Taxonomic uncertainty: causes, consequences, and metrics

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Abstract

Taxonomic uncertainty is prevalent across many biological groups. Yet, it remains overlooked in ecology, evolution, and conservation, leading to potential misinterpretations of biodiversity patterns. Here, we define taxonomic uncertainty, examine its root causes and consequences, and present metrics for its quantification. We argue that species should not be considered equivalent units in biodiversity research. To address this challenge, researchers need to (i) identify taxa with uncertain boundaries, (ii) track changes in species taxonomy, and (iii) incorporate taxonomic uncertainty into biodiversity studies. These tasks open new research opportunities for collaboration between taxonomists and other biodiversity scientists. Integrating taxonomic uncertainty into biodiversity research will improve the robustness of ecological models and conservation assessments, ultimately leading to a more accurate understanding of biodiversity.

Keywords: Species delimitation, error, taxonomy, macroecology, taxonomic stability

Highlights

- Taxonomic uncertainty is widespread across biological groups but often overlooked, leading to potential misinterpretations of biodiversity patterns.
- Taxonomic uncertainty arises from the interaction between biological processes shaping natural lineages and human efforts to name and classify them. Understanding its biological and cultural roots is essential for developing effective strategies to address its impact.
- Dealing with taxonomic uncertainty requires identifying taxa with uncertain boundaries, tracking taxonomic changes, and integrating this uncertainty into biodiversity analyses. This view challenges the assumption that all species are equivalent units of analysis.
- Addressing taxonomic uncertainty opens new interdisciplinary research avenues. Collaboration between taxonomists and other biodiversity scientists can improve the robustness of ecological models and conservation assessments and provide an accurate representation of biodiversity's complexities.

Taxonomic uncertainty in biodiversity research

Species (see Glossary) are the fundamental unit for studying biodiversity. Yet accurately describing and cataloguing species is an ongoing challenge. Many species – both extant and extinct – remain unknown to science [1,2]. Those formally described have been delimited using a variety of species concepts, criteria, and a variety of taxonomic methods [3,4]. Additionally, only a small fraction of described species have been re-evaluated through multiple lines of evidence [5]. As a result, even the best-known groups, such as birds and mammals, are subject to frequent taxonomic changes, which can profoundly impact downstream biodiversity research and conservation [6,7].

Rapid taxonomic changes are driven by technical and epistemological progress in taxonomy, which has recently reinvigorated this discipline [5,8]. However, taxonomic research remains heavily biased, with a few taxonomic groups and regions receiving disproportionate attention and several being understudied [9,10]. This disparity contributes to widespread uncertainty regarding the number and identity of species across taxa and regions [11–13]. Moreover, biases in taxonomic research result in varying degrees of uncertainty in species boundaries. Despite this shortcoming, biodiversity research treats species as equivalent units, representing unique biological entities.

Previous studies exploring the impact of taxonomic change on biodiversity research and conservation focus on how redefining species boundaries influences species counts, population sizes, and distribution ranges [13–16]. The broad interest in this topic [17, and many others] is justified because among the five tasks of taxonomy – **taxon** discovery, delimitation, diagnosis, description, and **specimen identification** [18] – **species delimitation** is perhaps the most challenging one. Several factors contribute to this complexity. For instance, defining species boundaries is inherently difficult, particularly for lineages in processes of divergence. Moreover, most groups lack comprehensive data on genetics, morphology, ecology, and behaviour, hindering the accumulation of robust evidence needed to establish species boundaries. Consequently, some degree of uncertainty is often associated with the delimitation of species boundaries. Although this uncertainty is increasingly acknowledged [5,11,19], clear guidelines on how to manage and incorporate **taxonomic uncertainty** into biodiversity studies are still lacking.

In this context, we offer a concise definition of taxonomic uncertainty (Box 1), examine its root causes (both cultural and biological), and discuss its consequences. In addition, we present key metrics and methodologies for quantifying taxonomic uncertainty and provide recommendations for scientists to address this prevalent bias in their research. Specifically, we focus on the uncertainty of species delimitation and how it can introduce bias and error into our perception of biodiversity patterns across time and space.

Box 1. Definition of taxonomic uncertainty

Taxonomic uncertainty has been widely discussed among taxonomists, (macro)ecologists, and conservationists, and the term has been used in different contexts (see Online Supplementary Material Table S1). Among taxonomists, it generally refers to the challenge of defining clear and unambiguous species boundaries [20,21]. For ecologists and conservationists, the term has a broader scope, encompassing uncertainty in species boundaries [9,22,23], discrepancies in species lists [24,25], and the proportion of unidentified or misidentified specimens in biological inventories, museum collections, and databases [26–28]. Typically, studies evaluate how these various sources of uncertainty affect biodiversity patterns and conservation assessments [29,30].

In general terms, taxonomic uncertainty can arise at any of the five tasks that make up the taxonomic process, as described by Favret [18]: taxon discovery, delimitation, diagnosis, description, and specimen identification (Figure 1). However, in the context of taxonomic uncertainty, species delimitation and specimen identification are especially critical because these tasks are tackled as hypothesis testing [18,20]. Once a hypothesis is proposed, it can be refuted or supported based on new data and evidence. Thus, different types of evidence or criteria can lead experts to produce different assessments of whether a given group of populations qualifies as a unique species or whether the correct name is assigned to a specimen.

Here, we define taxonomic uncertainty as the **degree of confidence in the hypothesis stating either (i) the delimitation of species boundaries, or (ii) the determination of a specimen's identity**. Lower confidence in these hypotheses corresponds to greater taxonomic uncertainty. Simply put, taxonomic uncertainty refers to the extent of our confidence in species boundaries and accurate identification of specimens.

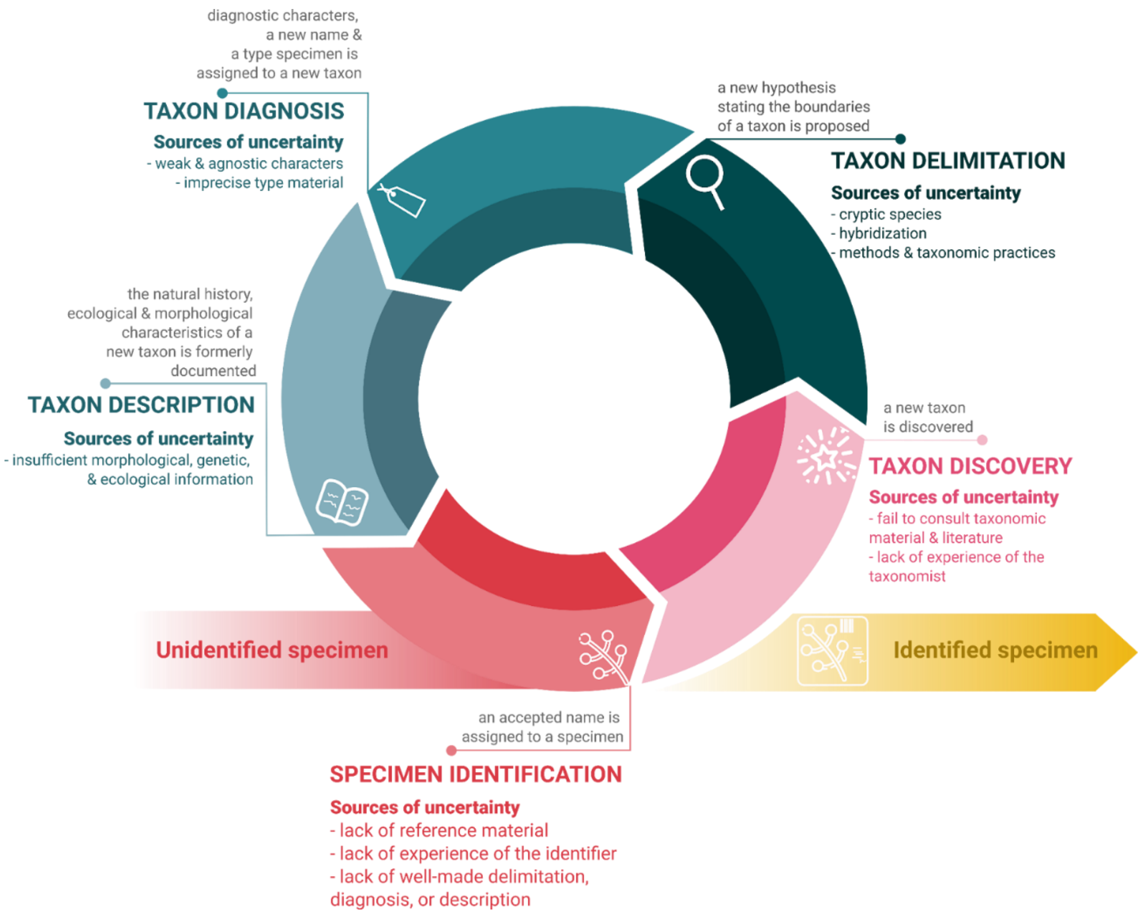

Figure 1. Taxonomic uncertainty across the five tasks of taxonomy (adapted from Favret, 2024). Taxonomic practice is a recursive and iterative process where the inability to assign a species name to a specimen may initiate a new cycle, potentially uncovering a new species or redefining the boundaries of an existing one. Note that uncertainty in any of the five tasks of the taxonomic process can affect the outcome of all subsequent tasks.

Causes of taxonomic uncertainty

Delimiting a species requires hypothesizing that a taxon, which is a human construct, represents a distinct evolutionary lineage [3,20]. However, a discrete human-defined taxon often does not perfectly align with continuously evolving biological lineages [20,31]. This misalignment is the core driver of uncertainty in species boundaries. Thus, uncertainty in species delimitation arises from the interaction between the biological processes shaping natural lineages and the human cultural framework and perspective of those attempting to recognize them.

From a cultural perspective, taxonomists rely on a variety of species concepts, criteria, and methods to determine species boundaries. Heterogeneity in the taxonomic practice across taxa, space, and time can lead to conflicting and competing species delimitation and classification. For instance, the phylogenetic species concept tends to recognize a larger number of narrowly defined taxa compared to non-phylogenetic species concepts [32]. Further, experts may interpret the same data differently depending on their practices and approaches [24]. For example, while “splitters” tend to recognize a greater number of species, “lumpers” often group closely related entities under fewer taxa [33].

From a biological perspective, defining species boundaries is particularly challenging for cryptic species and lineages with shallow divergence. These lineages typically experience recent speciation, explosive radiation, genetic introgression, or frequent hybridization events [20,34,35]. Molecular techniques, including phylogenetics and population genetics, have helped define many species boundaries [36,37]. However, numerous species complexes remain unresolved [5].

Biases in taxonomic uncertainty

The degree of taxonomic uncertainty depends on taxonomic effort and species’ biological characteristics [9]. Historically, taxonomic effort — i.e., investments in research capacity and use of integrative approaches — varies globally and is usually greater in temperate regions than in the tropics [10,38]. Additionally, tropical regions harbour more species, which requires significantly more research to reach the same level of taxonomic knowledge as temperate regions. As a result, taxonomic uncertainty tends to be higher in the tropics, a pattern known as the “latitudinal taxonomy gradient” [9].

Taxonomic effort also varies according to the characteristics of different taxa. Charismatic and conspicuous groups, such as birds, mammals, and trees, receive more attention and studies than cryptic and less appealing taxa [39,40]. Thus, historically understudied taxa, such as invertebrates, herbaceous plants and fungi, are expected to undergo numerous taxonomic changes as they are revised.

Additionally, some species characteristics (e.g., geographic range size, phenotypic variability, evolutionary distinctiveness) can also influence the degree of taxonomic uncertainty. For instance, widespread species with low phenotypic variability have been found to harbour substantial genetic diversity, revealing cryptic biodiversity in insects [41], fungi [42], marine invertebrates [43], and tropical plants [37]. Such characteristics make these taxa prone to being “split” into several species after a taxonomic revision.

Consequences of taxonomic uncertainty

The most significant consequence of taxonomic uncertainty is its potential to distort biodiversity patterns. This occurs because resolving taxonomic uncertainty often leads to taxonomic change, which can alter our understanding of the identity, number, geographic distribution, evolution, biological interactions, and environmental requirements of species [23,44]. For instance, splitting a taxon into multiple species increases species richness [15,37], potentially increasing beta diversity [13], endemism [22,45], and diversification rates [9,23,30], while reducing geographic range [13], population size [16], and niche and trait breadth [37,46] (Figure 2). In contrast, lumping two or more taxa into a single species decreases richness [47,48], possibly reducing beta diversity [13], endemism [22], and diversification rates [23], but may expand geographic range [13,27], population size [16], and niche and trait breadth [37]. In turn, moving a species into another genus or family (i.e., proposing a new combination) redistributes diversity within the involved taxa [49]. In this case, the taxon that receives the species increases its richness while the other taxon experiences a decrease.

Estimates of how many species remain to be described — a concept known as the Linnean shortfall [44,50] — are also affected by taxonomic uncertainty. Such estimates are typically derived from extrapolations of species discovery curves [51]. However, subsequent splitting or lumping inevitably impact these extrapolations, leading to an under- or overestimation of the shortfall [12,52].

Likewise, conservation strategies may be inappropriate if species limits are uncertain, as taxa requiring protection could be mistakenly recognized as less critical or vice versa [14,29]. When two or more taxa are lumped, the newly defined species may no longer require the same level of protection. Conversely, when a taxon is split into two or more species, the resulting species may need further protection. For instance, a taxonomic assessment of 870 species of Australian lizards and snakes revealed that 282 taxa (32%) require revision of their conservation status, and 38 taxa (4%) likely represent undescribed species that merit conservation concern [29].

Moreover, as taxonomy evolves, alternative classifications are proposed. Relying on different classifications to recover large-scale biodiversity patterns may lead to varying outcomes. For instance, the choice of the taxonomic database (e.g., Tropicos, GBIF) caused regional variations of 40% to 60% in bryophyte species richness across the Northern Hemisphere [53]. This problem can be addressed by comparing results using alternative classifications [7,13,47]. Additionally, inconsistencies among classifications can highlight taxa with tricky boundaries [e.g., 25], which can indicate unsolved taxonomic uncertainty.

Keeping biodiversity databases up-to-date with the most recent taxonomic classification is a demanding task that often requires re-evaluating each record [28]. This is particularly the case when a splitting is proposed for taxa with sympatric distributions. Consequently, the utility and accuracy of occurrence data for describing current species distributions depend highly on the timing of database consultations. For example, a decade-based comparison of 9,727 occurrence records of the Neotropical plant genus *Myrcia* DC. (Myrtaceae) present in two databases (2007 and 2017) showed that 27% underwent only nomenclatural changes, whereas 4% experienced either splitting or lumping [27].

The identification of specimens can also be compromised by uncertainty in species boundaries. Accurate specimen identification depends on unambiguous species delimitation and a precise diagnosis and description (Figure 1) [18]. Thus, selecting the type specimen and the diagnostic characters used to describe a species is critical, as these will influence the future identification of specimens within that taxon. If a type specimen lacks key diagnostic characteristics or does not represent a typical individual, further identifications result in errors [54].

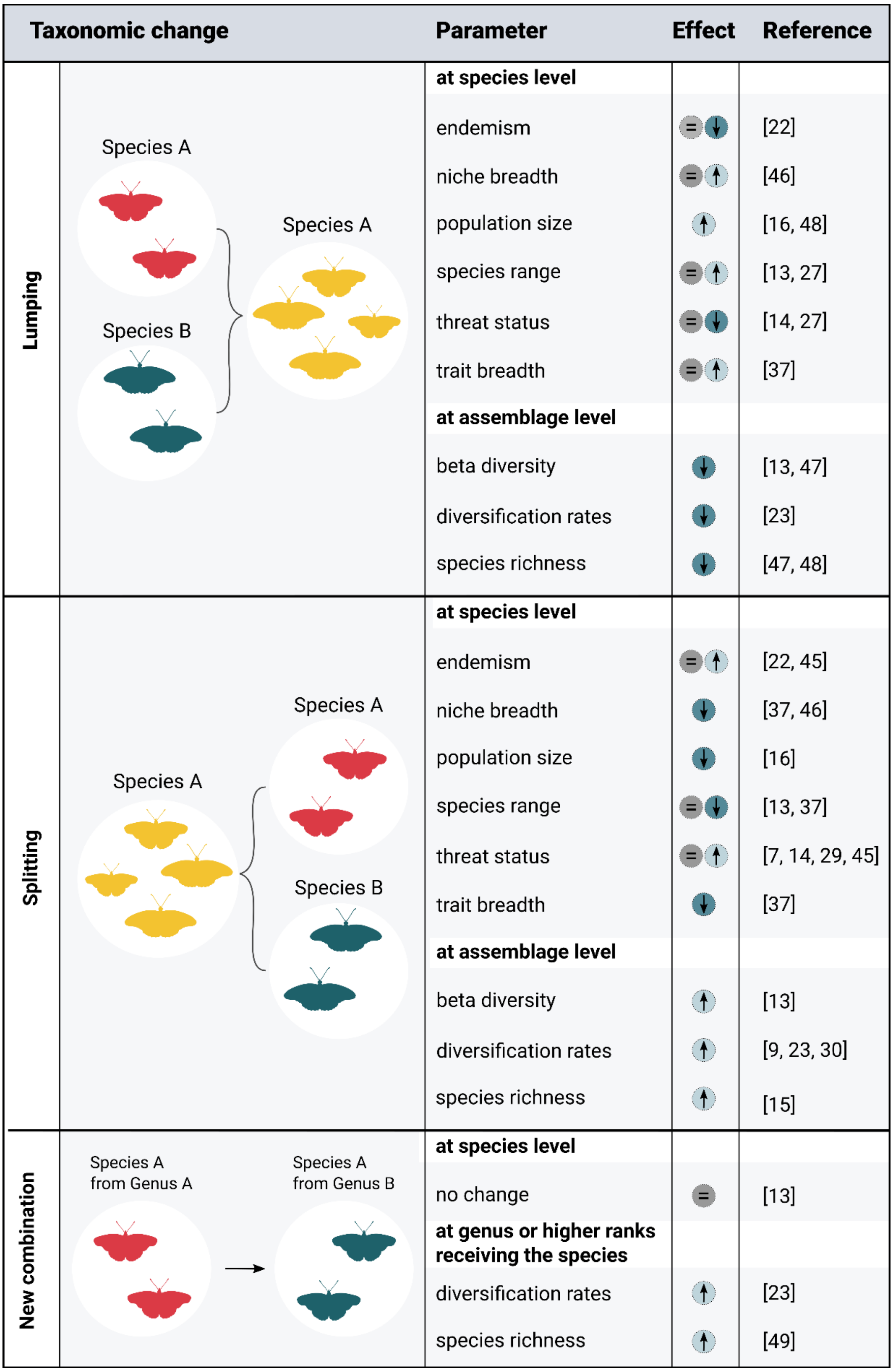

Figure 2. Taxonomic changes (lumping, splitting, and recombination) and their impact on biodiversity patterns and species threat status.

How to deal with taxonomic uncertainty

Mitigating all forms of taxonomic uncertainty requires investment in taxonomic research and training, particularly for understudied clades and areas. However, even with greater resources, taxonomic uncertainty will remain prevalent [19]. Furthermore, change is inherent to taxonomy. Thus, scientists need tools to deal with ambiguity in species boundaries and frequent changes in species taxonomy.

Next, we present seven metrics and group them into those that (i) quantify the degree of confidence in species boundaries, and (ii) track taxonomic history to infer taxonomic stability and predict future changes. Multiple metrics can be combined to address specific research questions.

Confidence in species boundaries

Taxonomists' assessment: The degree of confidence in species boundaries can be directly evaluated by consulting taxonomists of a given biological group [e.g., 29,30,55] These consultations can be performed through structured questionnaires, in which specialists can evaluate whether a taxon requires taxonomic revision or anticipate the potential outcomes of such revisions. Another alternative is to apply the Delphi method. This method gathers expert assessments anonymously and achieves consensus opinions through iterative rounds of questionnaires with feedback [56]. These consultations present challenges when they focus on groups with many species or a shortage of taxonomists. Nonetheless, such assessments capture the experiences and perceptions of taxonomists, as well as specific characteristics of taxa (e.g., species complexes) that are often unavailable in the literature or difficult to quantify using other metrics.

Effort in taxonomic revisions: Confidence in species boundaries can be assessed by quantifying effort in revisionary work (e.g., revisions, monographs). When a taxon has been repeatedly revised without any resulting taxonomic changes, it likely holds a widely accepted and well-established delimitation [57]. This effort can be quantified by assessing the frequency and timing of revisions for each taxon.

Thoroughness of species description: The reliability of species limits can be evaluated by considering the scope of information used to delimit a taxon. The rationale is that taxa delimited using a comprehensive set of information are more robust and less likely to undergo future taxonomic changes [58–60]. The scope of information justifying species boundaries can be assessed using variables such as the number of morphological characters measured, the lines of evidence integrated to delimit the taxon, and the number and geographical coverage of examined specimens. These variables can be obtained by consulting published taxonomic works. Although extracting textual information on species descriptions is time-consuming, AI-assisted text-mining offers an effective solution. So far, a few studies have assessed the thoroughness of species description, e.g., for birds [58], helminth [59], and squamate [61]. They indicate that species descriptions have become increasingly detailed over time.

Biological characteristics of the taxon: Certain biological characteristics make some taxa more prone to having uncertain boundaries. Closely related taxa with overlapping geographical distribution and similar ecological or morphological traits pose significant challenges for delimitation [9,36]. Identifying where such taxa occur and to which clade they belong can highlight biological groups and regions where taxonomic uncertainty is most pronounced. For instance, undescribed mammal species are more likely to be found among small-bodied taxa with large geographical ranges, which overlap with regions with high climatic variability [39]. Similarly, New World coralsnakes with small body sizes that occur in Central and North America seem more likely to undergo future splitting [30]. These studies show that integrating species characteristics with advanced modelling techniques can help to uncover taxonomic uncertainty.

History of taxonomic change

Congruence of species lists: Assessing the lack of congruence across species lists can highlight hotspots of taxonomic disagreement, indicating species for which boundaries remain uncertain [24,25]. For example, a study comparing 665 raptor birds across four species lists found that 212 (32%) were not consistently recorded in all lists [25], and may merit further taxonomic studies.

Digital name salience: When alternative classifications are proposed, multiple names may simultaneously apply for the same taxon. Additionally, a time lag exists between a new taxonomic proposal and its widespread acceptance and adoption. Digital tools provide methods for assessing the prominence of taxonomic names in the literature [62]. These tools, such as Ngram Viewer [63], allow scientists to evaluate the current level of consensus and temporal trends in the usage of competing taxonomic hypotheses, especially for taxa that have been extensively studied.

Taxonomic changes (splitting and lumping): Temporal trends in splitting and lumping offer insights into the taxonomic history of a group, providing means to evaluate taxonomic stability and gain insights into future changes [33,48,64,65]. Such temporal trends are often represented by curves of **synonymy** accumulation or synonym rates relative to all described species [e.g., 65]. Establishing such curves is straightforward, as the necessary data, i.e., a list of accepted species and their associated synonyms, are available on online platforms (e.g., The Catalogue of Life, World Flora Online, World Register of Marine Species). However, these platforms lack critical temporal metadata on synonyms, such as the year and publication in which species names were synonymized. Consequently, recovering historical trends in splitting or lumping requires consulting primary taxonomic literature. This work can be time-consuming. Yet, novel text-mining techniques may help to unlock this information. So far, studies reporting historical rates of splitting and lumping are scarce and restricted to a few groups [33,48,64].

Incorporating metrics of taxonomic uncertainty into (macro)ecological models and conservation assessments

Next, we suggest four possible ways that metrics of taxonomic uncertainty can be explicitly incorporated into biodiversity research.

(i) Bayesian and regression models: Metrics of uncertainty in species boundaries can be incorporated as priors into Bayesian statistical algorithms or as weight parameters in regression and classification models to describe macroecological patterns and inform conservation decisions.

(ii) Maps of biogeographical ignorance: Metrics of uncertainty in species boundaries can serve as an additional layer for building maps of biogeographical ignorance [66].

(iii) Sensitivity analysis: Metrics of uncertainty in species boundaries and rates of taxonomic change can be integrated into sensitivity analyses to assess the impact of taxonomic uncertainty on biodiversity patterns and species conservation status.

(iv) Spatial-temporal analysis: Patterns of splitting and lumping over time and across regions can be used to identify periods and areas of taxonomic instability, which can be incorporated into spatial-temporal models.

Concluding remarks

Centuries of taxonomic research, along with recent advances in analytical tools, have been pivotal in reducing taxonomic uncertainty. However, taxonomic efforts remain unevenly distributed across taxa and regions, and species boundaries in many clades are inherently ambiguous. Consequently, species should not be treated necessarily as equivalent units in biodiversity analysis. To address this challenge, it is essential to (i) identify taxa with uncertain boundaries, (ii) keep track of taxonomic changes, and (iii) explicitly incorporate metrics of taxonomic uncertainty in (macro)ecological studies and conservation assessments (see Outstanding questions). A comprehensive account of taxonomic uncertainty will not only enhance the robustness of macroecological models and conservation assessments but also provide a more accurate representation of biodiversity's complexities. This task strongly depends upon a close collaboration among ecologists, evolutionary biologists, taxonomists, and systematists.

Outstanding questions

(i) What do we gain from understanding the biological and cultural causes of taxonomic uncertainty? We discuss that both biological and cultural factors drive taxonomic uncertainty. Disentangling genuine biological complexity (e.g., cryptic species) from human-driven inconsistencies (e.g., different species concepts) can shed light on how to effectively address taxonomic uncertainty. While human-driven inconsistency can be overcome — albeit with some difficulty — biological complexity may be only partially resolved and, in some cases, remains inherently intractable given the methods currently available.

(ii) Can we achieve robust estimates of taxonomic uncertainty for all groups of organisms? We propose four approaches for quantifying uncertainty in species boundaries and three for assessing the history of taxonomic changes. Although these approaches can already be applied to a relatively small number of taxa, scaling them to encompass broader taxonomic coverage remains a challenge. Emerging computational tools offer promising pathways to overcome this limitation.

(iii) To what extent does taxonomic uncertainty contribute to the overall uncertainty in ecological models? We discuss that taxonomic uncertainty tends to be prevalent in taxa and regions receiving little taxonomic attention. However, we still lack a clear understanding of how much taxonomic uncertainty contributes to the overall uncertainty of ecological models. Identifying the degree of taxonomic uncertainty across taxa and regions would allow to assess the reliability of model outputs.

(iv) How can we break down the silos between ecologists and taxonomists to address taxonomic uncertainty? Interdisciplinary research is an effective way to enhance the dialogue between taxonomists and other biodiversity scientists. In practical terms, when providing a species list with associated synonyms, taxonomists could (i) explicitly state the year and publication in which species names were synonymized, and (ii) report the degree of uncertainty of each species delimitation in a standardized manner. In turn, users of this information should appropriately credit taxonomists. This would improve ecological models and give better visibility (and citation) for taxonomic works.

Glossary

Species: separately evolving metapopulation lineages.

Species delimitation: the proposal of a new hypothesis stating the boundaries of a species.

Specimen identification (or ***specimen determination*** according to Favret [18]): the assignment of a specimen belonging to a particular species.

Synonym: is one of two or more names that apply to the same taxon, but that is not the currently accepted one.

Taxon (***taxa***, plural): a taxonomic unit of organisms at any rank (e.g., species, genus, family).

Taxonomic uncertainty: refers to our degree of confidence in species boundaries and accurate identification of specimens.

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Author Contributions

LM, JS, and RJL led the writing; LF and TL searched for papers to compile Table S1; all authors contributed to the writing and revising the manuscript.

Declaration of generative AI and AI-assisted technologies in the writing process

GPT-4-turbo (OpenAI) was used for minor text editing. The authors take full responsibility for the content of the published article.

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List of figures

Figure 1. Taxonomic uncertainty across the five tasks of taxonomy (adapted from Favret, 2024). Taxonomic practice is a recursive and iterative process where the inability to assign a species name to a specimen may initiate a new cycle, potentially uncovering a new species or redefining the boundaries of an existing one. Note that uncertainty in any of the five tasks of the taxonomic process can affect the outcome of all subsequent tasks.

Figure 2. Taxonomic changes (lumping, splitting, and recombination) and their impact on biodiversity patterns and species threat status.