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Perspectives

Cryptic species diversity should not be trivialised

Abstract Cryptic diversity, defined as two or more distinct species that were classified as a single one due to morphological similarity, is believed to be a potentially important factor influencing future conservation decisions. A recent meta-analysis allegedly demonstrated that the proportion of cryptic species is almost evenly distributed among major metazoan taxa and biogeographical regions – a conclusion of potentially profound impact on biodiversity assessment and conservation. We argue that this result is the consequence of methodological error, and using the same data, show that the degree of cryptic diversity between metazoan phyla varies up to two orders of magnitude. Cryptic diversity is a non-trivial, genus level phenomenon that, because of its apomorphic nature, should not be generalised across all Metazoa.

Keywords cryptic diversity, cryptic species, Metazoa, phylogeny, biodiversity conservation

Introduction

The discovery of cryptic diversity, defined as two or more distinct species that were classified as a single one due to morphological similarity (e.g. Bickford *et al.*, 2007; Pfenninger & Schwenk, 2007) is believed to be a potentially important factor influencing future conservation decisions (e.g. Witt *et al.*, 2006). Bickford *et al.* (2007) predicted that ‘the discovery of cryptic species is likely to be non-random with regard to taxon and biome and, hence, could have profound implications for evolutionary theory, biogeography and conservation planning’. They base their forecast on data taken from disparate types of studies, and mainly anecdotal, rather than systematic and quantitative evidence. Conversely, Pfenninger and Schwenk (2007), inspired by this prediction, conducted a quantitative meta-analysis of 771 931 papers containing 2207 reports on cryptic species in several metazoan phyla. They rather unexpectedly concluded that the proportion of cryptic species is almost evenly distributed among major metazoan taxa and biogeographical regions when corrected for species richness and study intensity. In a recent review on cryptic biodiversity, Beheregaray and Caccone (2007) took a neutral stance toward this radical view, notwithstanding the profound impact it might have on biodiversity assessment and conservation.

If it were true that we can expect a predictable proportion of cryptic diversity in each metazoan group and biogeographical region, then that kind of systematic research, which is among the most expensive and time consuming (e.g. Lefébure

et al., 2006; Brown *et al.*, 2007; Elmer *et al.*, 2007) would become largely superfluous. Similarly, efforts to increase efficient population sampling, for example in the tropics, in arthropods, in subterranean environments, or wherever high cryptic diversity is expected, should be removed from the priorities of biodiversity agendas. It is precisely because the ‘... direct theoretical and practical consequences for global biodiversity estimates, conservation efforts and global taxonomic initiatives’ of the work of Pfenninger and Schwenk (2007) are potentially so profound that we think a fast response of the community is necessary to either corroborate and accept, or to refute them.

Here we show that the data used by Pfenninger and Schwenk (2007) actually imply a substantial variation of taxonomic cryptic diversity reaching up to two orders of magnitude, but argue that only genus- or lower-level studies can really reveal meaningful regularities of the cryptic diversity phenomenon.

A matter of scale

The notion of a homogeneous proportion of cryptic species in metazoan taxa rests upon linear regression models calculated from the following variables: (1) log-transformed number of cryptic species reports in relation to log-transformed number of species within a taxon (phylum, classes, or a pool thereof); (2) log-transformed number of publications in relation to the log-transformed number of species within a taxon; (3) residuals from both regressions (excess/deficit of taxonomic effort as independent, and excess/deficit of cryptic species reports as dependent variable). The third regression was used to explain a part of the variance of the first one.

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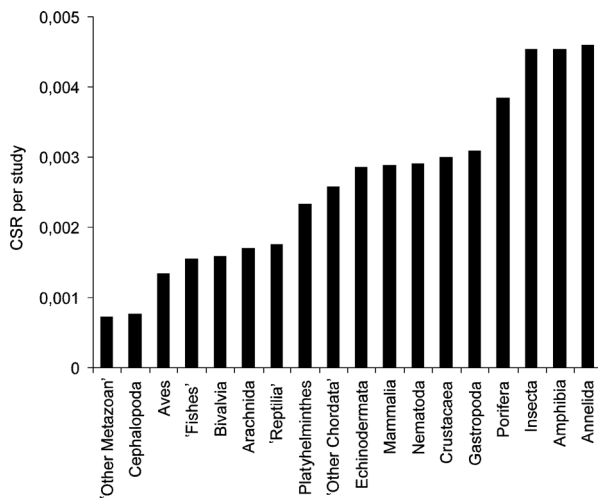


Figure 1 Cryptic diversity (in cryptic species reports, CSR, per published study) in major metazoan groups used by Pfenninger and Schwenk (2007), corrected for study intensity and taxon size. The extremes ‘other Mollusca classes’ and ‘other Arthropoda classes’ with diversity values of 0.0002 and 0.0226 CRS per published study, respectively, were omitted.

The log transformation obscures what the correlation ($R^2 = 0.53$ and 0.47) actually indicates: differences in proportions, measured on a linear scale. With species numbers ranging from 10^2 to 10^6 per group and the corresponding cryptic species reports from 1 to 10^3 , substantial variation in proportions could still be hidden behind a statistically significant correlation. Following the reasoning of Pfenninger and Schwenk (2007), we corrected the proportion of cryptic species reports per group by relative study effort expressed as number of papers per species. The values obtained differ between 0.0002 and 0.02 cryptic species reports per paper in ‘other Mollusca’ and ‘other Arthropoda’, respectively. (Both, cryptic species reports and number of all papers are a function of the same underlying taxon size, therefore the proportion of cryptic species reports corrected for study effort can be calculated directly as the quotient between cryptic species reports and number of all papers.) After removing the two extremes, cryptic diversity still spanned an order of magnitude (Fig. 1). Even within the vertebrates, a threefold difference in the corrected percentage of cryptic diversity between ‘fishes’ and amphibians is in our opinion enough to question the notion of a homogeneously distributed cryptic diversity among vertebrate classes.

Use of non-monophyletic groups

The groups forming the basis for the quantitative analysis by Pfenninger and Schwenk (2007) were selected and formed ad hoc. Beside well-established monophyletic groups, the data included ‘evolutionary’ paraphyletic taxa such as fishes, and even totally arbitrary ones, like ‘other arthropod classes’. The use of non-monophyletic groups of different taxonomic rank may lead to circular reasoning and affect the linear regression model. Pfenninger and Schwenk’s (2007) final conclu-

sion, ‘... morphological stasis upon speciation represents an evolutionary constant, independent of phylogenetic relation or ecological circumstances’, is based on pooled taxa whose relationships were explicitly ignored. Twenty-six out of 34 or so extant metazoan phyla including Cnidarians with 10 000 and Ectoprocts with 7000 species (Brusca & Brusca, 2003) were pooled into a single group called ‘Other Metazoan phyla’. Leaving aside the problem of ignored phylogenetic relationships, the obvious trouble with pooling the data a priori is that it requires the presumption of a uniform distribution of cryptic diversity. Hence, for the majority of metazoan phyla, the conclusions rest on circularity. Moreover, the log-transformation of species numbers biases the model towards more inclusive groups (for example phyla represented by many classes) because

$$\sum \log(\text{number of species within classes}) > \log\left(\sum \text{number of species within classes}\right). \quad (1)$$

Speciation processes should be studied at the rank of genus

The main fallacy of the top-down approach is that it ascribes post-speciation morphological crypsis as a trait to phyla and other higher taxa, and, by induction, assigns it to the Metazoa as a whole. By so doing, Pfenninger and Schwenk (2007) created a black box around the underlying speciations and associated processes. However, the astounding variety of speciation-related processes (e.g. Howard & Berlocher, 1998; Coyne & Orr, 2004; Dieckmann *et al.*, 2004) and the inherently apomorphic (derived) nature of the new traits evolving thereafter, speak much in favour of multiple origins and mechanisms generating cryptic species diversity. Every new genus and every newly colonised habitat may have their own level and pattern of cryptic diversity, requiring a specific investigation and conservation approach. Only when hidden in the black box, can these differences be manipulated to demonstrate that ecological circumstances have no influence and that cryptic diversity is homogeneously distributed over the globe.

Bickford *et al.* (2007) pointed out that extreme environments may harbour a higher degree of cryptic diversity due to selection reducing or eliminating morphological change accompanying speciation. However, neither Bickford *et al.* nor Pfenninger and Schwenk (2007) elaborated on cryptic diversity as a consequence of convergent or parallel morphological evolution under similar selection pressure. Similarities leading to this kind of cryptic diversity are independently derived and as such cannot possibly apply to some general pattern innate to all metazoans. Trontelj *et al.* (2008) have shown that this kind of cryptic diversity can play a major role in subterranean crustaceans. It is peculiar to a certain environment and certain taxa, and as such in stark contrast with the generalisations proposed by Pfenninger and Schwenk (2007).

Low proportions of cryptic species may indicate that the routine use of molecular techniques as a major tool for their discovery (Witt *et al.*, 2006) has been introduced relatively

recently. In such cases, correlating the proportions of cryptic species with the general study intensity measured by number of publications can lead to false conclusions. Also, it seems reasonable to believe that for most taxonomic groups the time of discovery of cryptic species has just begun (see Fig. 1 in Bickford *et al.*, 2007). Consequently, it is highly questionable whether the published studies suitable to detect cryptic species have sampled the Metazoa randomly and densely enough, both in a phyletic and ecological sense, so the hypothesis of non-randomness of cryptic diversity, even at the widest taxonomic and geographic scale, remains a challenge. Sound testing will only be warranted when genus-level studies on cryptic diversity accumulate to the point where non-trivial random representation of higher order taxa or biomes will be possible. At scales relevant for diversity estimates (e.g., between vertebrate classes) and conservation planning the body of evidence is clearly on the non-random side advocated by Bickford *et al.* (2007). The generalisation ‘that cryptic metazoan diversity predictably affects estimates of earth’s animal diversity’ (Pfenninger & Schwenk, 2007), and all its consequences should be treated most cautiously.

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