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Opinion

Finding Evolutionary Processes Hidden in Cryptic Species

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Cryptic species could represent a substantial fraction of biodiversity. However, inconsistent definitions and taxonomic treatment of cryptic species prevent informed estimates of their contribution to biodiversity and impede our understanding of their evolutionary and ecological significance. We propose a conceptual framework that recognizes cryptic species based on their low levels of phenotypic (morphological) disparity relative to their degree of genetic differentiation and divergence times as compared with non-cryptic species. We discuss how application of a more rigorous definition of cryptic species in taxonomic practice will lead to more accurate estimates of their prevalence in nature, better understanding of their distribution patterns on the tree of life, and increased abilities to resolve the processes underlying their evolution.

Cryptic Species – Taxonomic Oddities or Biologically Relevant Entities?

'Cryptic species' is a common and increasingly used term that refers to taxa that cannot readily be distinguished morphologically, yet evidence indicates they are on different evolutionary trajectories (Box 1). While researchers may not be able to visually recognize cryptic species as different species, the organisms can. Cryptic species are found on all major branches of the tree of life and probably represent a significant portion of undiscovered biodiversity [1–4]. As such, cryptic species might significantly add to our understanding of biodiversity, calling for increased conservation efforts [2,4–9]. Cryptic species are also important because they serve as an intellectual bridge connecting the study of taxonomy and phylogenetic pattern with ecosystems functioning, evolutionary processes, and macroevolutionary trends, including speciation, **parallelism** (see Glossary), **convergence**, and **stasis**. However, problems with the definition, among others the linkage to the species' taxonomic nomenclature history, and inconsistencies in the use of the term 'cryptic species' make it difficult to draw firm conclusions about their prevalence in nature and their implications for ecology and evolution.

Here, we discuss the general problem of defining cryptic species based on a literature survey that revealed the wide latitude in what researchers call cryptic species. Some authors have even suggested considering cryptic species as a temporary formalization problem of species delineation, rather than as a natural phenomenon [10]. To help mitigate the problem, we propose a more rigorous, multidimensional, and interdisciplinary approach for cryptic species. The approach focuses on better quantifying the extent of phenotypic **disparity** of taxa compared with the degree to which they have genetically diverged and exchanged genes (have evolved reproductive isolation). Standardizing the delineation of cryptic species will facilitate investigations into several outstanding questions concerning their biological significance (see Outstanding Questions). It will also lead to a better characterization and

Highlights

Current definitions of cryptic species are inconsistent and can lead to biased estimates of species diversity.

Cryptic species are often implied to represent taxa displaying low phenotypic disparity in relation to divergence time, but this relationship is usually not formally quantified.

Here we propose a quantitative framework, which provides a formal characterization of the intuitive concept of cryptic species.

The proposed framework facilitates understanding of evolutionary processes leading to and resulting from cryptic species and provides a basis for estimates and modeling of occurrences of cryptic species across taxa and environments.

The framework fosters a shift from pattern- to process-driven research concerning cryptic species.

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Box 1. Cryptic Species: History and Definitions

The English clergyman William Derham reported cryptic species in the avian genus *Phylloscopus* as early as 1718 [58]. Cryptic species have thus been recognized for several hundred years. In the last few decades the number of publications referring to cryptic species has increased dramatically (Figure IA), likely due to more researchers in the field and the increased use of genetic methods to distinguish taxa (Figure IB and, for example, [5,10]). However, criteria used in the literature to designate taxa as cryptic have often been vague and nonuniform. In the few cases where an explicit definition has been stated, the wording is often similar to that of Bickford *et al.* [5]: Cryptic species are 'two or more distinct species that are erroneously classified (and hidden) under one species name'. This taxonomy-based definition is often elaborated upon to highlight that cryptic species are morphologically indistinguishable [5,35]. Others have included an additional requirement of genetic divergence or distinctiveness between cryptic species ([15]; see Supplemental Table S4 online for a list of definitions). How genetically diverged populations must be to be considered cryptic species is usually not specified, but one can assume that this will be of the same magnitude as for non-cryptic species (e.g., a certain barcode gap) [5]. By contrast, several definitions seem to mostly follow trends and concepts related to the research topic of the paper or field of the researcher. For example, in speciation research, definitions tend to highlight reproductive isolation and the biological species concept [37]. Mayr [59], for instance, defined cryptic species as 'morphologically similar or identical natural populations that are reproductively isolated'. Other terms such as 'semi-cryptic', 'pseudo-cryptic', 'sibling', and 'hyper-cryptic' indicating different degrees of 'crypticity' have also been proposed [10], complicating the debate of the biological relevance of cryptic species. Regardless, our literature survey (Box 2) revealed that many cryptic species have been defined based on molecular data and taxonomic history, with little regard for actually quantifying morphological disparity.

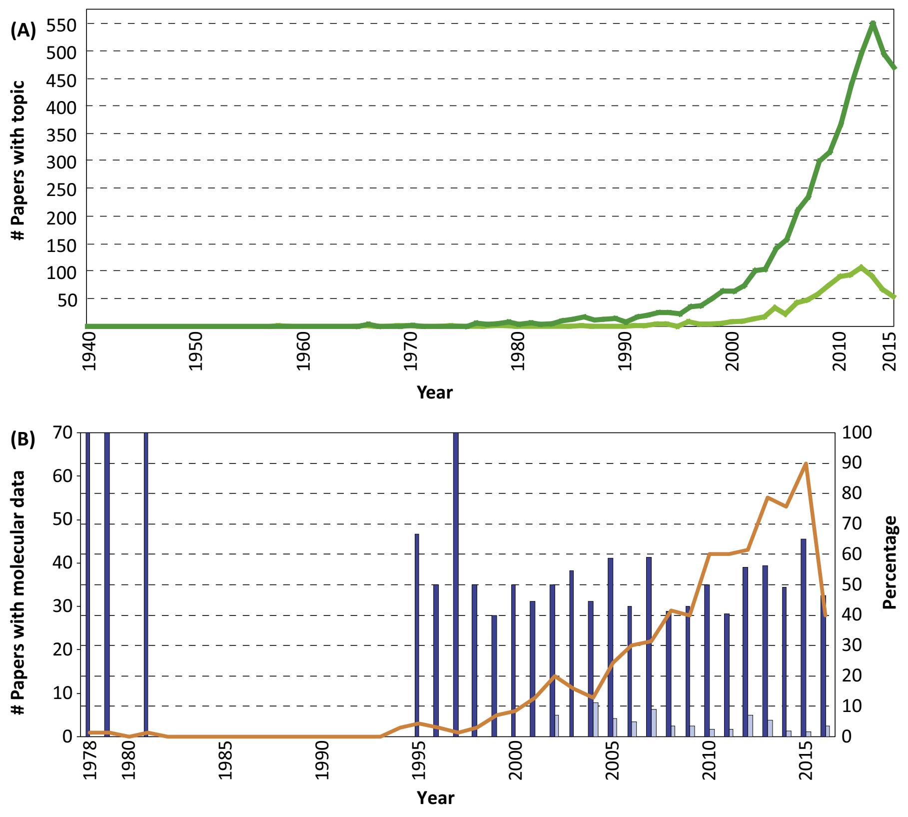

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Figure I. Scientific Publications on the Subject of Cryptic Species since 1940. (A) The number of papers found with the search term 'cryptic speci*' (dark green line) and 'cryptic speciation' (light green). Of note is the marked increase in publications since 1990. (B) The number of papers included in the literature survey (Box 2) that included molecular data in the study (orange line) is also increasing similar to the overall numbers in A. Dark blue bars indicate the percentages of molecular papers that analyzed more than one genetic marker and light blue bars indicate studies based on genomic data. Note that these percentages are not increasing through time.

understanding of the different types of cryptic species, from recently diverged to phylogenetically distant taxa. In doing so, conclusions concerning (i) evolutionary parallelism, convergence, and stasis; (ii) the role that cryptic species play in ecosystem functioning; and (iii) factors initiating and contributing to speciation can be more confidently accepted.

The Problem of Definition in Theory and Practice

Cryptic species have generated both taxonomic and evolutionary ambiguity. A frequently cited definition of cryptic species [5] describes them as two or more distinct species that were earlier classified as one. Hence, cryptic species are defined based only on their taxonomic nomenclature history. However, this is unsatisfactory because various biological factors or taxonomic artifacts might result in erroneous species lumping. In addition, it offers no guidance for how morphologically similar or by how many characters species should differ to be considered as cryptic. Moreover, one of the longest and most contentious debates in evolution concerns what constitutes a species. If biologists cannot even agree on what to consider different species, then how can we reach consensus on what represents cryptic species?

Our literature survey of 606 studies indicates that the lack of philosophical clarity translates into a serious empirical problem in the operational designation of cryptic species (Box 2, see Supplemental Material and Tables S1–S4 online). For example, 47% of them, even though claiming cryptic species status for taxa, presented no phenotypic data, while 25.3% reported at least one trait differing between cryptic species. Thus, morphological similarity is subjectively evaluated and rarely quantified to address how similar cryptic species are [11–13]. Moreover, nonmorphological phenotypes, such as behavior, were seldom considered (Box 2). In this regard, cryptic species designation was often pattern driven with a focus on morphological characters discriminating taxa and little else. When several phenotypic traits were assessed, analyses seldom extended to species beyond the focal cryptic species. This is relevant because rates of morphological evolution for cryptic 'ingroup' taxa should be substantially (statistically) reduced compared with non-cryptic taxa to be considered cryptic.

Glossary

Convergence: independent evolution of a derived character state between taxa from different ancestral traits [41].

Disparity: the morphological or phenotypic difference between taxa [60].

Most recent common ancestor (MRCA): the last ancestor genetically shared by a group of individuals.

Parallelism: independent evolution of a character state in different taxa from a similar and shared ancestral trait [41].

Pattern-driven research: research focusing on the detection of biological patterns in empirical data.

Process-driven research: research focusing on the underlying processes generating observed patterns.

Stasis: retention of the same ancestral character state over an extended period [41].

Symplesiomorphy: character state of the MRCA present in descendant taxa.

Box 2. Characteristics of Published Studies of Cryptic Species

Our literature survey was based on the ISI Web of Science 'Life Sciences' database, using the search term 'cryptic speci*' for 'Topic' on June 17, 2016. The initial search returned 6002 entries (see Supplemental Table S1 online), from which approximately 15% were discarded as they were either not research papers, did not use our search term in a taxonomic context, or were not written in English. From the remaining publications, 606 were randomly chosen (see Supplemental Table S2 online) and assessed according to (i) how cryptic species were defined; (ii) whether and which types of genetic markers were scored; (iii) the analyses conducted; and (iv) the conclusions that could be drawn (see Supplemental Material and Table S3 online for additional details). For these 606 papers, 72.4% involved animals, 7.5% plants, 10.1% fungi, and 6.4% other groups, including protozoans. Only 14.0% of the studies explicitly referred to a specific definition of the term 'cryptic species', indicating the degree of subjectivity in the field. Moreover, according to the Code, species – including cryptic ones – are only valid when accompanied by a formal description. However, only 19.3% of the studies provided such formal descriptions. This low number can be indicative of uncertainties of the species status, ignorance of taxonomic practice, or that the species were formally described elsewhere.

The majority of studies (84.2%) provided molecular data, but many (35.5%) used only one locus. In comparison, only 42.7% of the studies included explicit analyses of morphological data and 23.9% other phenotypic traits. Overall, 56.6% of the studies targeted mitochondrial loci and 52.6% nuclear markers. Of the studies using nuclear data, 48.3% contained results for multiple loci. Very few studies included genome-scale data (3.1%). The relative numbers of studies with more than one marker or genomic data have not increased in recent years (see Figure IB in Box 1). Most studies (73.9%) provided an estimate of genetic divergence of some form (e.g., distance estimates or phylograms) and included congeneric species in the comparison (61.4%). However, only 16.0% of the studies applied genetic dating methods to estimate the time to the MRCA and only 4.3% used fossil calibrations.

The genetic data provided in the surveyed studies were also of limited utility in cryptic species delineation. Of the 606 studies, 35.5% based cryptic species designation on only a single molecular marker, most often from the plastid or mitochondrion, and lacked information on phenotypic disparity. Only 15.4% of the surveyed studies combined different types of molecular markers with morphological and/or other phenotypic data, and compared genetic divergence of the cryptic taxa with other congeneric non-cryptic species. The results show that there is remarkable inconsistency in the operational designation of 'cryptic species' [5,14,15] and huge variation in the applied analytical rigor [11,16–21]. Taxonomic practice for identifying cryptic species thus requires attention if the term is to be useful for comparative studies.

With recent advances in high-throughput DNA sequencing, visualization/microscopy, and statistical analytical tools, there are no technological or methodological impediments restricting higher standards in the empirical investigation of cryptic species [22,23]. This is important as informed estimates of species diversity and speciation rates are crucial for understanding evolutionary processes and ecosystem functioning, and for developing effective conservation strategies and sustainable usage of ecosystem services [2,4–9]. Cryptic species are one component of these estimates. Estimates of cryptic biodiversity based on vague definitions are of little help and, like undiscovered species or lack of species lists, will be counterproductive. For example, in ecology and conservation research, cryptic species are usually taken at face value based on the original reports. In particular, studies investigating patterns of cryptic species distribution across habitats, taxonomic groups, or life history strategies are often based on meta-analyses [5,24–28]. Given the shaky foundation in which cryptic species appear to be subjectively defined, it is difficult to place much confidence in the conclusions drawn from such meta-analyses. Sympatric cryptic species might, for example, contradict the ecological paradigm of competitive exclusion [29,30], but based on the current state it remains difficult to decide whether this is specifically or generally true. Similar considerations apply to studies of parallelism, convergence, and stasis. Without better standardization of the designation of cryptic species including details about phenotypic variation, levels of genomic differentiation, and divergence times, it remains difficult to make proper inference about evolutionary processes. Such standardizations as suggested herein will substantially improve comparability across lineages, as taxonomic nomenclature traditions are replaced with studies quantifying variation in a similar manner within and across groups.

The Conceptual Framework

Accurate **pattern-** and **process-driven research** on cryptic species is possible. However, to accomplish this, a sound and consistent foundation for defining cryptic species is needed. We do not pretend to solve the cryptic species problem completely here, but offer a conceptual framework to alleviate the problem by combining phenotypic disparity and genetic divergence. The latter serving as a proxy for reduced gene flow and an estimate of the time since divergence from the **most recent common ancestor (MRCA)**. By doing so, we emphasize the importance of reduced gene flow between taxa and the establishment of reproductive isolation between sexually reproducing populations relative to the extent to which they have changed in morphological and other phenotypic characters. As we explain later, this approach facilitates studies of parallelism, convergence, and speciation. The proposed framework provides a yardstick for the standardization of cryptic species descriptions without getting too entangled in the issue of species concepts. We concentrate on sexually reproducing organisms, for which a metric of gene flow and divergence time versus phenotypic disparity are key considerations.

Our conceptual framework highlights two important elements for defining cryptic species (Figure 1). First, species have to be distinguishable, for example, as statistically separable

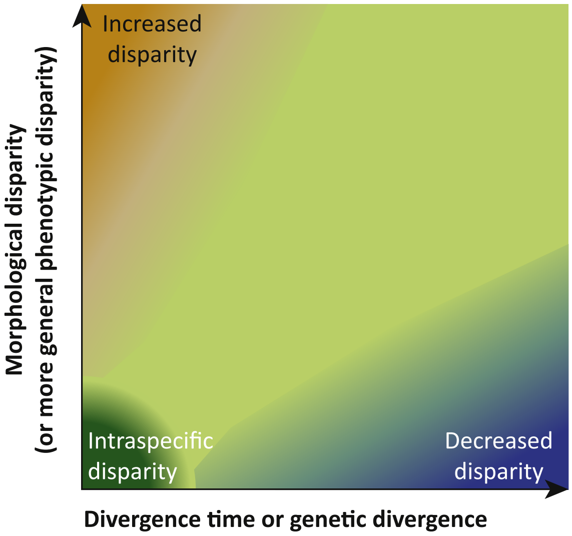

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Figure 1. Our Conceptual Framework for Cryptic Species. The *x* axis represents the time of divergence between taxa since their most recent common ancestor approximated by genetic divergence. The *y* axis represents phenotypic (morphological) disparity. Intraspecific variation (polymorphism) within a taxon is depicted by the dark green area in the lower left corner of the figure. The null hypothesis is that morphological disparity between taxa relative to sister species should increase proportionately with divergence time (light green area). However, morphological disparity could increase at a significantly higher rate than the null expectation due to, for example, a recent adaptive radiation (orange area in the upper left corner of the figure). Alternatively, morphological disparity could also be substantially lower than expected over time (blue area in the lower right corner), the hallmark of cryptic species.

and diverged genotypic clusters of individuals (reflecting reproductive isolation) that do not form diagnostic morphological clusters. Although estimates of reproductive isolation in nature are only truly possible for taxa that geographically overlap, data from laboratory crosses, when technically feasible, and other information can be used to help gauge the level of gene flow and reproductive isolation. One major consideration is the time point when diverging populations are considered as being genetically and reproductively distinguishable species (e.g., [31–35]), as this will affect conclusions about recently diverged species. Consequently, cases, where populations exhibit sufficient gene flow to not cluster distinctively using methods like STRUCTURE or genetic network analyses, should be considered, if at all, as races or ecotypes [34,36], rather than cryptic species [37].

Second, the temporal dimension of cryptic species should be recognized by their showing of statistically lower degrees of phenotypic (or more specifically morphological) disparity than non-cryptic relatives given similar divergence time estimates from their MRCAs (Figure 1). By placing morphological disparity directly in relation to time (genetic divergence), recognition of cryptic species can become divorced from taxonomic nomenclature traditions based on the numbers of previously recognized species (e.g., lumpers vs. splitters), and debates about levels of ‘crypticity’ [10] more nuanced.

Although these two components of defining cryptic species seem self-evident, they are seldom adequately performed to allow for quantitative comparisons. For example, the temporal dimension is frequently ignored [38–40] and, of the 606 studies in our survey, only 3.3% and 4.5% of the reported divergence events could confidently be regarded as young or old, respectively. For accurately determining genetic divergence, genome-wide sequence data are highly preferred for any group of taxa. However, very few studies applied genome-scale data (Box 2) [18,23]. Uniparentally inherited markers, such as the mitochondrial cytochrome oxidase subunit I gene (COI) – the target marker for DNA barcoding in animals – do not provide a comprehensive assessment of gene flow and reproductive isolation. There are several examples of high genetic divergence in COI that reflect deep population structure rather than species differences [18].

More importantly, to identify and quantify species that are cryptic from those that are not, detailed information about phenotypic disparity has to be related to genetic divergence, levels of gene flow, and reproductive isolation. Therefore, population to species-level morphological variation needs to be explicitly quantified to measure morphological disparity among cryptic species and their relatives as, for example, done in [41–43]. Available species descriptions can provide a good starting point for such morphological comparisons, providing information on both discrete and continuous characters. Depending on the data, appropriate methods for the quantification of morphological variation are available, including geometric morphometrics [44], landmark-free approaches such as the generalized Procrustes surface analysis [45], and multivariate analysis like nonmetric multidimensional scaling [46]. These methods and clustering, principal component, and discriminant function analyses should be employed to assess whether populations can be statistically distinguished from another or not. In addition, statistical tools like disparity through time plots [47] allow for testing whether morphological disparity between hypothesized cryptic taxa is significantly lower than expected given a null random walk expectation of drift. Tests of rate variation (e.g., variance ratio test) among hypothesized cryptic and non-cryptic lineages can also indicate whether morphological and other phenotypic traits (e.g., those related to behavior, life history, and physiology) deviate significantly from neutral expectation to statistically support cryptic species status for taxa. Note that hybridization has the potential to complicate analyses by reducing phenotypic disparity below levels seen for allopatric or completely reproductively isolated populations. However, it can generally be expected that proportional reductions in the level of genomic divergence would compensate for this and help to maintain the standardization of cryptic species delineation.

Currently, there are no studies that adhere completely to the proposed framework. There are several examples, however, where most of the requirements are fulfilled, for example, in studies of unicellular eukaryotes [48], cnidarians [41], annelids [42], mollusks [43], vertebrates [46], and plants [49]. However, the primary focus of these studies has been to find diagnostic characters. Phenotypic disparity was usually not cast in relation to other non-cryptic taxa and/or genetic divergence. One reason for this is that detailed examination of phenotypic and genetic variation in a comparative context, as proposed here, is time-consuming and not practical for projects whose primary focus is not the delineation of cryptic species (but then they should also refrain from assigning them). However, accurate rather than quick science is what should be aimed for, and when conducted properly, the proposed framework will provide the rigor to move beyond suggestive evidence to full and more standardized recognition of cryptic species.

Evolutionary Processes and Cryptic Species

Given a standardized and more accurate characterization of cryptic species, it is possible to examine their ecological and evolutionary implications in greater depth and with more confidence. For example, one question of interest is the extent to which cryptic species represent recently diverged versus more distantly related taxa. Other questions concerning evolutionary processes like parallelism, stasis, and convergence that are often considered primarily with respect to single traits [50–52] could also be extended to investigate whole phenotypes by more robust analysis of cryptic species. In this regard, underlying selective regimes might be expected to be more pronounced or generally constrained to impact the entire (or nearly entire) suite of phenotypic traits [53], to which the term ‘cryptic speciation’ has been misleadingly applied in recent years (Figure IA). We examine these questions in the following section.

Recent Divergence

In this case, hypothesized cryptic species are sister taxa or members of a species complex with short divergence times, which are too recent for substantial morphological differences to accumulate [37,54,55] (Figure 2A). In many of these instances, the rate of accumulation of morphological disparity might actually not differ significantly from older non-cryptic species (Figure 2A). In speciation research it is commonly assumed that in the early stages of speciation selection acts largely on physiological, immunological, reproductive, or behavioral traits rather than on morphology [16,17,19]. Hence, for very young species, similarity in morphology might not be unexpected and it could take additional time to visually observe differences between taxa [10]. However, recently diverged taxa showing significantly lower rates of morphological disparity might be constrained by stabilizing selection and represent early stages of stasis.

Parallelism

Cryptic species that evolved by parallelism are not sister taxa, but are phylogenetically separated from each other to such a degree that their similarity can no longer be considered **symplesiomorphic**, but rather independently evolved from morphologically similar ancestors (Figure 2B). In comparison to more closely related and younger non-cryptic species, morphological disparity changes less as the cryptic species evolve from one similar morphotype to another similar one (Figure 2B). However, if the evolution of the new morphotype in one lineage precedes the other lineage in time, morphological disparity will first increase and then decrease again (similar to the plot in Figure 2C). Regardless, ancestral character state reconstructions are important to distinguish between recent divergence, convergence, or parallelism, and to assess and test rates of morphological change. Swift *et al*. [41], for example, showed that similar morphologies for lake species evolved by parallelism in closely related scyphozoan species. Confirmation of parallelism begs the question of whether similar morphotypes evolved due to intrinsic (e.g., developmental or genetic constraints) or extrinsic factors (e.g., deterministic environmental pressures) confining the available morphospace to only one selectively advantageous solution.

Convergence

In this case, cryptic species are not closely related and their morphological similarity results from independent evolution of morphologically dissimilar ancestors (Figure 2C). At early stages of divergence, cryptic and non-cryptic species pairs are expected to show similar rates of morphological differentiation. However, at some point in time the cryptic species pairs would begin to converge morphologically (Figure 2C). Convergence as a mechanism for cryptic species is rare, but has been reported in the deep sea [56]. In contrast to parallelism, intrinsic factors are expected to be less important for convergence than extrinsic ones, as convergent evolution is assumed to have started from different genetic and developmental backgrounds.

Stasis

Under stasis, cryptic species are sister taxa or members of a complex that retain a high degree of morphological similarity over extended periods (Figure 2D). Hence, symplesiomorphies prevail for millions of years, and significantly longer than expected by random drift. For example,

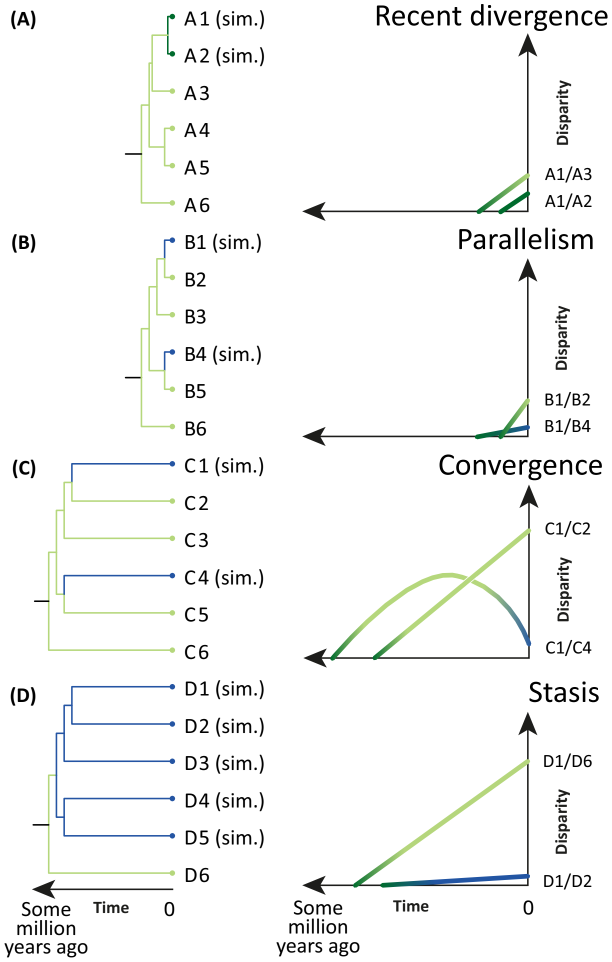

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Figure 2. Expected Signatures of Four Evolutionary Processes That Can Lead to Cryptic Species. The colors of lines in phylogenies and graphs correspond to the different areas in Figure 1 and species with similar (identical) morphotypes denoted with 'sim.'. Panels on the left denote the phylogenetic relationships among taxa, while the panels to the right depict the evolution of morphological disparity through time for pairs of cryptic and non-cryptic species (e.g., A1/A2 vs. A1/A3). (A) Recent divergence: cryptic species are very closely related and only recently diverged from each other. However, the rate of morphological disparity is not necessarily substantially different from that for non-cryptic species and, as such, these taxa may not actually represent cryptic species. The supposed cryptic species might indeed be on a trajectory, which with time might lead from the borders of the dark green area to the light green area in Figure 1. (B) Parallelism: the cryptic species are not very closely related to each other and the rate of morphological disparity for non-cryptic species is much greater than that for cryptic species. While disparity between non-cryptic species evolved from the dark to the light green area, disparity between the cryptic species progressed into the dark blue area of Figure 1. (C) Convergence: the cryptic species are also not closely related to each other. Initially, morphological disparity for cryptic species can change in a manner similar to that for the non-cryptic species pair. However, at some point, morphological disparity decreases for the cryptic species, while continuing to increase between non-cryptic taxa. Hence, in their past the level of disparity of the cryptic species was first within the light green area of Figure 1, but then evolved toward the dark blue area associated with the low level of disparity of cryptic species. (D) Stasis: the cryptic species are closely related to each other or are part of a species complex and diverged a long time ago. In comparison with non-cryptic species, the rate of morphological change is substantially reduced, as cryptic species evolved from the dark green to the dark blue area of Figure 1.

one cryptic complex of annelid worms has been shown to display little morphological variation over tens of millions of years [42]. The lack of morphological diversification could result from low standing genetic variation and/or developmental constraints on the morphospace [5,57]. It is also possible that the ecology of taxa showing stasis has remained relatively constant through time and strong stabilizing selection has retained a common, shared morphology. This raises the question of whether cryptic species tend to be ecological generalists versus specialists, the answer to which might hinge on how common adaptation to different environments underlies speciation and depends on morphological change.

Concluding Remarks

Current research practices regarding cryptic species require change. There is much insight to be gained by standardizing and increasing the rigor in the way that cryptic species are defined and studied. Current practices, however, do not allow firm conclusions to be made concerning the number and significance of cryptic species in nature or the evolutionary processes associated with them. Indeed, given the results of our literature survey it is likely that many reported cryptic species should not be considered as such. Consequently, there is a need for careful re-analyses of many proposed cryptic species complexes with more rigorous criteria to better assess their true prevalence in nature. We propose an interdisciplinary approach that involves combining comprehensive data on genomic and phenotypic traits to statistically test for significant differences in rates of phenotypic disparity (e.g., morphological disparity) between cryptic and non-cryptic species. This approach will standardize the designation of cryptic species in the literature for taxonomic and comparative purposes; eliminate the history of taxonomic nomenclature as a consideration; and enable meta-analyses based on comparisons involving taxa categorized as displaying similar versus differing levels of disparity, periods of divergence, and degree of reproductive isolation. Adopting the approaches we advocate will provide a more sound basis for policy making in conservation biology and make it possible to address a number of questions involving evolutionary parallelism, convergence, and stasis associated with cryptic species (see Outstanding Questions), helping to reveal the biological meaning hidden in cryptic species. Conducted across lineages, general principles and accurate predictions, for example, to what extent cryptic species prevail in certain groups or are affected by climate change can be deduced.

Outstanding Questions

What is the general relationship between phenotypic disparity and reproductive isolation and genetic divergence through time?

Do thresholds of phenotypic disparity indicating the presence of cryptic species exist or is the relationship a continuum, with taxa lying in the tail of the distribution warranting cryptic species status?

Which methods for assessing phenotypic disparity and their significance are most universally applicable and most powerful with regard to discerning cryptic species?

Is it possible to establish an *a priori* best-practice strategy for defining cryptic species across a broad range of diverse taxonomic groups?

Are there more cryptic species in certain branches of the tree of life, among taxa with certain life histories (e.g., generalists vs. specialists), or in certain habitats?

Which cryptic species are the results of recent speciation, parallelism, convergence, or stasis, and how common are they?

What are the relevant intrinsic and extrinsic factors affecting morphological evolution and to what degree do they affect the phenotypic landscape of cryptic species?

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Supplemental Information

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