description* does not serve taxonomy and should be discouraged.

The main argument put forward in favour of the minimalist approach is the unsubstantiated claim that it accelerates the naming of new species as a strategy to combat the taxonomic impediment (Sharkey et al., 2021a). Nevertheless, formal analyses of the impacts of integrative taxonomy did not find a slowing effect of integrating across multiple types of data for species delimitation and description (Pante et al., 2015). If anything, taxonomists should address bottlenecks imposed at different stages of the current taxonomic process, not replace it with subpar solutions. It is important to optimise taxonomic practice so that new descriptions are less likely to require revision in the foreseeable future, a goal that minimalist taxonomy is unwilling to achieve. Of note is that the proponents of the minimalist approach perform the minimum effort needed to barely conform to taxonomic naming conventions, leaving the more time and effort consuming tasks of providing the integrative redescriptions to "future revisers" (Sharkey et al., 2021a). For many taxonomists, professionals and non-professionals alike, the 'joy of discovery' and naming of species are major driving forces keeping them active in such an underfunded field. Not only is taking away this small reward from these researchers unfair, in the long run it further harms taxonomy by discouraging taxonomists from conducting research on certain groups.

Is morphology dead?

The gold standard in taxonomic species descriptions is still morphology, despite a sustained increase over the years in integrative studies that also include other data types (Pante et al., 2015; Bond et al., 2021). Morphology helps us connect all life, former and current. Most species that have evolved are now extinct and many of these were diverse, ecologically important, and distinct from their living relatives (Wiens, 2004). This means that if we do not take fossil lineages into consideration, we would be ignoring over 99% of the taxa that have ever lived (Novacek & Wheeler, 1992). Minimalist taxonomy effectively excludes palaeontology from our study of evolutionary history and species relationships. As argued several times by Wheeler (2008; 2009; 2018), taxonomy, although essential for environmental biology, is at heart an evolutionary science. Taxonomy seeks to recognize evolutionary history, to describe what makes species unique (not just what makes them identifiable) and what they share with other species, and to phylogenetically classify them. These goals are not achievable based on DNA alone, and certainly not with single (or few) molecular markers.

Furthermore, while morphology is one *type* of data, different phenotypic traits are the manifestation of hundreds or thousands of genes, whose expression is channelled during development and filtered by ecological constraints of each species over evolutionary time. Thus, morphology is a rich source of information for robust taxonomic inference, although not without its own limitations. One of the frequent criticisms against morphology is the existence of cryptic species, which might reflect low resolution of traditional characters rather than a real absence of morphological differences should higher resolution methods be employed.

Integrative taxonomy is dead, long live integrative taxonomy!

What can be done to avoid one type of data from misrepresenting species diversity? The solution lies in integrative approaches. Olave et al. (2014) concluded that without integrating multiple lines of evidence, interpreting what DNA-based approaches actually delimit will remain ambiguous. Integrative approaches narrow the parameter space where species are undetected in groups differentially diverging along different data type axes (Edwards & Knowles, 2014), and over-splitting is avoided especially if delimitations are congruent across different methods (Carstens et al., 2013). Furthermore, the use of integrative data also provides coherence between species detection and description (Edwards & Knowles, 2014), which should help ease the taxonomic impediment. There are multiple recent examples in which integrative strategies were successful at delimiting species, even in the case of complex evolutionary histories, morphological crypsis and hyperdiverse groups (e.g., Abdala et al., 2021; Arthofer et al., 2013; Brasero et al., 2020; Chaplin et al., 2020; Costa & Katz, 2021; Feliciano et al., 2021; Gebiola et al., 2012; Lima et al., 2020; Newton et al., 2020; Papakostas et al., 2016; Puillandre et al., 2012; Wachter et al., 2015; Weston et al., 2020). Furthermore, reanalysis of COI barcode clusters ("BINs") computed by BOLD Systems (Ratnasingham & Hebert 2007) already indicate minimalist species are unstable, which would require redescription with additional evidence (Meier et al., 2022).

How would real-world examples have been affected by the minimalist approach?

Our objections to the minimalist approach are best illustrated by real-world examples. We argue that the approach produces species descriptions that are not usable by the taxonomic community, would alienate non-professional taxonomists (who represent the majority in some groups) and parataxonomists, does not address the true bottleneck of species discovery as opposed to species description, and in the long run would slow down species descriptions instead of speeding them up.

Much of the earlier discussion surrounding the use of DNA barcoding has occurred on theoretical grounds (e.g., Moritz & Cicero, 2004): what would the performance of DNA barcoding be, given the behaviour of mitochondrial DNA or the levels of divergence observed between species? How would DNA taxonomy impact species discoveries? We are now at a stage where we can directly assess the potential use of DNA barcoding in driving taxonomy, in particular in hyperdiverse groups. We take as our real-world examples tropical parasitoid wasps, African Great Lakes' cichlids, and European butterflies. We feel these represent good test cases. Hyperdiverse taxa such as parasitoid wasps were the target group for the minimalist approach. Cichlids and butterflies are well-studied, with barcode data available, which allow *de facto* statements about applicability of a DNA barcoding-based minimalist approach.

Ichneumon wasps. Consider Ichneumonidae as a group that contains more species than its sister family Braconidae. Dal Pos and Rousse (2018) described a new species of *Genaemirum* Heinrich, 1936 based on the dichotomous key by Rousse et al. (2016), which in turn was based (with modification) on the extensive work by Heinrich (1967), who provided the first and, so far, only taxonomic treatment of all Afrotropical genera of the subfamily Ichneumoninae (over 400 genera and 4300 species worldwide). Johansson (2020) described five new species of Diplazontinae from Sweden after Klopfstein's (2014) revision of the group. Di Giovanni et al. (2018) identified a new species of the genus *Misetus* Wesmael, 1845 thanks to the key to the genera of Phaeogenini by Selfa and Diller (1994). Di Giovanni et al. (2015) and Di Giovanni and Reshchikov (2016) were able to fill the gaps of distribution of Ichneumonidae in Italy and record several species new to the country using the morphological keys and diagnoses provided by different European authors (e.g., Tereshkin, 2009). Moreover, many other taxonomic revisions are expected to be extremely useful in the years to come (e.g., Pham et al., 2020; Rousse et al., 2013). Sorting through an estimated >100,000 specimens of Ichneumonidae wasps from Uganda, morphological analysis of 456 individuals of the subfamily Rhyssinae resulted in a review of all Afrotropical rhyssines and the description of two new species (Hopkins et al., 2019). The sorting into morphospecies was possible due to a previous review by Rousse and van Noort (2014) of 30 previously described individuals and twelve known species.

Without morphology, an identification key would be replaced by the necessity to DNA barcode all specimens. The alternative of barcoding just some specimens would require splitting them into preliminary morphospecies to select which specimens to barcode. This rather defeats the stated purpose of minimalist descriptions, which is to save time and effort. Based on the examples mentioned above, morphological keys can be extremely functional for identifying even hyperdiverse taxa, and the idea that they do not work lacks factual support. For example, it is doubtful Varga (2020) would have described a new Kenyan rhyssine species, had there not been multiple morphological characters and an identification key available. We do recognize that morphological keys are not always convenient, accurate, or easy to use, and do sometimes require specialised terminology and some expertise to understand and implement. However, this is a good argument for integrating molecular data and investing in taxonomy and taxonomic training to improve both knowledge of species in such taxa, and the quality and ease of use of data to make keys more reliable, not as an excuse to abandon integrative studies. One recent example on how keys can be made more efficient is given by Fernandez-Triana (2022).

The central argument of increased speed has not been properly demonstrated by the minimalist taxonomy either. One important time sink pre-dates the act of describing species, and is 'hidden' in the form of sampling, building expertise and initial sorting of diversity usually based on morphology (known and unknown), as also recently noted but then not quantified by Fernandez-Triana (2022). For instance, it took Hopkins et al. (2019) several years to separate the parasitoid wasps, about a year to sort the rhyssines into species and write the descriptions. A *very* generous estimate would be that three months would have been saved using a minimalist approach, out of a total of at least three years at the cost of slowing down future work by established taxonomists and preventing new taxonomists from arising.

African Great Lakes' cichlids. The most spectacular examples of adaptive radiation in extant vertebrates are arguably the cichlids inhabiting the African Great Lakes (e.g., Gante & Salzburger, 2012). While the cichlid faunas from Lakes Malawi and Victoria are still mostly undescribed and number in the hundreds, the cichlid assemblage from Lake Tanganyika is comparatively well-known. In this older lake, the circa 250 species belong to 16 tribes defined on morphological grounds and confirmed by molecular data. These species radiated in situ from a common ancestor about 9.7 Ma (Ronco et al., 2020; 2021), of which ~86% are described, and the remaining awaiting formal treatment are mostly 'known unknowns' (Ronco et al., 2020).

In a test of the potential of DNA barcoding of the Tanganyikan assemblage, out of 96 species of littoral cichlids assayed, Breman et al. (2016) successfully *identified* only 73% of the valid species included. The potential for *discovery* was not much better, either underestimating by ~30% (70 hypothetical molecular operational taxonomic units (MOTUs) using the General Mixed Yule Coalescent) or overestimating species-level diversity by ~10% (115 hypothetical MOTUs using the Automatic Barcode Gap Discovery method). BINs are thus a poor proxy to species in the case of Tanganyikan cichlids.

The likely reasons for this poor behaviour of DNA barcoding in identifying or delineating Tanganyikan cichlids reported by Breman et al. (2016) stem from a combination of introgression and incomplete lineage sorting (i.e., sharing of haplotypes across species and apparent polyphyly; e.g., Brawand et al., 2014; Gante et al., 2016; Nevado et al., 2011), associated with fast cladogenesis observed in speciose groups (i.e., lack of universal resolution of the barcode at the species level). The results certainly do not reflect major issues with species validity, as morphology and nuclear genomes both support the vast majority of the species recognized (Ronco et al., 2021). Thus, limitations of DNA barcoding are overcome with an integrative approach to identification and delineation.

Considering that these difficulties are readily apparent in the oldest of cichlid radiations, a minimalist DNA taxonomy would be deemed unfeasible in younger radiations such as those of lakes Malawi and Victoria, which are far more speciose and have been boosted by ancient hybridisation (Malinsky et al., 2018; Meier et al., 2017). Species boundaries permeable to introgression (in particular of mtDNA) and rapid cladogenesis are attributes of hyperdiverse groups. These are the groups for which Sharkey et al. (2021b) claim a minimalist DNA taxonomy would speed up naming of new species, although that would be done at the cost of rigour, accuracy, or reliability in identifying or delineating new species.

Butterflies, other insects, and the 'Wolbachia effect'. There is no other insect group so intensively studied as European butterflies, save perhaps *Drosophila* Fallén, 1823. Given the attractiveness of European butterflies and the long history of their study, we know a lot about their distributional changes, ecologies and life histories. This was followed by the emergence of national and international barcoding programs (e.g., Lukhtanov et al., 2009; Dincă et al., 2011; Hausmann et al., 2011; Dincă et al., 2015; Litman et al., 2018; Dincă et al., 2021). In this well-known group, species delineation methods revealed a portion of polyphyletic, paraphyletic or barcode-sharing species. For example, Dincă et al. (2011) showed that in 180 Romanian butterfly species, only 162 species formed separate barcode clusters, three species pairs shared barcodes, four species were paraphyletic, two species pairs were polyphyletic and eight species had intraspecific divergence (p-distances) over 2.0%, which, according to the minimalist approach, would merit their description as a complex of cryptic species for which morphology 'fails'. Similar numbers were obtained for other countries (Hausmann et al., 2011; Dincă et al., 2015; Litman et al., 2018). Recently, a compilation of 22,306 sequences of 459 European butterfly species (97% of known European species) was analysed by Dincă et al. (2021). In this dataset, the 459 species were assigned to 441 BINs, in which 65 BINs were taxonomically discordant, and 16 were singleton (i.e., not including any other sequences), 69 species shared barcodes and 56 species had a divergence greater than 2.5%.

A comparable picture arose for the North American butterfly fauna (D'Ercole et al., 2021): in the 814 American butterfly species, 573 species (out of 755 with more than 2 specimens) formed distinct clusters, 151 species were polyphyletic or paraphyletic, 125 species shared barcodes and 79 species had a divergence greater than 2.5%. An analogous analysis of dragonflies, a genetically distant insect order, produced similar results (Geiger et al., 2021), indicating that such patterns of non-monophyly are widely distributed among insects, and they might be even much broader: in an often-cited review on mitochondrial phylogenies of closely related animal species groups, over 20% of ~2,300 species assayed showed species-level paraphyly or polyphyly (Funk & Omland, 2003). This would result in an unacceptably high percentage of incorrectly described species should only DNA barcodes be used to delineate species.

Mutanen et al. (2016) explored the amount of bias in European Lepidoptera in barcode paraphyly and polyphyly. They investigated 4,977 species (41,583 specimens) and found 465 non-monophyletic species using a neighbour-joining method and 469 species using the Maximum Likelihood method of tree reconstruction. These can be explained by over-splitting or cryptic speciation (estimated at 31.8%). However, they also recognized that non-monophyly increases when more specimens are investigated and is higher if the species are relatively young.

Such large-scale studies serve as a background for detection of cryptic diversity. The ideal procedure to follow them up with and produce new species identifications would include sequencing nuclear DNA, searching for morphological and life history traits, and (ideally) microbial screening. This array of techniques was used when delineating the European species of *Spialia* Swinhoe, 1912 (Hernández-Roldán et al., 2016). In many cases, the issues of barcode non-monophyly can be solved with detailed studies at intraspecific- and closely related species-group levels. Some butterfly species display mtDNA over-splitting: *Thymelicus sylvestris* (Poda, 1761) has six mitochondrial lineages, but these are not recovered by ddRADseq data (Hinojosa et al., 2019). An analogous pattern was observed in *Melitaea didyma* (Esper, 1778) (Dincă et al., 2019). *Melitaea ornata* Christoph, 1893 includes two separate mitochondrial groups and one of them clusters with its sister species *Melitaea phoebe* (Denis & Schiffermüller, 1775), whereas nuclear genes clearly distinguish two species (Tóth et al., 2017). Younger groups, where speciation is ongoing, can display incomplete lineage sorting, identifiable by an absence of a predictable biogeographical pattern (Funk & Omland, 2003; Toews & Brelsford, 2012). The introgression of mitochondrial DNA occurs via hybridisation, which is observable in the butterfly genus *Colias* Fabricius, 1807 (Wheat & Watt, 2008).

In addition, mitochondrial DNA inheritance patterns of arthropods and filarial nematodes are affected by the co-inherited bacteria *Wolbachia* Hertig, 1936 (e.g., Hurst & Jiggins, 2005). Ahmed et al. (2015) estimated the presence of endosymbiotic *Wolbachia* in 80% of Lepidopterans, with 25–33% infected individuals. As *Wolbachia* interferes with reproduction of its hosts, it might cause a swift spread through a population, hitchhiking one mitochondrial type. Mitochondrial clades with a deep divergence associated with the presence/absence of *Wolbachia* were observed in both *Phengaris nausithous* (Bergsträsser, 1779) and *P. teleius* (Bergsträsser, 1779) (Ritter et al., 2013). If two bacterial strains are present, they could each bear a different mitotype, causing a deep mitochondrial split, as observed in American *Coenonympha tullia* (Müller, 1764) (Kodandaramaiah et al., 2013). Furthermore, *Wolbachia* might mediate introgression, as hypothesised for *Iphiclides podalirius* (Linnaeus, 1758) and *I. feisthamelii* (Duponchel, 1832) (Gaunet et al., 2019). *Wolbachia* screening might support past hybridisation events as in *M. phoebe* and *M. ornata* (Tóth et al., 2017), and *Pseudophilotes baton* (Bergsträsser, 1779) and *P. vicrama* (Moore, 1865) (Sucháčková Bartoňová et al., 2021).

Large datasets, compiled and extended in Mutanen et al. (2016) and Dincă et al. (2021) demonstrate what would happen if the minimalist approach would have been used. The minimalist approach would have accepted barcode-delimited species largely as is, without taking into account morphological and life history traits (as in the examples above), studying intraspecific or closely related species group variation in detail, or checking for the effect that *Wolbachia* could have on results. In the majority of cases, barcodes succeed in assigning specimens into proper taxonomic species, but they still have their limits for a substantial portion of taxa. It is fair to assume that a similar portion of species would have been inaccurately delimited in other, less explored insect groups. We have to consider that the amount of non-monophyly reflects the number of investigated specimens and that it depends on species age, i.e., low divergence in young species and high divergence in old species (Mutanen et al., 2016).

DNA barcode-based minimalist taxonomy does not address the taxonomic impediment

Are the false negative and false positive rates for cichlids, butterflies and dragonflies discussed above acceptable in the face of the pressing need to name vanishing biodiversity? One could argue that a large proportion would still be correctly named using only a DNA barcode. One problem with a minimalist DNA approach is that we would be completely blind as to which taxa might or might not be properly named. In other words, given the paucity of taxonomic information gathered by minimalist DNA taxonomy, invalid taxa would effectively be 'unknown unknowns' – we know they would exist but we would not easily know which ones they might be without an in-depth reanalysis of the entire group (see Meier et al., 2022). Thus, the amount of taxonomic work needed to assess which species are actually valid would surmount the work needed for a proper first pass using an integrative approach, even considering incremental contributions and subsequent efforts as new taxa are discovered. Furthermore, it is doubtful that taxonomy end-uses, such as conservation and management actions, would gladly be based on such high numbers of erroneously named and improperly circumscribed species, in particular since we ought to preserve and manage morphological and ecological diversity as much as molecular (i.e., barcode) diversity.

A path forward

Much emphasis has been placed in automation of molecular analyses and DNA barcoding has been surfing this wave. Sequencing technologies have witnessed great progress, as we quickly moved from automated Sanger sequencing, to 'next generation' short read sequencing, to 'third generation' long read sequencing in just two decades. One recent application that combines barcoding and high throughput sequencing is metabarcoding of environmental DNA (eDNA) for biodiversity monitoring. Metabarcoding of eDNA allows the simultaneous assessment of barcodes of multiple taxa present in the environment, for example from water, soil or air samples, as evidence of organisms' presence (Taberlet et al., 2018). A newer metagenomics approach is being developed that extends this principle to any type of DNA present in the environment (i.e., beyond barcodes), with gains in detection sensitivity, accuracy and precision, even when applied to multicellular eukaryotes (e.g., Alves et al., 2019; Curto et al., in prep). These high throughput approaches enable not only detecting known biodiversity (i.e., formerly characterised barcodes or genomes in known, previously described species), they also show a great potential for *discovering* unknown molecular diversity. Such environmental metagenomics data could sensibly direct follow-up integrative studies towards targeting the collection of potential new taxa (to which the newly found molecular diversity belongs to), effectively closing the gap between known and unknown biodiversity.

Much less focus has been put on one of the bottlenecks to taxonomic studies: morphological analyses. In particular, one area that could benefit from automation, speeding up informative species descriptions, and ameliorating the taxonomic impediment, would be automated morphological classification and character *discovery*. Over the last decades we have seen considerable advancements in deep learning computational methods such as convolutional neural networks (CNNs) and other types of networks (e.g., Gaston & O'Neil, 2004). In particular, CNNs learn to extract relevant features from photographs without human intervention (e.g., Kaya et al., 2019; Valan et al., 2019). On the one hand, these methods could speed up routine identifications of a large proportion of taxa, freeing taxonomists for more creative and critical tasks. Specimens that do not fit the groups being classified could be flagged for more in-depth identification by taxonomists, with the potential for discovering new groups and undescribed species (e.g., Yang et al., 2021). On the other hand, as CNNs are classifying individuals, they are 'learning' about traits that group similar individuals and separate them from other groups. Thus, these methods have a great potential for *discovering* traits that discriminate between different species, facilitating species descriptions and highlighting traits that an experienced and dedicated taxonomist can test for applicability, including of cryptic taxa for which traditional characters have low resolution; of course, the goal is not that CNNs replace an experienced taxonomist, but rather provide additional information (e.g. highlighting potentially useful traits, verbal descriptions of the traits) that would speed up the process and enrich taxonomic descriptions. An investment on rapid automatised biodiversity assessment was also recently proposed by Ahrens et al. (2021).

Soon it might be possible to not have to make difficult choices between thoroughness and speed of taxonomic treatments, in particular if cost and technology continue progressing at a steady pace. For instance, robotic coupling of sorting and classifying, photographing, and sequencing barcodes (without destroying the specimens in question) has recently been implemented for very small insects (Srivathsan et al., 2021; Wührl et al., 2021). The initial investment might be steep for individuals, but probably within the reach of institutions and research projects dedicated to monitoring and describing biodiversity. Progress in this area should allow addressing the taxonomic impediment without sacrificing rigour, utility or quality for speed and quantity.

Bioinformatics could also play a major role in next-generation taxonomy and enhancement of species discovery. A promising example is a user-friendly, specimen-based toolkit called 'iTaxoTools 0.1′ (Vences et al., 2021a). This software, based on open-source Python code, includes tools focusing on species delimitation and diagnosis and centred around specimen identifiers, and at its current stage contains GUI versions of six species delimitation programs (ABGD, ASAP, DELINEATE, GMYC, PTP, tr2) and a simple threshold-clustering delimitation tool, along with new Python implementations of existing algorithms, including tools to compute pairwise DNA distances, ultrametric time trees based on non-parametric rate smoothing, species-diagnostic nucleotide positions, standard morphometric analyses, etc. This innovation could greatly accelerate the rate of species discovery in hyperdiverse taxa in the future, without compromising the quality of the descriptions.

Another important aspect is the cost associated with taxonomic activities (either personnel, robotics for morphology, DNA barcoding, computing power, or collection management), in particular if we are to adopt new strategies to speed them up. In the current model, it is undeniable that funding goes where perceived publication impacts are, and these are increasingly being measured as paper citations, which in turn translate into journal impact factors. The most direct way of recognising the importance of taxonomic work would be to make citations of species descriptions or other relevant taxonomic treatments (as argued elsewhere by Meier, 2017) mandatory for each taxon the study focuses on. In a digital era, publication page limits and word limits should be extended to allow the citing of original descriptions or taxonomic revisions of focal species studied. Considering that taxonomic descriptions are scientific hypotheses (Pante et al., 2015), and that current scientific practice rightfully calls for citing all relevant literature (e.g., statistical software), it is only fair that taxonomic literature receives equal treatment. Increased funding is necessary to address shortages of trained taxonomists, and challenges faced by Natural History museums and the utilisation of the biological collections they hold (e.g., Ebach et al., 2011; Pinheiro et al., 2019; Dupérré, 2020; Engel et al., 2021).

A frequently hidden aspect of DNA barcoding reliability is that it is only as good as the assignment of names to barcoded units. That requires careful identification of the individuals that are barcoded, using original descriptions, subsequent revisions and keys, and ideally also examination of original type material. That rigour is seldom practised or explicitly stated, especially in labs focussed mainly on genetic or genomic analysis, where morphological identification skills are not honed, and where more work is done with tissue samples than with actual specimens. Misidentification of the material that later winds up serving as the barcode reference for a species can cause knock-on errors for decades, until a mismatch between the type material and the application of the name is discovered. Even when a great deal of rigour has been applied to the original assignment of DNA barcodes to species names, DNA sequences from historical type material have resulted in surprises that have necessitated synonymisations and replacement names (e.g., Vences et al., 2021b). In the absence of that rigour, such mistakes will certainly be more common and necessitate even more revisionary work. For this reason, we argue that vouchering of DNA barcoded specimens in public museum collections should be the norm.

Finally, as we have discussed above, morphological comparison with existing nomina can be difficult in truly cryptic clades, or where the historical type material is damaged, ambiguous, or immature. However, it is no longer the case that the assignment of such names must necessarily be left to convention or best guesses. Major strides have been made recently in sequencing historical type and non-type material, some well over a century old, or fixed in DNA-degrading chemicals like formalin, and often based on very small quantities of tissue, in what has been dubbed museomics (e.g. Erpenbeck et al., 2016; Ruane & Austin, 2017; Evans et al., 2019; McGuire et al. 2018; Rancilhac et al. 2020; Scherz et al., 2020; Call et al., 2021; Straube et al., 2021a, 2021b; Vences et al., 2021b). This means that DNA barcodes (and indeed substantial parts of the mitochondrial and nuclear genomes) can be sequenced from old types, and used to more confidently assign names to lineages. As discussed above (and argued by some of us elsewhere; Zamani et al., 2021), assignment of previous names should take priority over the establishment of new names, in order to reduce the strain on the taxonomic community.

Conclusions

As already argued by Wheeler (2008), taxonomy (i.e., species description) is different from instant species identification and should be considered a science of its own, with its own set of hypotheses to test. However, minimalist taxonomy relegates taxonomy to a mere service for other sciences. How can we move forward from this? Do we really need to consider taxonomy just a tool for the end-user, ignoring the epistemology that sets taxonomy apart from other sciences? Probably the best way forward is to set aside any baseless claim of superiority of one data type over another and focus instead on building communities with the intention to create a collaborative environment where researchers with different sets of skills and passions can thrive. However, this means setting aside ego and personal achievement for a greater good: the discovery and study of what is left of the Earth's biodiversity. Is this achievable? Our response to this is affirmative. The ichneumonid community, as an example, was formally reignited in 2019 in Basel (Klopfstein et al., 2019) with the aim to reduce the taxonomic impediment of the group by gathering people with different skill sets. Time will tell if the community will last, but the simple fact that it has been built points to the fact that collaboration, sharing data, diversifying the fields of knowledge and building bridges are achievable and, even more importantly, desirable actions.

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