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Opportunities and challenges presented by cryptic bryophyte species

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Abstract

Cryptic bryophyte species exhibit a decoupling in the degree of morphological and molecular divergence, as a result of different processes, from recent divergence to stasis. Here a body of cryptic species literature comprising 110 papers published between 2000 and the end of 2018 is reviewed. Most studies of cryptic species focused on northern hemispheric taxa, but we do not yet have sufficient studies to assess whether a geographic bias in the distribution of cryptic species exists, and we don't know how many cryptic bryophyte species there might be globally. Fully two-thirds of all studies on cryptic bryophyte species rested their claims of morphological crypsis on previous taxonomic investigations, without revision of morphology to confirm cryptic species status. There is more than one kind of morphological crypsis, and while quantification of morphological patterns can contribute to our understanding of crypsis this is a commonly neglected component. Hybridisation is possibly an under-appreciated contributor to cryptic species, but inference of hybridization has been limited by study design. Opportunities exist in the application of geometric morphometric methods and next generation sequencing technologies to overcome intrinsic limitations in traditional morphological and molecular data sources. The usage of 'cryptic species' as a tool to flag instances where traditional species concepts are deficient devalues the term, and a distinction between genuine crypsis and business as usual revision of species circumscription should be re-established and maintained.

Introduction

Cryptic bryophyte species

It is widely acknowledged that species circumscription in bryophytes, and liverworts in particular, is challenging due to their lack of structural complexity in comparison with the sporophyte-dominant lineage of land plants (Heinrichs *et al.* 2009; Medina *et al.* 2012). Crypsis is therefore a matter of perspective, and can be prone to personal perception over rigorous definition. Morphological differences among species are often subtle, and may be difficult to apprehend in the absence of molecular data corroborating their significance (Cargill *et al.* 2016). The modular growth of bryophytes adds to this challenge by increasing the scope for the expression of intra-individual variation, which may further erode differences between species. Investigations into bryophyte species circumscription tend to bundle the different aspects contributing to the challenge under the phrase 'cryptic species'. The goal of this review is to investigate reportedly cryptic bryophyte species with reference to recently published insights that contribute to our understanding of what cryptic bryophyte species are, how they arise, and what we can learn from them. The review addresses three themes:

1) How the term 'cryptic species' has been used in bryophyte studies, and how that use has been justified.

2) What cryptic species can tell us about evolutionary processes, and what we can learn by studying them.

3) How our approach to characterizing and understanding cryptic bryophyte species can be improved.

To pursue these themes, a literature review was conducted. ISI Web of Knowledge Core Databases was searched using the keyword phrase 'cryptic AND bryophyte', which returned 128 results (search conducted 5 January 2019), of which 110 were included in the literature review. The 18 excluded studies either did not treat cryptic species directly or were not accessible. For each study the morphological and molecular data sources and methods of analysis were scored, as were the provision of a definition for cryptic species and the presentation of taxonomic implications. The discussion that follows considers the results of this bryophyte-specific survey within the context of the broader body of cryptic species literature, with reference to the key themes identified above.

What are cryptic bryophyte species?

Generally, cryptic species exhibit a decoupling between the degree of morphological and molecular divergence (Fiser *et al.* 2017; Struck *et al.* 2018). A definition of cryptic species was provided by 25% of the 110 studies published between 2000 and 2018 included in the survey (Table 1). A lack of morphological difference among cryptic species was a common theme across definitions provided by surveyed literature, most of which emphasized a lack of morphological diagnosability alongside genetic distinctness, but often without specifying precisely how that genetic distinctness was structured. Some definitions did imply a distinct genetic structure, for example 'Cryptic species were groups of related species' (Myszczynski *et al.* 2017). Some studies make the point in their definition of cryptic species that the lack of morphological differences does not necessarily hold upon detailed re-examination of morphology (Medina *et al.* 2012).

Where do cryptic species occur and how many are there?

The very first cryptic species of bryophyte was identified with molecular techniques in European *Conocephalum conicum* (L.) Dumort.by Szweykowski and Krzakowa (1979), and by 2001 seven cryptic moss and seven cryptic liverwort species were known (Shaw 2001), all had been identified when data from molecular sources indicated reproductive isolation between individuals that exhibited no significant morphological differences. Since 2001 there has been a proliferation of cryptic bryophyte species in published literature. In some cases the reproductively isolated groups had been previously recognized as morphs, such as the small and large morphs of *Conocephalum conicum.* Several studies have focused on reproductive relationships across intercontinental disjunctions in distribution, and geographic regions from which cryptic bryophyte species have been reported. These regions include North America (Therrien *et al.* 1998; Shaw 2000; Medina *et al.* 2012), Europe (Hedenäs *et al.* 2014), Asia (Bechteler *et al.* 2016), Africa (Ahonen *et al.* 2005), and Australasia (Cargill *et al.* 2013); but few studies treat cryptic species from South America and the African continent. Most studies of cryptic species come from northern temperate regions, a result that may be confounded by a geographical bias in investigative effort, but we do not yet have sufficient studies to assess whether such geographic bias exists, and we don't know how many cryptic bryophyte species there might be globally.

How can we identify cryptic species?

Cryptic bryophyte species have been reported for all three main bryophyte groups. A brief discussion of one example from each will suffice to illustrate the diversity of contexts and approaches to their identification and resolution. In a study of the hornwort genus *Megaceros* Campb. in Australasia, Cargill *et al.* (2013) tested the hypothesis that plants from Australia and New Zealand sharing the same spore ornamentation belonged to the same species by including a range of individuals from Australia, New Caledonia, and New Zealand in a phylogeny based on three molecular markers (nrITS, *rbc*L, *trn*L–F). Spore ornamentation did not delimit a monophylum but was associated with three different lineages, comprising species from New Zealand, Tasmania, Macquarie Island, mainland Australia, and New Caledonia. Phylogenetic diversity on both sides of the Tasman Sea was higher than expected, and taxonomic implications of the investigation were presented including the description of the new species of *Megaceros austronesophilus* Cargill & Seppelt from Tasmania and Macquarie Island.

In a study of the North American liverwort *Frullania asagrayana* Mont. by Ramaiya *et al.* (2010), 88 samples were genotyped using 13 microsatellites. Individuals were plotted in PCoA, resulting in two clusters whose reproductive isolation was tested with admixture analyses performed by STRUCTURE (Pritchard *et al.* 2000). The number of private alleles in each group and the admixture analysis indicated substantial reproductive isolation, but five individuals expressing genetic make ups intermediate between groups suggested gene flow from a southern group to the predominantly northern group, but none in the opposite direction (Ramaiya *et al.* 2010).

In an explicit test for intercontinentally distributed cryptic species Vigalondo *et al.* (2017) included individuals from recently discovered populations of the moss *Orthotrichum acuminatum* H.Philib. in Africa and eastern North America in a phylogeny with previously known European populations and scored 87 qualitative and quantitative morphological characters to test group membership on both data sets. Individuals from all three continents formed a monophylum without significant internal phylogenetic subdivision, and grouped into a single morphological cluster in PCA, so confirming *Orthotrichum acuminatum* as having a disjunct distribution spanning three continents. In this case the species was not a cryptic complex, but the same approach applied to other *Orthotrichum* Hedw. species has returned that result (e.g. Medina *et al.* 2012).

Molecular data

Molecular data sources

Before the year 2000, isozymes formed the basis of most molecular datasets by which cryptic bryophyte species were recognized. Isozymes are visualized by gel electrophoresis of protein extracts, different proteins separate, can be scored, and so inform allele frequencies against which reproductively isolated groups can be identified by possession of recurring allele combinations. Molecular sequence data was first applied to cryptic *Mielichhoferia* Nees & Hornsch. species alongside isozyme data, and the two data sources delimited the same groups (Shaw 2000). While isozyme use continues either alone or in combination with molecular sequence data (4 studies since 2000), Sanger sequencing of one or more loci has become standard practice (77 studies), and nearly all studies now establish molecular groups by phylogeny inference from a molecular dataset wherein multiple individuals are sampled per species. Seventy percent of studies published since 2000 include Sanger sequencing (Fig. 1), and the number of molecular markers employed in a single study shows a general increasing trend through time. Single marker studies were prevalent between 2000 and 2004, but since 2005 three- and four-marker studies (58 total) dominate. These markers encompass both nuclear and chloroplast genomes, but only three studies within those captured by the literature survey included a marker from the mitochondrial genome. The chloroplast markers used were from a small group of loci: *trn*L-F, *rps*4, *mat*K, *rbc*L, and all bar three studies employed a single nuclear marker, nrITS, meaning relationships were effectively assessed using two gene trees, the chloroplast being uniparentally inherited (Jankowiak *et al.* 2005; Jankowiak-Siuda *et al.* 2008), probably through the maternal lineage (Natcheva and Cronberg 2007).

One limitation associated with sequence data for fixed loci, including nrITS and *trn*L–F is that they have slower rates of molecular evolution than sequences from alternative sources such as inter-sequence simple repeats (ISSRs) which, like allozymes, may exhibit recurring fixed differences among reproductively isolated groups (Vanderpoorten *et al.* 2003; Spaguluno *et al.* 2009; Ramaiya *et al.* 2010). Their capacity to identify reproductive isolation in instances where population divergence is recent, or where population size slows coalescence to reciprocal monophyly, is therefore limited. Other molecular data sources used to infer cryptic species since 2000 include AFLPs (1 study: Fernandez *et al.* 2006), RFLPs (1 study: Wachowiak *et al.* 2007), and microsatellites (5 studies: e.g. Szövényi *et al.* 2008). One study within the surveyed literature used allozymes (Bijlisma *et al.* 2000), and four others employed isozymes, alone or in combination with other molecular data sources (Szweykowski *et al.* 2005; Buczkowska *et al.* 2012; Wyatt *et al.* 2013); only one study used RAPDs (Cronberg 2000).

Next generation sequencing (NGS) makes large quantities of informative sequence data readily accessible. NGS such as anchored / targeted enrichment methods (Lemmon *et al.* 2012) can sample hundreds of loci using small samples of herbarium material that may be one hundred or more years old (Hart *et al.* 2016), which has potential to inform relationships at all levels. NGS is already employed to understand relationships among land plants (Gates *et al.* 2018), but no studies of cryptic bryophyte species published between 2000 and 2018 used next generation sequencing technologies. The transfer of NGS technologies to cryptic bryophyte species has started (Myszczynski *et al.* 2017) and will be the next phase in the application of methodological innovation for understanding patterns of geographic diversity and reproductive relationships in bryophytes. However, the resolution of fine-scale population genetic structure afforded by genomic data could lead to rampant over-splitting of species when genetic variation is partitioned among populations (Isaac *et al.* 2004; Oliver *et al.* 2015; Sukumaran and Knowles 2017; Coates *et al.* 2018). We will then recover genetically distinct groups sharing the same morphology that are not cryptic species (Doughty *et al.* 2018; Moritz *et al.* 2018). Genome scans can assist by measuring gene flow among populations, but whether restricted gene flow indicates ephemeral or enduring isolation cannot be assessed from genetic structure itself (Sukumaran and Knowles 2017). The simple identification of population genetic structure is alone insufficient basis for the proposition of cryptic species because there is a broader population genetic context that determines the significance of observed differences. This broader context can have an historical component. For example, in the modern context during glacial-interglacial cycling, populations may experience transient reproductive isolation through climate-mediated range contraction, allowing genetic divergence to occur. Accumulated differences could dissolve when climate restriction is relaxed, and populations regain genetic contact. This context dependency is also true for patterns of morphological variation and difference.

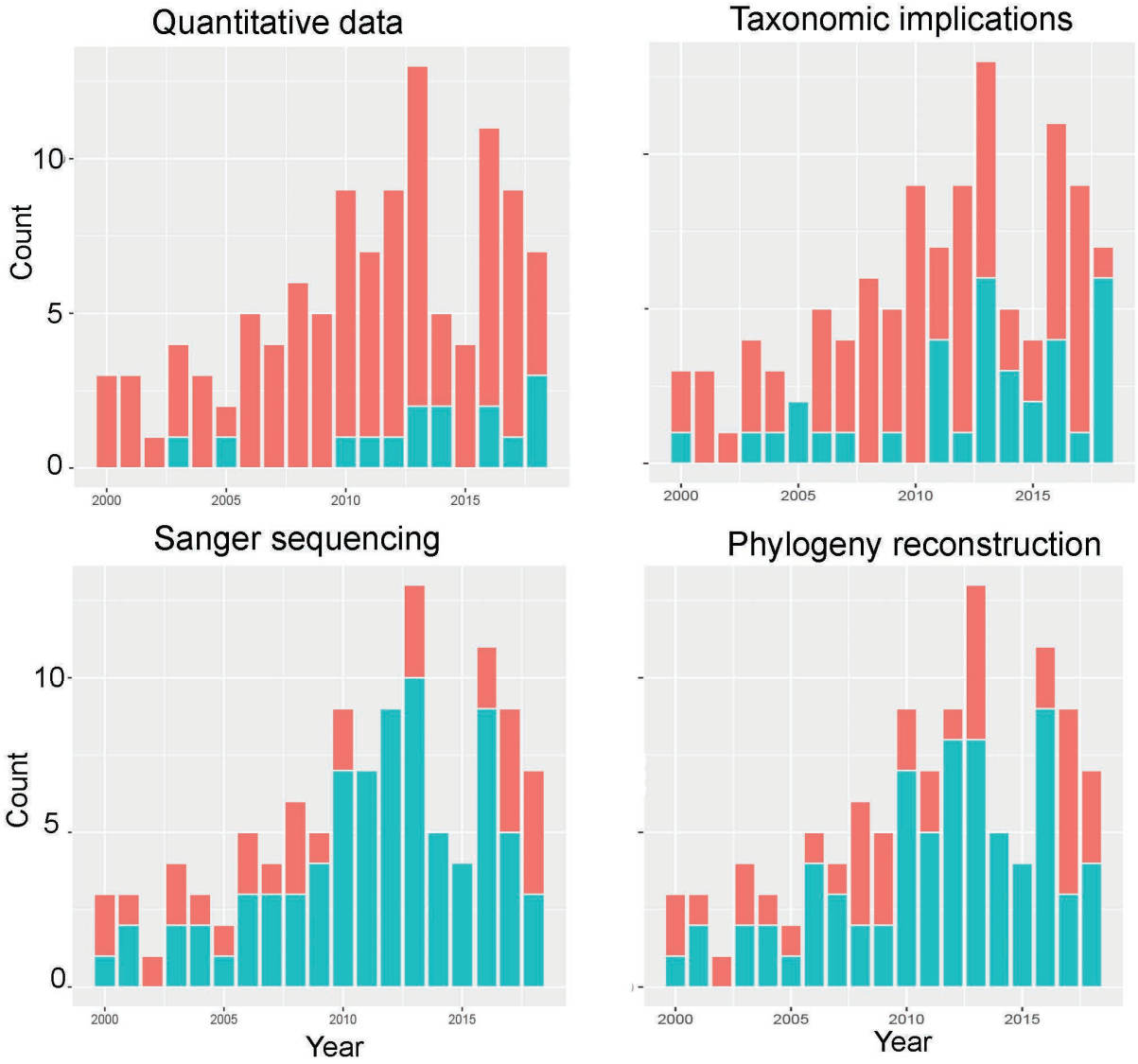

Fig. 1. Histograms showing year of publication for 110 cryptic bryophyte species papers included in this literature review. Blue sections indicate papers containing the feature A: Quantitative data; B: Taxonomic implications; C: Sanger sequencing; D: phylogeny reconstruction.

The focus on sequence data from a suite of loci has meant that phylogeny reconstruction has become the primary mode of data analysis in studies of cryptic bryophyte species; 70% of studies published between 2000 and 2018 employed this approach (Fig. 1). Other methods have been employed but less frequently, for example distance-based analysis of sequence alignments, and presentation of dendrograms based on Neighbour-joining algorithms to achieve and represent groups was used in 16 studies. Statistical parsimony (Templeton *et al.* 1992) to construct non-hierarchical haplotype networks from an alignment of DNA sequence data was used in 18 studies (e.g. Hedenäs and Eldenas 2007; Hedenäs *et al.* 2014).

Molecular criteria for cryptic species recognition.

It follows from the diversity of data sources employed to achieve groups from molecular data that a diversity of criteria for group delimitation have been employed. Isozymes, ISSR, RFLPs and AFLPs all inform genetic identity by resolving recurring allele combinations that circumscribe distinct genetic groups, though the kinds of alleles differ. Alignments of sequence data are information rich structures that illuminate both genetic identity and history. One or both of these components are employed by a variety of methods to inform species circumscription. Automatic Barcode Gap Detection (Puillandre *et al.* 2012) takes a genetic distance matrix derived from a sequence alignment, or other genetic data, and examines the distribution of all pairwise distances among samples. In matrices of pairwise genetic distance containing multiple representatives of each species, the distribution of distance values is bimodal with peaks corresponding to intra-specific distances and

inter-specific distances (Hebert *et al.* 2003, 2004). The gap between the two modes allows individuals to be assigned to genetic groups independent of any other knowledge of relationships (Puillandre *et al*. 2012). This property makes ABGD a suitable approach for identifying primary species hypotheses to test against additional evidence within an integrative taxonomic framework; even though empirical studies have demonstrated that ABGD tends to under-estimate the number of species (Luo *et al*. 2018).

There are also a number of tree-based methods. Genetic groups can be identified by visual inspection of tree topology alone, but replication of these groups may not be possible. The focus on phylogeny reconstruction, as an aid to species circumscription, is not restricted to bryophytes and neither is the challenge of circumscribing species. Hence, a range of algorithmic methods for species assignment based on tree shape, including generalised mixed Yule coalescent (GMYC) (Pons *et al.* 2006; Fujisawa and Barraclough 2013), Poisson tree processes (PTP) (Zhang *et al.* 2013) and Bayesian Phylogenetics and Phylogeography (BPP) (Yang 2015) have been developed in response to the universality of a phylogenetic approach to the question of inter-individual relationships. A phylogeny containing multiple samples per species will contain branching due to both phylogenetic and coalescent processes, therefore a threshold separating these two branching processes should be identifiable. In time-calibrated phylogenies this threshold takes the form of a significant increase in the slope of lineage-through-time plots corresponding to the packing of intra-specific branches onto the tree. This threshold time can then be used in conjunction with topology to assign individuals to genetic groups independent of any other knowledge of their relationships. Like ABGD, tree-based approaches provide a useful platform for deriving primary species hypotheses that can be tested against additional data within an integrative framework. However, empirical and simulation studies have demonstrated that GMYC and PTP tend to over-estimate the number of species within a phylogeny (Paz and Crawford 2012; Pentinsaari *et al.* 2017; Renner *et al.* 2017; Luo *et al.* 2018). GMYC is based on assumptions of non-recombination, so is appropriate for single-gene trees rather than phylogenies (Pons *et al.* 2006), but whether concatenation of linked markers from a linked and predominantly non-recombining genome such as the chloroplast, to estimate a chloroplast 'gene' tree (as in Renner *et al.* 2017), is acceptable has not been specifically addressed.

Morphological data

Morphological data sources

A wide range of characters from both gametophyte and sporophyte generations have been used to circumscribe species, but generally species circumscriptions emphasize qualitative characters. There are exceptions, species circumscription in some genera, including *Leucobryum* and *Rhynchostegium* (Vanderpoorten *et al.* 2003; Hutsemékers *et al.* 2012) is reliant upon quantitative characters. Differences in size and shape, by their continuous nature, exhibit spectrum-like patterns of variation that have been challenging to accommodate within a conceptual framework that strives for discrete species whose member individuals correspond with a typical form (Hedenäs *et al.* 2014). Attaining precise species circumscription has often come at the cost of accurate delimitation, by which I mean groups that benefit from precise definition using thresholds, within continuously varying characters, may suffer by not reflecting real-world biological entities.

Species circumscription often focuses on character systems acknowledged as informative within a lineage, for example patterns of cell differentiation and wall architecture in Sematophyllaceae, lobule teeth morphology in Lejeuneaceae (Pócs 2016), spore ornamentation and thallus anatomy in Ricciaceae (Cargill *et al.* 2016). Sometimes cryptic species are missed through this lineage-specific character system focus. For example, cryptic species of *Homalothecium* Schimp., indistinguishable by gametophytic traits, can readily be separated by sporophyte morphology (Hedenäs *et al.* 2014). Detailed revision of morphological variation in lieu of phylogeny reconstruction can yield subtle yet significant differences from a range of character systems, which are often impossible to apprehend independent of an informative *a priori* grouping of individuals. These usually manifest as differences in patterns and parameters of size and shape variation.

Sometimes a few select characters used by previous studies to circumscribe species have been scored and mapped onto a phylogeny in an effort to demonstrate the impossibility of morphological species circumscription (Hartmann *et al*. 2006). Generally such reassement of morphology is in qualitative and subjective terms, though there are exceptions (see for example Pätsch *et al.* 2010; Hedenäs *et al.* 2014)

Morphological criteria.

How has decoupling between morphological and molecular divergence been measured, and what has it been measured against? A recent comprehensive review of cryptic species literature by Struck *et al.* (2018) found a shortfall of morphological criteria for crypsis, of 606 papers surveyed 47% presented no phenotypic data, and another 25% reported at least one trait difference between cryptic species, implying the cryptic species were often morphologically diagnosable, even if they had been historically confounded.

The bryophyte literature surveyed exhibits similar patterns, with 67% of studies presenting no phenotypic data. Only 33% (37) of studies surveyed included a re-examination of morphology and of those, less than half (13, or 12% of the total studies) included collection and analysis of quantitative character data (Fig. 1). Two thirds of all bryophyte studies rested their cryptic species claims on previous reports, usually the taxonomic investigations that had produced the hypotheses of relationship under scrutiny, without revision of morphology to confirm cryptic species status. The vast majority of these studies assumed that prior morphological assessment had been comprehensive and effective.

These paired assumptions are not always justified, and indeed most of the bryophyte cryptic species themselves demonstrate this. In morphological studies of bryophytes, the characters assessed often have been selected based on published precedent, and fairly relaxed criteria of morphological unity have been applied to the results of those investigations. Two weaknesses are introduced to morphological studies as a result.

1) Lack of comprehensiveness. Taxon circumscriptions within a particular lineage may be dominated by a limited number of character systems. For example, in the thallose liverwort *Riccia*, spore morphology and thallus anatomy have been heavily weighted in taxon circumscription (Na-Thalang 1980; Perold 1999). This weighting followed widely applied assumptions of phylogenetic conservatism in characters from the sporophyte generation, and an assumption that complex gametophytic structures were difficult to evolve, so had a single origin (Schuster 1992). The resulting subgeneric classification forced unrelated individuals sharing these features into the circumscription of single species, which molecular data inevitably rendered polyphyletic (Cargill *et al.* 2016). Spore morphology has also been widely employed in other taxonomic studies of hornworts (Campbell 1982, 1984; Hässel de Menéndez 1990), and species circumscriptions for Asian-Pacific *Megaceros* were heavily reliant upon spore morphology (Cargill *et al.* 2013). Hasegawa (1983) synonymized many species based on continuity in spore size and ornamentation across the Asia-Pacific region, on the grounds that observed differences in spore morphology resulted from phenotypic plasticity. Hasegawa (1983) also regarded variation in many other aspects of form as environmentally induced, and therefore uninformative with regards to species circumscription.

2) Lack of effectiveness. Many studies emphasize the interpretation of constancy in one or more critical character systems as evidence supporting circumscription of single species. The opposite view, where morphological differences are interpreted as polymorphisms, in support of circumscription of single species also occurs (So 2002, 2005). The latter interpretation has usually been motivated by the observation of morphological continuity and overlap in size and shape variation between individuals differing in other characters. The impression of overall similarity imbued by spectrum-like variation in gross morphology overrides the resolution of the real diversity indicated by differences in less conspicuous, but no less significant, facets of morphology (Heinrichs *et al.* 2004). This seems to have been a pervasive issue in the interpretation of morphology, and has had two outcomes. Firstly, a reduction in species diversity when actuated in the interpretation of morphological data when morphology alone is the basis for taxonomic revision. Secondly, increases in accepted species diversity when variable species claims have been re-examined by molecular and morphological data in combination (for example Heinrichs *et al.* 2010; Renner *et al.* 2018). However, in these instances most of the resulting revised species hypotheses may not be in any way cryptic, as in the *Radula buccinifera* (Hook.f. & Taylor) Gottsche, Lindenb. & Nees complex (Renner *et al.* 2013a), and the application of the term is then inappropriate. By applying the term cryptic species as a way of highlighting historical instances of ineffective morphological study, we both reduce the value of the term and lose focus on what cryptic species can tell us about evolutionary patterns and processes.

Some studies recognize this incongruity, and use other terms like pseudo-cryptic, semi-cryptic, unnoticed or overlooked, alongside or in place of 'cryptic' (Heinrichs *et al.* 2010; Medina *et al.* 2012, 2013). Bryophyte cryptic species studies confirm one of the main themes in the review of Struck *et al.* (2018), that the lack of operational clarity and consistency represents a serious empirical problem for cryptic species designation.

What causes cryptic species to form?

Before we can ask what causes cryptic species to form, we must establish what types of crypsis have been observed. A conceptual framework for understanding and defining cryptic species was proposed by Struck *et al.* (2018) that described the relationship between phenotypic disparity and genetic or temporal divergence which, when combined with phylogeny, defined four general patterns of phylogenetic discordance with morphological unity (Fig. 2). Struck *et al.* (2018) emphasized the link between effective characterization of patterns and subsequent process-driven research into the underlying causes explaining lack of phenotypic differences.

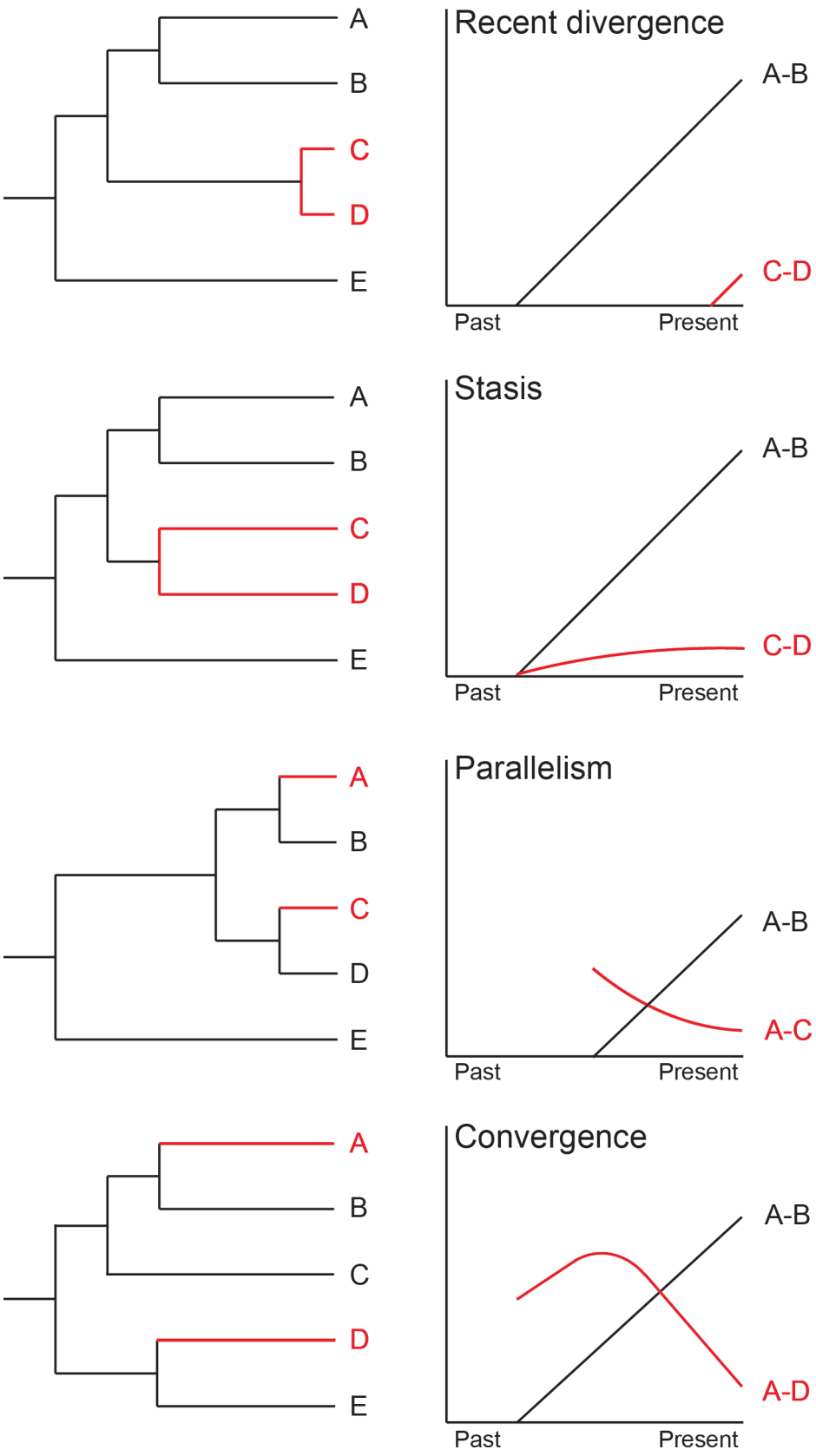

Fig. 2. Four processes leading to cryptic species, expressed in terms of disparity through time associated with different phylogenetic relationships characterizing each. Modified from Struck *et al.* (2017), with a different representation of convergence than the original.

Identifying the type of crypsis requires both phenotypic and genetic data, the first to gauge the degree of phenotypic divergence, the second to assess the time-course of reproductive isolation. These two data components are then assessed within a temporal and phylogenetic context, to establish which of the four general

patterns of phenotypic crypsis is at hand. These general patterns are summarised below, along with examples of the range of processes that produce them, following Struck *et al.* (2018). Some putative instances of each from the bryophyte literature are provided where phenotypic and genetic data is consistent with each pattern.

Recent divergence.

Relatively young sister species may have had insufficient time for phenotypic differences to arise and accumulate. Northern and Southern groups of *Frullania asagrayana* are one example of recently diverged groups that exhibit no morphological differentiation (Ramaiya *et al.* 2010). Lineages within the *Frullania tamarisci* (L.) Dumort. complex represent another, wherein slight morphological differences circumscribe separate lineages (Heinrichs *et al.* 2010).

Stasis

Relatively old sister species share the same phenotype (Smith *et al.* 2011). Crypsis may have a number of causes, including extrinsic factors such as stabilizing selection, niche conservatism, or intrinsic factors such as genetic inertia, lack of genetic variation, or developmental constrains. Phenotypic stasis over geological time has been reported for the moss *Helicophyllum torquatum* (Hook.) Brid. based on morphological similarity between fossil and extant individuals (Kubilius *et al.* 2018).

Convergence

Relatively unrelated species share the same phenotype, each having evolved from phenotypically dissimilar ancestors. The phenotype of each cryptic species is independently derived, and not an inherited symplesiomorphy. Because species converge from different phenotypic, genetic and developmental backgrounds, extrinsic factors are expected to be more important. The *Lejeunea tumida* Mitt. complex comes close to an example of cryptic species generated by convergence in liverworts. Four species in two pairs on each side of the basal-most node within *Lejeunea* Lib., were attributed to a single species prior to study by morphological and molecular data, and do exhibit considerable overlap in gametophyte size and shape (Renner *et al.* 2010, 2011). However, as discussed below these species do not qualify as morphologically cryptic.

Parallelism

Parallelism describes equivalent phenotypic shifts experienced by relatively closely related pairs of sister species. The phenotype of each cryptic species is independently derived, and not an inherited symplesiomorphy. Species converge from similar phenotypic, genetic and developmental backgrounds, and extrinsic or intrinsic factors may contribute to evolution.

Emergent properties of phylogenies, including variation in rates of phenotypic evolution, may be produced by stochastic processes (Raup and Gould 1974). It is therefore necessary to test whether observed crypsis could be generated by chance, by comparison with expectations under an appropriate null model (Raup 1977). The possibility that observed patterns of phenotypic disparity have been produced by chance should be eliminated before seeking mechanistic explanations (Raup and Gould 1974). The rates of morphological evolution for cryptic species produced by stasis should be significantly lower than non-cryptic species. There have been few studies of rates of morphological evolution in liverworts. The only relevant study, on *Leptoscyphus* Mitt., measured rates of state transition in the order of millions of years, so on geological timescales (Devos and Vanderpoorten 2008). Other studies have inferred stasis over tens of millions of years on the basis that amber inclusions have been assigned to extant species (Kubilius *et al.* 2017). Estimating and testing rates of morphological evolution requires the age of divergences among species, yet only 10% of surveyed cryptic bryophyte studies were time-calibrated. Time-calibration has remained a vexing issue for bryophyte studies. However the generation of more comprehensively sampled phylogenies, particularly those based on bait-capture datasets (e.g. Wolf *et al.* 2018), and the discovery and documentation of fossil species in amber (Heinrichs *et al.* 2014, 2015a, 2015b, 2016, 2017), will both alleviate the shortage of dateable nodes that currently constrains phylogeny-based studies of the timescale of morphological evolution.

What can we learn from cryptic species?

Thirty studies (27%) addressed taxonomic implications of their identification of cryptic species by modifying species circumscriptions in response to their results. This is on the low side given that studies of cryptic species tend to falsify pre-existing species hypotheses, and reflects the difficulty of proposing a revised circumscription for entities of challenging morphological delimitation. The range of operational definitions applied to the term 'cryptic species' indicates it has been applied to a diversity of scenarios, and that critical components of the definition can be highly subjective (Table 1). So what are the patterns or trends?

Table 1. Published definitions for cryptic species, 2001-2018.

Authors	Definition
Myszczynski *et al.* (2017)	cryptic species are groups of related species that are virtually identical or morphologically very similar, with unclear morphological boundaries between them
Baczkiewicz *et al.* (2017)	Cryptic species are taxa which are characterized by distinctive genetic differences, different ecological preferences and the complete or nearly complete absence of morphological variations
Schwarzer and Joshi (2017)	genetic groups or cryptic species within existing morphospecies with restricted genetic exchange
Hedenas (2017)	lineages that are molecularly as distinct as those of the morphologically recognized species but which lack (known) morphological distinguishing features
Renner *et al.* (2017)	cryptic species – instances where morphology fails to provide a reliable basis for inferring relationships because separate lineages are not characterized by morphological differences
Karlin and Robinson (2017)	it is difficult, if not impossible, to separate the three taxa at the macroscopic level and also at the microscopic level (Karlin *et al*. 2011). Thus they collectively form a cryptic species complex
Schebin *et al.* (2016)	morphological similarity between genetically distinct bryophytes
Caparros *et al.* (2016)	distinct species have been erroneously classified (and hidden) under one species name
Li *et al.* (2015)	incongruity between morphological species concept and molecular evidence
Bakalin and Vilnet (2014)	complex genetic structure has been discovered for some morphologically circumscribed species with quite extensive, e.g., intercontinental, distributional ranges
Hedenas *et al.* (2014)	lineages that are well defined genetically but appear to be indistinguishable by normally used morphological features, and are hence termed "cryptic taxa"
Yu *et al.* (2013)	biological entities with reproductive isolation and/or genetic divergence without recognizable morphological disparity
Medina *et al.* (2013)	complex genetic structure that suggested the existence of several cryptic species (Shaw, 2001; Heinrichs *et al.* 2009), that is, species that are supposedly indistinguishable by comparative morphology
Ludwiczuk *et al.* (2013)	Populations on a separate continent can be described as morphologically different subspecies, varieties, or species, or they can be described as cryptic species demonstrating significant genetic subdivision, without morphological divergence
Renner *et al.* (2013)	Occasionally, distinct lineages exhibit no qualitative character differences
Stech *et al.* (2013)	heterogeneity between rates of molecular versus morphological evolution seems to be evident in bryophytes, partly leading to a hidden molecular diversity and cryptic speciation
Medina *et al.* (2013)	an assemblage of species that are indeed morphologically distinguishable, but would have been considered merely cryptic without morphological re-evaluation
Dong *et al.* (2012)	molecular variation without concordant morphological differentiation
Heinrichs *et al.* (2011)	genetic divergence without accompanying morphological disparities and thus cannot be identified using the traditional morphological species concept
Fuselier *et al.* (2011)	taxa that are similar morphologically but phylogenetically divergent to an extent that they appear to be different biological species
Pokorny *et al.* (2011)	morphologically cryptic phylogenetic structure within widespread taxonomic species
Kreier *et al.* (2010)	molecular differentiation without accompanying morphological differentiation)
Vanderpoorten and Shaw (2010)	Retention of a constant morphology despite genetic divergence over millions, or even tens of millions of years, has been termed 'cryptic speciation'
von Konrat *et al.* (2010)	the assumption of a congruence between speciation processes and accumulation of morphological disparity between sister species
Heinrichs *et al.* (2010)	biological species whose genetical distinction is not reflected in conspicuous morphological disparities
Patsch *et al.* (2010)	"cryptic" diversification [i.e. molecular diversification without accompanying morphological diversification
Fuselier *et al.* (2009)	However, genetic and morphological evolution can occur at different rates, and vicariant populations can undergo significant genetic subdivision without morphological divergence, a process known as cryptic speciation
Heinrichs *et al.* (2009a)	Genetic variation without concordant morphological variation has usually been regarded as an indication of cryptic speciation
Heinrichs *et al.* (2009b)	Genetic variation without concordant morphological variation has often been regarded as an indication of cryptic speciation
Shaw (2001)	morphological uniformity may belie complex underlying genetic structure
Fiedorow *et al.* (2001)	Because they are impossible to distinguish morphologically, they could not be recognized by formal taxonomy; thus we treat them as two cryptic species

Patterns of morphological variation

Four processes, each associated with different patterns of phylogenetic discordance, may contribute to cryptic species formation. With which patterns of morphological discordance might these phylogenetic processes be paired? Would quantification of the pattern of morphological discordance contribute to our understanding of evolutionary history? Cryptic species implies morphological unity among two or more species. That there is more than one kind of morphological unity is demonstrated by the definitions published in cryptic species studies.

We can think about the relationship between morphospaces occupied by two or more species in terms of two parameters, the mean and the variance (Fig. 3). When the same mean and variance are shared by two species, we have morphological unity. When either or both the mean and variance differ, we have morphological overlap, the degree of which varies depending on the relative separation of means and magnitude of variance. When the magnitude of difference in means exceeds the combined variance, the two species occupy non-overlapping morphospaces, they are morphologically discrete. This applies to single morphological characters, and multivariate morphological space. A morphological species concept founded on strict discontinuity would, in our simplified example, only recognize as species those with non-overlapping variation. All the others from this example would, given the definitions published in literature, be regarded as cryptic species. The point is that not all cryptic species are the same. They exhibit different degrees of morphological overlap, and one may be nested within the range of morphological variation expressed by another. A traditional approach to species circumscription may only recognize as species those bounded by morphological discontinuity. The term 'cryptic species' as currently employed, is applied to all others.

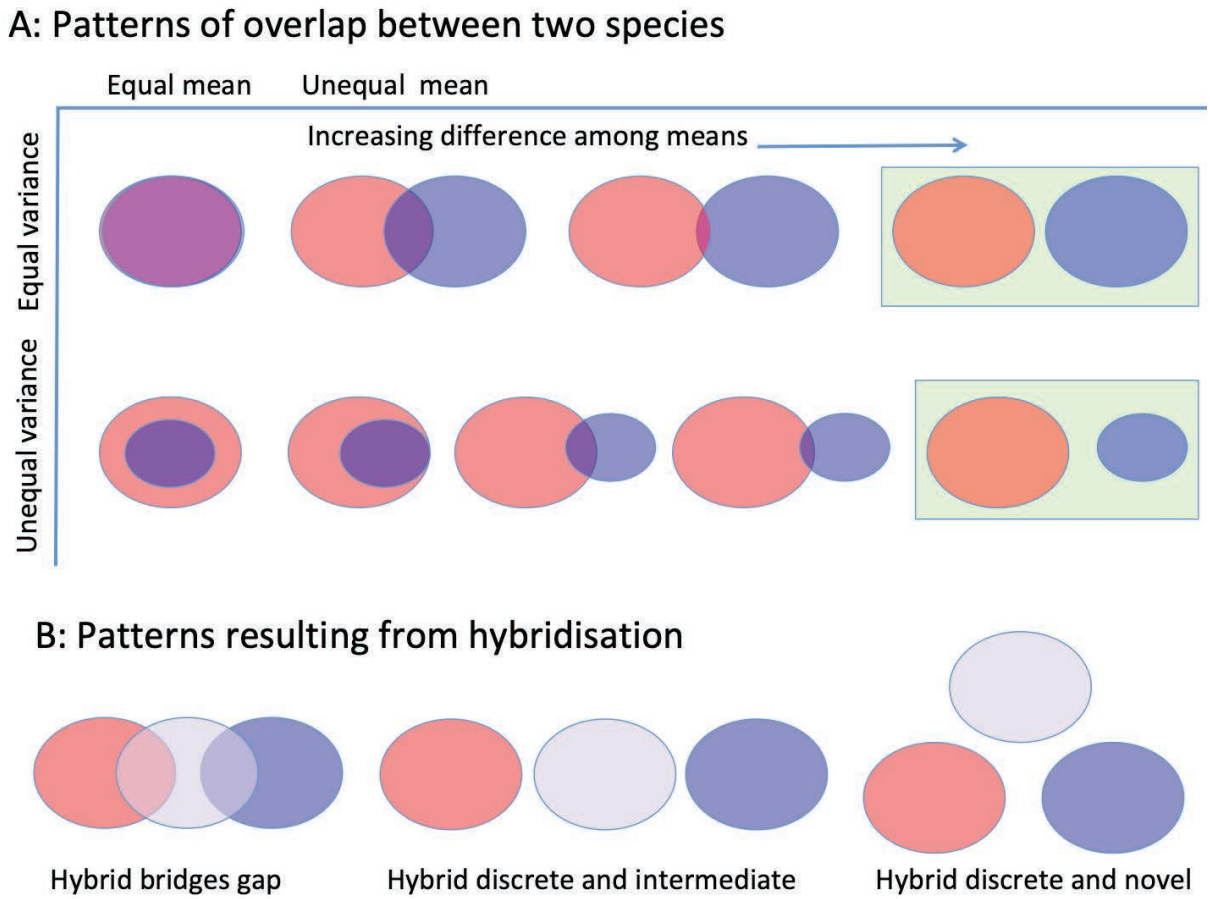

Fig. 3. Patterns of morphological variation among two species showing patterns of continuity and overlap expressed along axes of differences in mean and variance, the green boxes highlight instances where the magnitude of difference among means exceeds the combined variation of both species, in other words morphological discontinuity, which would be recognized as separate species under a traditional morphological species concept.

Intergradation of size and shape variation complicates both species circumscription and individual identification (Vanderpoorten *et al.* 2003; Pätsch *et al.* 2010; Hutsemékers *et al.* 2012). Cryptic species are, by some definitions, hidden by complicated patterns of morphological variation (Bickford *et al.* 2007). If interpreted loosely

enough, this definition could apply to a substantial proportion of all bryophyte species. Bryophyte species are often circumscribed against size and shape discontinuities, but intra-specific variation in some aspects of form may exceed inter-specific differences (Renner *et al.* 2013b). In that situation, traditional approaches to interpretation of morphology, which tend toward rigid fixation on discontinuity, may struggle to profitably employ these data sources to circumscribe or identify species. Complicated patterns of continuity and overlap may actually have the perverse outcome of devaluing qualitative differences in other structures that are capable of circumscribing morphological clusters, possibly due to the over-riding impression of morphological flux that size and shape variation enforce (So 2005). An additional and non-trivial complication is that one person's 'obelliptic' is another's 'obovate', such are the difficulties delimiting discrete subsets of a continuum to which we affix descriptive nouns, as any consideration of the application of ovate in the botanical literature will attest. Shape is difficult to describe, yet subtle shape differences often circumscribe 'cryptic' species (Renner *et al.* 2018). Traditional morphometric methods that seek to quantify shape all do so by proxy, on the basis of metric measurements of various dimensions comprising shape, and so conflate size with geometry (Viscosi and Cardini 2011). Geometric morphometric methods (GMM) allow the geometric component of form to be extracted and considered on its own merits and in isolation from others (Bookstein 1996; Dryden and Mardia 1998). As such, geometric morphometrics present a powerful suite of tools for understanding shape differences in the context of phylogeny (Sidlauskas 2008), species (Viscosi 2015), ontogeny (Klingenberg 2016), and biotic interaction (Klein *et al.* 2017). Geometric morphometric methods have not been widely applied to bryophytes, despite the repeated claim that they are character poor, and despite the need for accurate quantification of shape within the context of intra- and inter-specific variation and difference.

In bryophytes, a lack of morphological differentiation may not necessarily result from lack of available morphospace (Bickford *et al.* 2007), rather one of expansive intra-individual variation (e.g. Renner *et al.* 2013b, 2018). Due to their modular construction by iterative replication of the same fundamental structural unit, bryophytes, and leafy liverworts in particular, 'freeze' the spatial and temporal variation introduced to growth and development through environment by genotype interactions in contemporary form (Renner *et al.* 2013b). Individual shoots may then express the full spectrum of module morphologies and, indeed, within *Lejeunea* most phenotypic variation in gametophyte size and shape was partitioned within individuals. Variation within individuals contributed 55% of shape variation and 45% of size variation (as measured by sums of squares in an unbalanced experimental design), and differences among individuals contributed another 30% of shape variation and 19% of size variation (Renner *et al.* 2013b). Disconcertingly, inter-specific differences in size and shape contributed only 27% of shape and 25% of size variation. A similar pattern emerged in study of *Plagiochila* (Dumort.) Dumort., in a complex of species having hierarchically structured shoot systems (Renner *et al.* 2018). In this complex 51.7% of variation was explained by differences between primary, secondary, and tertiary shoots, which together comprised single bipinnate shoot systems. Only 29.7% of variation was explained by inter-specific morphological differences, and again, intra-individual variation swamped inter-species differences and confounded traditional approaches to species circumscription (Engel and Smith Merrill 2010; Renner *et al.* 2018). Fully balanced and nested experimental designs using next generation morphometric methods have the potential to quantify the partitioning of morphological variation at all levels within the structural hierarchy of bryophyte diversity, from individual shoots to species and higher monophyla. Such studies are labour intensive, but insights into variation partitioning, particularly as they pertain to morphological crypsis, would be valuable.

However, despite often considerable intra-specific variation, significant signal can be extracted from phenotype using GMM such that the *parameters of variation themselves*, rather than discontinuities in the distribution of variation, can be used to circumscribe species. A direct translation from GMM to species circumscription has not been attempted independent of other data sources, but the utility of GMM for species circumscription and identification in instances of overlapping size and shape variation is demonstrated by their ability to identify individuals belonging to the *Plagiochila arbuscula* (Brid. ex Lehm. & Lindenb.) Lindenb. complex using leaf shape alone, and to assign type specimens to resolved species using the shape of single leaves (Renner *et al.* 2018). The quantification of shape variation allows us to assess the degree of morphological overlap among species, and perhaps explore the possibility of a mathematical quantification of what it means to be cryptic, defined by the now entirely observable parameters of phenotypic variance and mean.

The power of GMM could be applied to reverse engineer the detection of cryptic bryophyte species. Most studies of morphologically cryptic species have proceeded from knowledge of genetic structure to tests of phenotypic unity, when the latter has been included. Because bryophytes exhibit hierarchically structured modular growth, it may be possible to utilize the partitioning of size and particularly shape variation to test hypotheses of species circumscription, despite morphological continuity and overlap, by employing Gaussian mixture modelling (Fraley and Raftery 2002) in combination with rater analysis (Fleiss 1971). Given a complex of phenotypically variable and confusing forms, by measuring replicate structures for each

individual the hypothesis of intra- or inter-individual partitioning of variation can be tested (e.g. Renner *et al.* 2009). The beauty of these methods in combination is that mixture modelling achieves replicable phenotypic group assignment for each module, and the individual to which modules belong is usually unambiguous. If intra-individual polymorphism explains variation, then there should be no correlation between phenotypic cluster membership and individual membership, whereas a significant rater correlation indicates that different individuals form different phenotypic clusters. While neither is incompatible with the existence of cryptic species the latter demonstrates that variation is partitioned among individuals into more than one phenotypically circumscribable group. The genetic isolation of this group can then be assessed.

Process of evolution

Confusing patterns of morphological variation in the African *Sphagnum mendocinum* Warnst. and *Sphagnum planifolium* Müll. Hal., and the amphi-Pacific *Sphagnum australe* Mitt. and *Sphagnum falcatulum* Besech., were demonstrated to result from a history of alloploid hybridisation (Karlin 2014; Karlin and Robinson 2017; Karlin *et al.* 2009, 2011, 2013, 2014). In this elegant series of studies, ploidy was inferred from the pattern of microsatellite alleles, whose utility had been demonstrated by Ricca *et al.* (2008). For example, thirteen of fifteen microsatellites had two alleles in *S. slooveri*, suggesting it is a gametophytic allodiploid (Karlin *et al.* 2014). Furthermore, microsatellites and nucleotide sequences indicated that *S.* × *australe, S.* × *slooveri* A.Eddy, *S.* × *planifolium*, and *S.* × *falcatulum* were all inter-subgeneric hybrids (Karlin 2014; Karlin *et al.* 2013, 2014). The resultant mixing of genomic contributions and morphology contributed to the history of taxonomic confusion associated with each species. Extensive morphological overlap between *S. cuspidatum* Ehrh. ex Hoffm. and previously undetected allodiploid *S.* × *falcatulum* and allotriploid *S.* × *falcatulum* had contributed to historically variable treatments of *Sphagnum* subg. *Cuspidata* Lindb. , wherein up to 17 species were recognised (Karlin *et al.* 2013). Reticulate evolution in *Sphagnum* L. was demonstrated by Shaw and Goffinet (2000), and reticulate evolution events at species level have been identified in several other bryophyte lineages. The true moss *Cinclidium stygium* Sw. has an allopolyploid origin with *C. arcticum* (Bruch & Schimp.) Schimp. and *C. latifolium* Lindb. as parents (Wyatt *et al.* 2013); the Pelleid simple thalloid *Pellia* × *borealis* Lorb. has an allopolyploid origin with two cryptic species within *Pellia epiphylla* (L.) Corda as parents (Ordzykoski *et al.* 1996); and the leafy liverwort *Plagiochila* × *britannica* Paton is an allodiploid hybrid having *P. porelloides* (Torr. ex Nees) Lindenb. and *P. asplenioides* (L.) Dumort. as parents (Barbulescu *et al.* 2017). Other allopolypoids are known from the moss genera *Plagiomnium* T.J.Kop. (Wyatt *et al.* 1988), *Rhizomnium* (Mitt. ex Broth.) T.J.Kop. (Jankowiak *et al.* 2005), *Atrichum* P.Beauv. (Perley and Jesson 2015), and *Polytrichastrum* G.L.Sm. (Derda and Wyatt 2000).

Why are known allopolyploid hybrids numerically biased toward *Sphagnum*? In *Sphagnum* multiple low-copy nuclear markers have been routinely employed, and cloned. More broadly across bryophytes the general focus has been on phylogeny reconstruction, the routine use of a single nuclear marker in most bryophyte phylogeny reconstruction, and the emphasis on polyphyly and paraphyly over reticulation in hypothesis testing. Generally, hybrids have been identified using standard phylogeny reconstruction methods when gene tree incongruence is detected. For example, conflict between nuclear and chloroplast gene trees provided unequivocal evidence for the hybrid origin of *Plagiochila* × *britannica* Paton (Barbulescu *et al.* 2017). The same kind of incongruence suggested the North American *Porella platyphylloidea* was of hybrid origin (Heinrichs *et al.* 2011), but this has not been sufficiently investigated. For many allopolyploids, however, this locus-by-locus approach may obscure the occurrence of alleles from the different subgenomes that contributed to complex allopolyploid hybrids, and concatenation of sequences from different evolutionary lineages introduces noise into phylogenetic datasets, which then erodes signal and resolution (Karlin *et al.* 2014). Cloning has been the standard method to establish sequence identity of nuclear homeologues, but this is expensive and laboratory intensive work (Rothfels *et al.* 2017). Nuclear ITS is popular because it is easy to obtain PCR product, and is variable across intron sequences. However, genome-wide concerted evolution of nrITS (Alvarez and Wendel 2003) may remove the signal of subgenome contribution. Unintentional limitations imposed by the design of phylogenetic studies themselves may be contributing to low detection rates of reticulate evolution events in bryophytes, particularly in complexes of cryptic species exhibiting confusing patterns of morphological variation. Indeed there have been previous calls for inclusion of additional nuclear markers (Heinrichs *et al.* 2011). The extent to which hybridization may be contributing to both cryptic morphological species, and intractable patterns of morphological variation and overlap, is currently unknown, precisely because the potential for this contribution has not been fully appreciated (Karlin *et al.* 2014).

In another group of spore-bearing plants, ferns, reticulate evolution has significant implications for interpreting morphological variation. Considerable morphological variation within the fern previously known as *Polystichum richardii* (Hook.) J.Sm. was the result of morphological overlap between two diploid species of *Polystichum* Roth introduced by their allopolyploid hybrid (Perrie *et al.* 2003). Reticulate evolution contributes both morphological and ecological intermediacy (Perrie *et al.* 2003; Meimberg *et al.* 2009), which has been repeatedly demonstrated in many fern families (Vogel *et al.* 1998; Perrie *et al.* 2010; Ohlsen *et al.* 2014a,b; Rothfels *et al.* 2014; Sigel *et al.*

2014), and is acknowledged as a significant diversification process in Pteridophytes (Sigel 2016). To this end, a bioinformatics pipeline for disentangling sequences from different subgenomes in hybrid polyploid complexes has been developed (Rothfels *et al.* 2017) that could be applied to bryophytes.

Species circumscription practices

Cryptic species have always been intertwined with species circumscription practices. Species concepts in the 19th Century were influenced by the assumption that plants from geographically disparate regions would belong to different species. Trans-oceanic distances were often vast, and the variety of dispersal modes employed by bryophytes were not yet appreciated (Lewis *et al.* 2014). Modelling studies have shown that virtual microbes ≤20 mm, sizes common in bryophyte spores, have airborne lifetimes averaging half a day or more when released at the surface, and are therefore widely dispersible (Wilkinson *et al*. 2012). In liverworts, one of the greatest exponents of a geographical species concept, was Franz Stephani (Gradstein 2006), who was a prolific describer of new species in the late 19th and very early 20th Centuries. This geographical perspective was widely rejected by mid to late 20th Century bryophyte taxonomists working with morphological data who found, in many instances, that plants described from different continents could not be reliably distinguished using morphological characters. Many bryophyte species were then revised to have broad inter-continental distributions (Schofield and Crum 1972). In the absence of evidence for long-distance dispersal, these disjunctions were explained in terms of vicariance linked to the emergent theory of plate tectonics. The advent of data on relationships from molecular sources enforced another change of perspective, when broadly distributed species were shown to harbor complex genetic structuring (Shaw 2001), and cryptic species became part of the rejection of the paradigm that held bryophyte species as ancient, continent-riding 'sphinxes' of the past (Shaw 2001). In a way, cryptic species were exactly what 19th Century bryologists implied, reproductively isolated species on different continents that were difficult to distinguish with morphology. For a period during the early 2000's, the term cryptic species was used to highlight these instances where intercontinentally disjunct species exhibited significant geographical genetic substructuring, consistent with the existence of more than one species (Shaw 2001), and this usage remains current in bryology (e.g. Medina *et al.* 2013). However, another rather different use has been made of cryptic species in more recent literature, as a way of flagging the rejection of established species by new molecular evidence (Bickford *et al.* 2007). The latter cryptic bryophyte species have their roots in inappropriately broad morphological species concepts, given genetic data demonstrating reproductive isolation within both geographic and ecological settings (Szweykowski and Krzakowa 1979; Shaw 2001). Often these rejected species concepts (e.g. Heinrichs *et al.* 2009, 2010; Cooper and Renner 2014; Renner *et al.* 2010, 2013a) were founded on strict morphological discontinuity, under which species correspond with discrete phenotypic clusters. Using the term cryptic species in that context should now be rejected as overly simplistic given the repeated demonstration of morphological continuity and overlap among distinct lineages demonstrated by studies combining molecular and morphological data (Hutsemekers *et al.* 2012; Hedenäs *et al.* 2014; Renner *et al.* 2018). We are increasingly forced to acknowledge that strict morphological discontinuity is an inappropriate criterion for species diagnosis and circumscription in bryophytes (Renner *et al.* 2018), and cryptic species studies highlight the recursive nature of hypothesis-testing embedded within systematic and phylogenetic studies.

Species names are placeholders for hypotheses of relationship (Hey *et al.* 2003; Fitzhugh 2005); they encapsulate and distinguish different evolutionary lineages delimited by character data (Fitzhugh 2005). As hypotheses of relationship, species make predictions about expected patterns that can be tested against new data sources. We expect morphological and genetic data to identify the same groups within a test set of individuals. When this is the case, the empirical content of our hypotheses of relationships increases, because they are capable of explaining observed patterns across a greater body of data (e.g. Vigalondo *et al.* 2015). When this is not the case, we have grounds for rejecting our original species hypotheses (e.g. Medina *et al.* 2012, 2013). Reconsideration of morphological data may yield character differences previously overlooked, so facilitating revised morphological circumscription for new hypotheses of relationships. This outcome increases the empirical content of the revised hypothesis because it can now explain patterns across a larger body of data. Additional observations from ecology, chemistry, physiology, anatomy, and genomics can be incorporated as further tests of group membership predicted by the species hypothesis (de Queiroz 1998). The process of reciprocal illumination, whereby species hypotheses are progressively refined by additional observations, and old observations revised as species hypotheses are refined, manifests in this integrative loop.

Revising morphological species circumscriptions when morphology is reconsidered in lieu of molecular data is part of good taxonomic and systematic practice. That hypotheses of morphological homology, and morphological species circumscriptions can be revised in the light of greater knowledge of relationships and more sophisticated morphological analyses should not surprise us, especially considering that some of these hypotheses are decades old, predating both the articulation of homology criteria that fuelled the phylogenetic revolution, and evidence that contributed to our emerging recognition of the role of long distance dispersal in

contemporary distributions. We should therefore maintain a clear distinction between this business-as-usual outcome, and instances of genuine crypsis.

Recommendations

1) Cryptic species have precise meaning, bounded in genetic and morphological terms. Cryptic species should therefore be identified by the combination of morphological and molecular data. The current practice of resting claims of morphological crypsis on existing species circumscriptions should be discontinued.
2) The integrative loop combining new molecular and morphological evidence should be completed before a claim of morphological crypsis is levelled, and then applied only to those species that resist attempts to refine their morphological circumscription, and so cannot be diagnosed on morphological data alone.
3) Why the term cryptic species is being used should be clearly articulated.
4) A distinction between genuine crypsis and business-as-usual revision of species circumscriptions should be re-established and maintained.

We need to work toward a perspective whereby we seek to understand patterns and parameters of morphological variation for what they are – the products of environment by genotype interactions. Environment and genotype maintain a constant dynamic interaction that may be reinterpreted at every reproductive event.

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