Cryptic species and their evolutionary significance

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Abstract:	<p>Cryptic species are detected at an ever-increasing rate, mainly due to the application of molecular data. While the impact of this hidden diversity on macro-ecology and conservation biology is widely recognized, its evolutionary significance is rarely. In recent years it became apparent that definitions of cryptic species are too ambiguous to allow the differentiation between natural phenomena from human-made artefacts. Hence, recently a unifying conceptual framework has been proposed highlighting the necessity to test the degree of reduced phenotypic disparity in cryptic species. Within this reduced disparity also lies the evolutionary significance, as cryptic species can be regarded as the opposite of adaptive radiations. Specifically, studies on evolutionary stasis can substantially benefit from including these by addressing both patterns of reduced disparity and processes resulting in the lack of phenotypic evolution. Additionally, this will allow connecting macro-evolutionary and paleontological studies with micro-evolutionary investigations of genotype-phenotype linkage.</p>

1 **eLS**

2 **Cryptic species and their evolutionary significance**

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7 **Advanced article**

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10 molecular data. While the impact of this hidden diversity on macro-ecology and
11 conversation biology is widely recognized, its evolutionary significance is rarely. In
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18 stasis can substantially benefit from including these by addressing both patterns of
19 reduced disparity and processes resulting in the lack of phenotypic evolution.
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21 with micro-evolutionary investigations of genotype-phenotype linkage.

22

23 **Key words:**

24 Taxonomy; Speciation; Recent divergence; Parallelism; Convergence; Stasis;
25 Paleontology; Morphology; Phenotype; Adaptive radiations

26

27 **Key Concepts:**

- 28 • Cryptic species are phenotypically highly similar species.
- 29 • Species complexes resulting from taxonomic artefacts should not be considered
30 as cryptic species.
- 31 • To identify cryptic species, first one should establish species boundaries and only
32 then study processes resulting in phenotypic similarity.
- 33 • Cryptic species could result from recent speciation, parallelism, convergence or
34 stasis.

- Evolution of cryptic species through stasis holds the potential to enlighten us about deceleration of phenotypic evolution.
- Cryptic species (shallow morphological differences, pronounced genetic divergence) could be considered as the opposite of adaptive radiation (pronounced morphological differences, shallow genetic divergence).

Introduction:

Taxonomy, the discipline dealing with the delimitation of biological units, remains one of the most contentious and laborious disciplines in biology, yet it represents a fundamental step before understanding underlying evolutionary processes. Interestingly, taxonomical considerations already had a strong impact on Darwin's line of argument concerning evolution (Darwin, 1859). He had already pointed out the problem of delineating species properly, and that the progress from populations to species is a contiguous scale with respect to the variability that can be observed at different levels, rendering it difficult to delineate species boundaries with certainty. The debate about this problem is still vibrant today and the debate about species concepts and how to apply them is in full fledge (for details see DOI: 10.1002/9780470015902.a0001744.pub2). In the last decades the discussion about cryptic species has been added to this debate, highlighting the necessity to delimitate independently evolving units to understand evolutionary processes.

The concept of cryptic species has been applied as early as 1718 by the English clergyman William Derham focusing on the avian genus *Phylloscopus* (Winker, 2005) and Mayr (1963) coined the term sibling species for cases, where the species are either sister or very closely related to each other. However, the detection of cryptic species really took off with the advent of employing sequence data in delineating species boundaries on a much broader scale since the early 1990's (Struck et al., 2018b; see DOI: 10.1002/9780470015902.a0003608.pub2 on barcoding). Since then, cryptic species have been detected at an ever-increasing pace and across all habitats on Earth and the entire tree of life including fungi, algae, plants, protists, invertebrates, but also primates, amphibia, reptiles and crustaceans (e.g., Bickford et al., 2007; Pfenninger and Schwenk, 2007; Perez-Ponce de Leon and Poulin, 2016; Hawksworth and Lücking, 2017). Accordingly, cryptic species seem to represent an overlooked, yet substantial part of biodiversity with far-reaching implications for ecological research such as diversity estimates, pest control, fisheries management and conservation efforts as well as research in model systems (Bickford et al., 2007; Caputi et al., 2007; Bernardo, 2011; Pante et al., 2015; Fišer et al., 2018). However, like with any new emerging concept in biology, the term cryptic species is often applied with very different meanings and hence has different implications. This, among others, affects the general conclusions, which can be drawn concerning cryptic species. Due to the different meanings the conducted meta-analyses usually compare apples with oranges (Struck et al., 2018b; Struck et al., 2018a). Therefore, it became noticeable that a unifying theoretical framework is needed for studying cryptic species, which then would also allow for drawing more general and solid conclusions about the ecological and evolutionary significance of cryptic species. Only such conclusions are then able to provide meaningful contributions to, for example, conversation management or health issues stemming from cryptic species.

1 **Towards a unifying conceptual framework for cryptic species**

2 The first attempt towards a unifying conceptual framework of cryptic species was
 3 accomplished by Bickford et al. (2007). They defined cryptic species as "two or more
 4 distinct species that are erroneously classified (and hidden) under one species name".
 5 This broad definition was quickly applied in several studies and became the most
 6 commonly used one, as it is easily applicable due to its tight link to the taxonomic
 7 history of the species. That is, it strictly requires that the species complex is formally
 8 described as a single species before. However, this also entails a caveat associated with
 9 different schools of taxonomic practice (DOI: 10.1038/npg.els.0003093). For instance, in
 10 taxonomy some schools favour splitting species even in cases of only little support, while
 11 others would rather lump these together as a single species (the splitter vs. lumpers
 12 debate). Hence, some groups would be more prone to have cryptic species only due to
 13 different taxonomic practices. For example, the newly described *Marphysa aegypti*
 14 (Annelida) from Egyptian waters was previously recorded as *M. sanguinea* (Elgetany et
 15 al., 2018). Even though both species are morphologically substantially different from
 16 each other, they could be called cryptic species or at least pseudo-cryptic species, while
 17 in truth the previous records suggest only sloppy taxonomic practices. On the other
 18 hand, molecular data supported the traditional assignment of species within the genus
 19 *Polygordius* (Annelida) based on geographic regions (Ramey-Balcı et al., 2018), despite
 20 the indistinguishable adult morphology of *P. lacteus* from *P. neapolitanus* and *P. jouinae*
 21 from *P. triestinus*. Nonetheless, both species pairs could not be considered cryptic
 22 species given the provided definition by Bickford et al. (2007). Moreover, others pointed
 23 out that recent definitions of cryptic species are often linked to and depend on the
 24 applied species concept (Pante et al., 2015; Sukumaran and Knowles, 2017; Fišer et al.,
 25 2018; Heethoff, 2018). Given these non-biological aspects, several studies introduced
 26 slightly different concepts such as pseudo-cryptic, hyper- or mega-cryptic species (e.g.,
 27 Adams et al., 2014; Cornils and Held, 2014; Nygren et al., 2018).

28 Hence, in recent years there has been an increased debate again what constitutes a
 29 cryptic species. Ultimately, Korshunova et al. (2017) argued "to avoid the terms
 30 "cryptic"/"pseudocryptic" species as a reference to a "natural phenomenon" because it is
 31 obscuring multilevel character diversity within a complicated taxonomy-dependent
 32 framework" and instead "to use the term "cryptic species" only for a temporary
 33 formalization of the problems with delineation of the species from the same geographic
 34 region, when those species demonstrate significant molecular phylogenetic differences,
 35 but are hardly distinguished morphologically, ethologically, etc.". A recent literature
 36 survey found that only 14% of the studies actually provided or applied an explicit
 37 definition of cryptic species adding to the problem of uncertainty in the assignment of
 38 cryptic species (Struck et al., 2018b). Of these, all were explicitly or implicitly taxonomy-
 39 based like the Bickford et al. (2007) definition. Additional criteria such as usage of
 40 molecular data, sympatric occurrence, reproductive isolation, reduced gene flow, or no
 41 morphological differences were included in the definitions. Moreover, another problem of
 42 assigning cryptic species based on these definitions is that the species delineation
 43 process is intermingled with the assignment of the term "cryptic". As a consequence, all
 44 problems associated with species delineation (DOI:
 45 10.1002/9780470015902.a0003456.pub2) also automatically apply to the assignment.
 46 In summary, the assignment of a species as cryptic species depends on many non-

1 biological factors such as the applied definition and species concept as well as the
2 taxonomic tradition resulting in much uncertainty about what constitutes a cryptic
3 species and if it is a natural phenomenon or only a human-made artefact. This problem
4 has dire consequences for meta-analyses investigating the impact of cryptic species in
5 biodiversity studies (e.g., Perez-Ponce de Leon and Poulin, 2016; Poulin and Pérez-Ponce
6 de León, 2017), and for the understanding of biological processes.

7 Two general assumptions, which were at least implicitly applied in the practical
8 procedures, were evident from the literature (Struck et al., 2018b). First, given the
9 species concept cryptic species were generally thought to be "true" species and, second,
10 these species were so similar in the taxonomically relevant phenotypic characters that
11 they were not or hardly distinguishable from each other. Therefore, Struck et al. (2018b;
12 2018a) provided a new definition for cryptic species reflecting these two assumptions.
13 The process of assigning cryptic species was separated into two clearly separated steps
14 in contrast to the previous attempts. At the first step, it has to be established that the
15 species are truly species given the applied species concept. In Figure 1 the white circles
16 indicate cases, which would not be considered species and accordingly also not cryptic
17 species. Hence, this first step is not different from any other species delineation process,
18 independent if these entities are cryptic or not, but it has the advantage that the pitfalls
19 associated with this process are confined to the proper step and are not carried over to
20 the next step. The second step consists in showing that the species are phenotypically
21 more similar to each other than one would expect given the time that has passed since
22 their last common ancestor (or the level of genetic divergence as a proxy for time).
23 These species should hence be called cryptic species only if this level of phenotypic
24 disparity is significantly lower than expected. The red circles in Figure 1 represent such
25 cases, while the orange and yellow circles do not. This second step is the crucial step in
26 the framework with respect to cryptic species as here the actual assignment occurs. The
27 definition is property-based and independent of the taxonomic history of the species at
28 hand. Specifically, it does not matter if the species have been described as only one
29 before or not. Studies across taxa, habitats, life strategies and so forth can be based on
30 comparable categories like similar applied species concepts, levels of disparity, or
31 genetic divergence instead of taking cryptic species at face value allowing more robust
32 conclusions about the impact of cryptic species.

33 **Evolutionary significance of cryptic species**

34 Understanding the tempo and mode of speciation, and the drivers of phenotypic
35 diversification are major objectives in biology (Rabosky and Adams, 2012). Therefore,
36 identifying and quantifying contrasts between phenotypic disparity and genetic
37 divergence has become popular in recent decades. Cases such adaptive radiations where
38 morphological disparity outpaces genetic divergence received considerable attention
39 (DOI: 10.1038/npg.els.0001782). Adaptive radiations generally rely on open ecological
40 opportunities like appearance of new resources, evolution of key innovations or
41 colonization of new areas followed by specialization to the open niches and speciation
42 (Losos, 2010). Cryptic species as defined by the aforementioned framework can be
43 regarded as the exact opposite to these radiations, being characterized by a strongly
44 reduced phenotypic or at least morphological disparity in comparison to the observed
45 genetic divergence (yellow vs. red circles in Fig. 1).

If high rates of phenotypic variation have the potential to result in radiation of organisms and occupation of different evolutionary niches – “high evolvability” – then low phenotypic disparity as observed in cryptic species can be seen as a paradox as theory predicts that clades with high evolvability supersede clades with low evolvability (Estes and Arnold, 2007; Rabosky and Adams, 2012). Clades of cryptic species should have a lower “adaptive zone” and occupy less ecological space and, hence, be replaced by clades with a potential to evolve and adapt faster (Rabosky and Adams, 2012). As evolvability is generally considered as a measure of evolutionary success (e.g., Rabosky and Adams, 2012) the question arises why so many cryptic species are observed nowadays, which supposedly lack any phenotypic or at least morphological evolution. Several suggestions have been put forth to explain lack of phenotypic evolution in general and especially considering macro-evolutionary patterns (Futuyma, 2010). These include, among others, genetic and developmental constraints, source populations impeding specialization (meta-population dynamics), repeated bottlenecks decreasing standing genetic variation, large populations, stabilizing selection, ephemeral, stressful or fluctuating environments, evolutionary stable configurations, or niche conservatism (e.g., Maynard Smith, 1983; Eldredge et al., 2005; Futuyma, 2010; Haller and Hendry, 2014; Chomicki and Renner, 2017). However, the lack of phenotypic evolution has received considerably less attention in evolutionary biology than its opposite, adaptive radiations, especially at the micro-evolutionary level, and empirical and experimental evidence for any of the suggestions is low so far. While cryptic species can be ideal systems to inform us on the causes of reduced phenotypic disparity, much needs to be done. First, the evolutionary processes resulting in cryptic species must be identified. Then it can be investigated in how far the different causes mentioned above influenced these processes. Four different processes have been suggested to result in cryptic species: recent divergence, convergence, parallelism and stasis (Swift et al., 2016; Struck et al., 2018b).

Evolutionary Processes I: Recent divergence

The most common, but unproven assumption is that cryptic species follow recent speciation and that they did not yet have enough time to accumulate substantial phenotypic, especially morphological differences (Knowlton, 1993; Reidenbach et al., 2012). For example (Fig. 2), in the malaria vector *Anopheles gambiae* (Hexapoda) two forms, the M (now recognized as *A. coluzzii*) and S form, are recognized, which seem to be reproductively isolated (Reidenbach et al., 2012). They are at an early stage after speciation differing in an inversion on chromosome-2, which seems to be associated with their ecological differences (Simard et al., 2009). The M form mainly exploits stable larval habitats with high level of stressors; the S form exploits unpolluted, predator free, ephemeral habitats associated with seasonal rainfall (Reidenbach et al., 2012). Ecological experiments suggest that these forms seem to outcompete each other in their respective environment and respond to predation differently (Diabaté et al., 2008). Hence, in the M and S forms other traits than morphology are under selection.

Speciation is not necessarily accompanied by morphological change in the early stages as selection acts largely on physiological, immunological, reproductive or behavioural traits (Bensch et al., 2004; Damm et al., 2010; Derycke et al., 2016). Allopatric speciation while remaining in one particular ecological niche or habitat might lead to the building-up of non-adaptive divergence without morphological change. As a result

recently diverged species can remain morphologically identical following initial divergence (Korshunova et al., 2017). In these cases of recent divergence cryptic species are nothing special to other species pairs as the speciation event is very recent and generally no or little phenotypic change, particularly in morphology, is expected this shortly after the speciation unless there is a strong selection towards different adaptive optima. Moreover, such cases cannot provide much insight into the supposed lack of phenotypic evolution.

Evolutionary Processes II: Convergence & Parallelism

Phenotypic similarity could also stem from convergence or parallelism (Swift et al., 2016; Struck et al., 2018b). In both cases the cryptic species evolved the same phenotypes independently of each other. While for convergence the immediate ancestors of the cryptic species were dissimilar from each other as well as to the extant cryptic species, for parallelism the ancestors were similar to each other, but dissimilar to the extant cryptic species. One example (Fig. 3) comprising both convergence and parallelism occurs in the *Mastigias* species complex (Scyphozoa) (Swift et al., 2016). *Mastigias* species occur in both coastal waters including coves and lagoons ('ocean' phenotypes), and in small-bodies of salt water without an open connection to the ocean ('lake' phenotypes). The 'lake' phenotypes evolved both by parallelism and convergence from the 'ocean' phenotypes. In some cases, the 'lake' phenotypes evolved from the same 'ocean' phenotype (parallelism) and in others from different 'ocean' phenotypes (convergence). Similarly, selective pressures from predators, led to parallelism in the Holarctic *Enallagma* species (Hexapoda) (Stoks et al., 2005). Cases of convergence of cryptic species were also found in the Deep Sea (Vrijenhoek, 2009).

As for the case of recent divergence the evolutionary processes of convergence and parallelism cannot contribute to our understanding of the lack of phenotypic evolution, as phenotypic change occurred. Nonetheless, these cases can help us understand how reduced phenotypic disparity evolves. Importantly, it indicates that reduced phenotypic disparity and lack of phenotypic evolution are not necessarily the same. For convergence and parallelism specifically the question arises what are the driving factors that the cryptic species independently evolved to the same phenotypes? Is it due to intrinsic (e.g., developmental constraints) or extrinsic ones (e.g., extreme environments) confining the available phenotypic landscape to only one solution in the respective situation? Contrary to parallelism, intrinsic factors are expected to be less influential than extrinsic ones in convergence, as evolution starts from more distinct genetic backgrounds. However, maybe even for convergence developmental constraints constrict the available phenotypic landscape more than expected.

Evolutionary Processes III: Stasis

In contrast to the other three processes, under phenotypic stasis cryptic species retain similar phenotypes for millions of years. The literature survey by Struck et al. (2018b) revealed that stasis in cryptic species may occur at least not substantially less than recent divergence and seems to be an important process in the evolution of cryptic species. A prominent example (Fig. 4) is provided by the *Cavernacmella* complex (Gastropoda) on the Ogasawara islands (Japan) (Wada et al., 2013). The '*C. minima*' phenotype occurs in five clades on the different islands of the archipelago (i.e.,

1 Mukojima, Chichijima, and Hahajima). These represent cryptic species and are unaltered
 2 for over 3 million years. In contrast, within the clade of these cryptic species are also
 3 five species, which are morphologically distinct from the '*C. minima*' phenotype. This
 4 indicates that enough time passed to accumulate morphological differences under certain
 5 conditions. This release from morphological arrest might indicate the absence of
 6 developmental constraints. Similarly, cichlids have demonstrated the potential for burst
 7 of morphological evolution and stasis (Seehausen, 2006). Other examples of stasis
 8 comprise *Stygocapitella* (Annelida), *Diporiphora* (Squamata), *Mastigias* (Scyphozoa), or
 9 *Cletocamptus* (Crustacea) species complexes (Rocha-Olivares et al., 2001; Smith et al.,
 10 2011; Swift et al., 2016; Struck et al., 2017). *Stygocapitella* is an example of long
 11 lasting morphological stasis. *Stygocapitella* individuals live between sand grains, by the
 12 foot of the dune, at a depth of about 0.5-1 meter and can be found on beaches in all
 13 major coastlines with the exception of tropical regions (Westheide, 2008). Molecular data
 14 suggest the presence of several cryptic species at the different coastlines and even
 15 though rigorous morphological reinvestigations discovered minimal phenotypic
 16 differences among the deeply divergent clades, these are estimated to have diverged
 17 about 300 to 100 million years ago (Struck et al., 2017). As such, the *Stygocapitella*
 18 complex seems to be under morphological stasis with slight morphological
 19 differentiations having occurred more than 100 million years ago. It is certainly
 20 challenging to address why these species did not change morphologically while closely
 21 related ones did, and why no phenotypic differences became fixed in the gene pools just
 22 by chance (e.g., due to recurrent bottlenecks).

23 Hence, cryptic species such as the presented examples are ideal systems to investigate
 24 stasis using extant taxa. These systems allow addressing both patterns of reduced
 25 phenotypic disparity and the process leading to the absence of phenotypic evolution. The
 26 term stasis is most often used in macro-evolutionary and paleontological studies and less
 27 in micro-evolutionary ones using extant taxa. In macroevolution and paleontology it
 28 became popularized as an argument for punctuated equilibria (DOI:
 29 10.1038/npg.els.0001774), where evidence from fossil timelines lasting for millions of
 30 years questioned the power of selection. However, recent efforts have focused on
 31 integrating stasis at the micro-evolutionary level (e.g., Hansen and Houle, 2004; Estes
 32 and Arnold, 2007). Futuyma (2010) reviewed many of these models including stabilizing
 33 selection, lack of genetic diversity, genetic and developmental constraints, ecological
 34 niche tracking and niche conservatism. Other potential, non-exclusive explanations for
 35 stasis or arrested evolution have been put forward specifically for more specific scenarios
 36 or habitats. For example, for the interstitial realm, that is the space between the sand
 37 grains in marine sediments, one potential explanation stems from the 'plus ça change,
 38 plus c'est la même chose' (The more it changes, the more it is the same) model
 39 (Sheldon, 1996). This model regards morphological stasis as a response to widely
 40 fluctuating physical conditions, which are stable on geological timescales. This fits the
 41 interstitial realm, as this is characterized by wide variations in pH, salinity and moisture
 42 at short timescales, but this fluctuating characteristic has remained similar for millions of
 43 years ago (e.g., Westheide, 1977). It has also been suggested that the phenotypic
 44 landscape of species with limited morphological differentiation such as, e.g., some
 45 worms or fungi are too small to allow for change (e.g., Bickford et al., 2007). In
 46 contrast, another suggestion is that intraspecific variation of traits is high and allows for

1 coping with broader ranges of ecological differences, while the traits fluctuate around a
2 stable mean (Voje, 2016).

3 **Conclusions**

4 Studying cryptic species has great potential to further our understanding of evolutionary
5 processes as outlined above, but also with respect to research in macroecology and
6 conservation biology (Fig. 5) (Bickford et al., 2007; Bernardo, 2011; Pante et al., 2015;
7 Fišer et al., 2018). However, to accomplish these goals a pre-requisite is that what is a
8 cryptic species can be determined with certainty. It is important to differentiate cryptic
9 species complexes from those complexes arising from taxonomic biases or malpractice.
10 Only the former will be able to inform us on biological processes in evolution and ecology
11 as they reflect true natural properties. A two-step conceptual framework to accomplish
12 this has been provided and hence the theoretical foundation been laid. However, the
13 literature survey by Struck et al. (2018b) also clearly showed that methodological
14 improvement is needed in all aspects to achieve this. Often the phenotype is not studied
15 at all, only a single, uni-parentally inherited genetic marker is used, and/or the results
16 are not set in relation to time or other non-cryptic species to assess if they are really
17 exceptionally different from them. Moreover, biology is transforming into a 'big data'
18 science including among others high-throughput sequencing technologies, which allows
19 us to apply population genomic and phylogenomic methods independent of the study
20 object and hence provide much broader data basis for their conclusions (Fig. 5).

21 On the other hand, improved delineations of cryptic species will result in and contribute
22 to an improved understanding of the causes of evolutionary processes like convergence,
23 parallelism and stasis (Fig. 5). Again, the applications of genomic and transcriptomic
24 approaches studies on cryptic species can aid in linking genotypic change to phenotypic
25 alterations or lack thereof. Similarly, improved delineations will result in improved
26 biodiversity assessments allowing better modelling of macroecological processes.
27 Moreover, an improved understanding of the evolutionary processes shaping cryptic
28 species allows a better assessment of ecological changes and its evolutionary
29 consequences over space and time. Summarizing the research on cryptic species should
30 address the following questions to contribute to our understanding of the evolution of
31 reduced phenotypic disparity and how this affects the macroecological processes in
32 different habitats:

- 33 1) Which species complexes are only taxonomic oddities, and which are truly cryptic?
- 34 2) Which cryptic species are the results of recent speciation, parallelism, convergence or
35 stasis, and how common are they?
- 36 3) What are the relevant intrinsic and extrinsic factors affecting phenotypic evolution of
37 cryptic species and to what degree do they affect their phenotypic landscape?
- 38 4) Are there more cryptic species in certain branches of the tree of life, among taxa with
39 certain life histories (e.g., generalists vs. specialists), or in certain habitats?
- 40 5) How affect cryptic species the composition and stability of ecosystems or vice versa
41 how vulnerable are cryptic species due to these effects?

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42

43 Glossary:

- 44 Cryptic species: Different species, which are morphologically very similar or identical.
- 45 Parallel evolution: Evolution of the same set of morphological traits from one ancestral
- 46 set of traits.
- 47 Convergent evolution: Evolution of the same set of morphological traits from different
- 48 ancestral set of traits.
- 49 Stasis: Maintenance of morphological similarity during long time scales.
- 50 Morphology: The form or structure of the external characters of an organism.

1

2 **Figures and Tables:**

3 **Figure 1.** Unifying conceptual framework based on Struck et al. (2018b). The x-axis
 4 represent time since divergence from the last common ancestor. Often genetic
 5 divergence is used as proxy for this. The y-axis represents the degree of phenotypic
 6 disparity. The dark blue area is the area of ongoing speciation and hence no species
 7 boundaries have been established yet (white circles). The light blue area indicates
 8 evolution between pairs of species (orange circles) as it is intuitively assumed. That is
 9 phenotypic disparity more or less increases linear with time. The orange area reflects
 10 cases (yellow circles) in which phenotypic evolution occurs at a much higher rate than
 11 anticipated such as. The green area represents cases (red circles) of significantly
 12 reduced phenotypic disparity given time as it is the case in the cryptic species.

13 **Figure 2.** Schematic representation of the *Anopheles* example for recent divergence
 14 (based on the results of Reidenbach et al 2012). The left panel exemplifies the recent
 15 divergence of the two cryptic species. In the middle the genomic inversion at
 16 chromosome 2 is shown and the right one lists the ecological differences observed
 17 between the two species.

18 **Figure 3.** Schematic representation of the *Mastigias* example of parallelism and
 19 convergence based on the results by Swift et al. (2016). The phylogenetic relationship
 20 between the two morphotypes (oceanic and lake; indicated by the two icons) is shown
 21 to the left. Swift et al. (2016) regarded the origin of the two lake morphotypes within the
 22 Chinese Sea as well as two within the Pacific Islands & South Philippinean Seas as
 23 examples of parallelism as they originated from the same oceanic species. In contrast,
 24 they concluded that the other lake morphotypes to each other as well as to these
 25 previous ones evolved by on convergence as they originated from different oceanic
 26 species.

27 **Figure 4.** Schematic representation of the *Cavernacmella* example for stasis given the
 28 results of Wada et al. (2013). Wada et al. (2013) recognized a total five cryptic species
 29 as well as five morphologically distinct, non-cryptic species within them (indicated by the
 30 different forms and colours; icons are relative in size to each other). The occurrence of
 31 these ten species is indicated as well as their life-history and habitat (epigean and
 32 cave-dwelling; indicated by the two icons).

33 **Figure 5.** Schematic representation how different biological disciplines can contribute to
 34 the research of cryptic species and thereby increase our understanding of macro-
 35 ecological, evolutionary and genomic patterns and processes.

36

37 **All 5 figures do not require permission as we generated them.**

For Review Only

Parallelism Convergence

Multidisciplinary research on cryptic species