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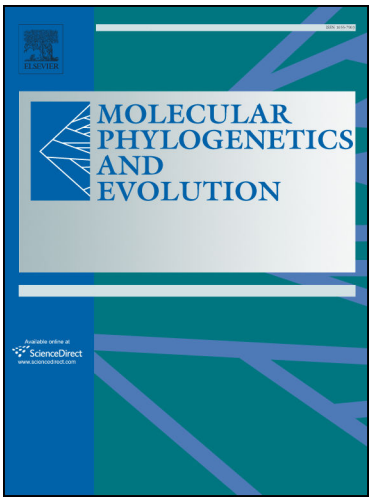

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Reassessing the role of morphology in bryophyte phylogenetics: combined data improves phylogenetic inference despite character conflict

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Abstract - Morphological data has gained renewed attention and has been shown to be crucial in clarifying the phylogenetic relationship in a wide range of taxa. In the last decades, phylogenetic analyses of sequence-level data have radically modified the systematic schemes within bryophytes (early non-vascular land plants) and have revealed a widespread pattern of conflict with morphology-based classifications. Yet, a comprehensive evaluation of character conflict has not yet been performed in the context of combined matrices. In this study, we evaluate the impact of morphology on bryophyte phylogeny following a total-evidence approach across 10 published matrices. The analysed matrices span a wide range of bryophytes, taxonomic levels, gene sampling and number of morphological characters and taxa. Data conflict was addressed by measuring: (i) the topological congruence between individual partitions, (ii) changes in support values of the combined data relative to the molecular partition and (iii) clade stability. The association between these measures and the number of morphological characters per taxon (N_c/T ratio) and the proportion of non-fixed characters (i.e., inapplicable, polymorphic and missing data) was explored. In the individual partition analyses, the N_c/T ratio correlated positively with the topological congruence in six to seven datasets depending on the weighting scheme. The proportion of non-fixed cells had a minor influence on congruence between data partitions. The number of characters and proportion of non-fixed data varied significantly between morphological datasets that improved congruence between data types. This variation suggests that morphological datasets affect the results of combined analyses in different ways, depending on the taxa studied. Combined analyses revealed that, despite the low congruence values between partitions, integrating data types improves support values and stability. However, while non-fixed data had no negative effect on support values, stability was reduced as the proportion of non-fixed cells increased. N_c/T ratio was negatively associated with support values and it showed ambiguous responses in stability evaluations. Overall, the results indicate that adding morphology may contribute to the inference of phylogenetic relationships of bryophytes despite character conflict. Our findings suggest that merely comparing (a) morphology-based classifications with molecular phylogenies or (b) the outcome from individual data partitions can misestimate data conflict. These findings imply that analyses of combined data may provide conservative assessments of data conflict and, eventually, lead to an improved sampling of morphological characters in large-scale analyses of bryophytes.

Keywords: Bryophytes; Character conflict; Morphology; Phylogeny

1. Introduction

In recent years, along with advent of genomic data, morphology has gained renewed attention by systematists interested in its potential as a source of evidence in large-scale phylogenetic analyses of vascular plants (Coiro et al., 2018), arthropods (Giribet, 2016) and vertebrates (Houle et al., 2010; Hsiang et al., 2015; Laing et al., 2017; Simões et al., 2016). The role of morphology in phylogenetics has been long debated based on the observed homoplasy and non-fixed data (i.e., polymorphism and missing data); attributing different impacts to each of these data properties (Bull et al., 1993; Wiens, 1995; Baker et al., 1998; Wiens, 1998,a; Gatesy and Arctander, 2000; Scotland et al., 2003; Wiens et al., 2003; Smith and Turner, 2005; among others). Several authors have discussed these properties from different perspectives and using both simulated and empirical data without reaching a consensus (Farris, 1983; Sanderson and Donoghue, 1989; Desutter-Grandcolas et al., 2003; Scotland et al., 2003; Wiens et al., 2003; Smith and Turner, 2005; Flores-Olvera et al., 2011; among others). Despite this lack of agreement (*but see* Wiens, 2003, 2004; Wiens and Morrill, 2011), some authors are still suspicious about using morphology as they consider it to be an unreliable source of data based on its homoplasy and the difficulty to assess homology among taxa (Scotland et al., 2003).

The earliest representatives of the embryophytes (i.e., land plants), broadly referred to as bryophytes, include plant species characterised by a conspicuous non-vascular gametophyte and a dependent sporophyte. There are three morphologically distinct lineages of bryophytes: hornworts (Anthocerophyta), liverworts (Marchantiophyta), and mosses (Bryophyta). Even though the inter-relationships among these three lineages are still dubious, recent analyses have suggested that bryophytes are monophyletic or that mosses + liverworts form a clade sister to hornworts + vascular plants (Puttick et al., 2018; Wickett et al., 2014). If bryophytes are monophyletic, this poses a problem for inferring the ancestral character states of embryophytes. At present, classifications schemes within the major lineages of bryophytes are mostly based on the analyses of sequence-level data (Cox, 2018; Crandall-Stotler et al., 2009; Goffinet et al., 2009; Goffinet and Shaw, 2009). Usually, these molecular analyses resulted in classifications that differed markedly from previous morphology-based proposals: [e.g., acrocarpous mosses (Bryaceae; Holyoak and Pedersen, 2007), pleurocarpous mosses (Buck et al., 2000), complex thalloid liverworts (Boisselier-Dubayle et al., 2002)].

Phylogenetic studies in bryophytes have stressed the incongruence between morphology and molecules (*see review in* Cox, 2018; Goffinet and Shaw, 2009; Heinrichs et al., 2009). A common explanation to account for this incongruence is that the homoplasy observed in morphology is due to selective forces (Buck, 1998; Buck et al., 2000; Crandall-Stotler et al., 2009; Goffinet et al., 2001; Goffinet and Buck, 2004; Pedersen and Hedenäs, 2002; Yu et al., 2013). This is based on the assumption that similar environmental requirements act as the main evolutionary pressure driving the morphological convergence between unrelated species (Barrett and Graham, 1997; Flores et al., 2017b; Heinrichs et al., 2009; Ranker et al., 2004; Yu et al., 2013). In epiphyllous liverworts, for instance, Yu et al. (2013) found incongruent outcomes between their hypothesis of relationships based on molecular data and previous morphology-based hypotheses; thus, suggesting rampant homoplasy in these ecologically similar taxa. Drastic patterns of morphological variation provide obstacles for taxonomists. While morphology may be highly conserved between species (e.g., Shaw et al., 2003), it can vary between population of a given species as well (i.e., polymorphic characters; e.g., Crum and Anderson, 1981; Bischler, 1998; Shaw and Allen, 2000; Draper et al., 2007; Karlin and Robinson, 2017). For example, Shaw and Allen (2000) discovered that labile characters within species of *Fontinalis* Hedw. contribute to character conflict in this genus. From a systematic point of

view, intraspecific variation has been regarded as potentially restricting the assessment of homology, discovery of synapomorphies and recognition of taxa (Scotland et al., 2003; Seppelt and Kanda, 1961; Shaw et al., 2003; Shaw and Allen, 2000; Wiens, 2004).

Nevertheless, empirical studies conducted on a broad range of taxa have suggested that morphology may still contribute to inferring phylogenetic patterns at a variety of taxonomic levels regardless of their homoplasy (Flores et al., 2017a; Gatesy and Arctander, 2000; Lee, 2009; Schneider et al., 2009; Wahlberg et al., 2005). In their analysis of vascular plants, Bremer et al. (1999) showed that morphological data alone generally recover few clades with significant support values (>75). However, they pointed out that the number of characters influences support values. Data sets with fewer characters generally have lower support values, and the number of available morphological characters is limited by the structural complexity of the organisms being studied. Indeed, support values are higher in large data sets that result from the combination of molecular and morphological data (Bremer et al., 1999, 2001). In a recent study on complex thalloid liverworts, Flores et al. (2017a) showed that both robustness of phylogenetic analyses and diagnoses could be improved by supplementing sequence-level data with large numbers of morphological characters. Along with the enhanced robustness and amended diagnoses, Flores et al. (2017a) indicated that down-weighting morphological characters in such large matrices could increase the congruence between data types.

However, the extent of character conflict and its relationship with character sampling and group (= *clade*) support can be complex. It has been shown that combining data may lead to higher support values than those obtained from individual conflicting partitions (Gatesy et al., 1999b; Gatesy and Arctander, 2000). In his study on lizards, Lee (2009) depicted that individual partitions were unable to solve deep-node relationships and retrieved spurious groups. Conversely, character interaction between these different data types yielded consistent estimations (Lee, 2009). The results by Gatesy et al. (1999), Gatesy and Arctander (2000) and others (Bremer et al., 1999; Bull et al., 1993; Guillerme and Cooper, 2016), suggest that character interaction, rather than just the number of characters, might determine net support in combined data. At present, however, character conflict has rarely been measured in phylogenetics analyses of bryophytes including morphology. Earlier attempts to evaluate character conflict between data types have relied upon comparisons of consistency indices and visual scrutiny of topological differences (e.g., Boisselier-Dubayle et al., 2002; Crandall-Stotler et al., 2005). While the consistency index has been criticised for being dependent on the number of states per character (Archie, 1989), visual comparisons of competing topologies do not provide quantitative estimations of conflict. Consequently, the contribution of morphology in the context of combined data is still underexplored in bryophyte phylogenetics.

In this study, the role of morphology in bryophyte phylogenies is revisited. To the best of our knowledge, the first assessment on the impact of the number of characters and non-fixed data on data conflict in bryophyte phylogenies is herein conducted. Specifically, we address whether the number of morphological characters and proportion of non-fixed cells is associated with (a) the topological congruence among individual data partitions and, (b) changes in support values and (c) clade stability after adding morphological data to the molecular data. Our analyses showed that (i) increasing the number of morphological characters usually improves congruence between data types when the interaction between data partitions is not considered. After combination, morphology contributed to (ii) group support and (iii) stability. As opposed to the number of characters, non-fixed data was more influential on group stability than on group support or topological congruence. The results achieved suggest that the common practice of comparing morphology-based classifications to molecular trees can be misleading and may obscure the

recognition of groups with enhanced stability and support values. Ultimately, the outcomes call into question previous statements on the value of morphology to infer the phylogenetic relationships in bryophytes.

2. Methodology

In order to evaluate the role of morphology and non-fixed characters, data conflict was explored across 10 published matrices on both the complete set of characters (i.e., combined data) and the individual data partitions (i.e., morphology and molecules; Table 1). Character conflict was investigated through the following assessments: *topological congruence* between individual data partitions, *changes in support values and resolution* and *clade stability* in combined data. Although recent implementations of the Mk model allow morphology to be analysed using Bayesian approach, the results and assumptions of model-based methods are still controversial (Goloboff et al., 2017; O'Reilly et al., 2016). Our study, thus, relies on the use of parsimony that has been widely employed in combined phylogenetic analyses.

Phylogenetic analyses were performed based on parsimony as optimality criterion as implemented in TNT 1.5 (Goloboff and Catalano, 2016); a software designed for the efficient analyses of massive datasets (*see review in* Giribet, 2005). Searches were conducted under both equal weighting (ew) and extended implied weighting (iw). Under iw, the strategy consisted of weighting characters according to their homoplasy and proportion of missing entries; assuming that each missing entry had half the homoplasy of an observed entry (P = 0.5; Goloboff, 2014). Weighting against homoplasy has been shown to improve the analyses of morphological data (Goloboff et al., 2008), and has been frequently used in combined analyses (Flores et al., 2017a; Legg et al., 2013; Mirande, 2016). Given the lack of a clear criterion to select a proper concavity constant value, in each analysis under iw the concavity was randomly chosen from the range 5-15. Driven tree searches were conducted by using new technologies (Goloboff, 1999; Nixon, 1999) using five Random Addition Sequence (RAS) trees as starting points per hit, ending the search when the best score was hit four times. Group support was assessed with *symmetric resampling*, calculating support as the difference in the raw frequency between the groups in question and their most frequent contradictory group (GC; Goloboff et al., 2003). Other resampling measures (e.g., bootstrapping) are prone to be distorted by the relative weight of characters and, thus, they may lead to over- or underestimations of support values (Goloboff et al., 2003). Since symmetric resampling is not affected by the relative weight of characters (Goloboff et al., 2003), we consider this resampling measure to be superior to other methods for assessing support values.

2.1. *Datasets*

The studied datasets involve morphological and molecular characters obtained from the original published studies. The criterion for selecting these datasets consisted in evaluating matrices wherein authors have reported conflict between data types and that included a minimum of 30 and 1000 morphological and molecular characters, respectively. Following this criterion, 10 combined datasets were chosen from the respective journals (renamed D1-10; Table 1). While a single selected dataset was taken from a recent study (Flores et al., 2017a), nine were derived from earlier studies (Table 1). Although analysing more recent data would be advisable, earlier datasets also offer two advantages. First, in some cases these earlier studies represent "classic" data upon which much of the present knowledge about each group is based (e.g., De Luna et al., 1999; Pedersen and Hedenäs, 2003). Second, data conflict for some

groups was first reported in these studies (e.g., Crandall-Stotler et al., 2005; Hyvönen et al., 2004). Therefore, analysing character conflict and their relative contribution in these foundational datasets could prove crucial for reassessing the role of morphology in bryology. The selected morphological matrices were either directly downloaded from the respective online supporting data or compiled *de novo* from the journals publications. Regarding the molecular data, when it was not available for download, the original sequences were obtained from GenBank following the vouchers provided by the authors and aligned with Mafft (Katoh et al., 2002) through the pipeline GB2TNT (Goloboff and Catalano, 2012). All major groups of bryophytes (except for Anthocerotophyta, for which combined data was not found) were sampled in these analyses: pleurocarpous and acrocarpous mosses and, thalloid and leafy liverworts.

The ratio between the number of morphological characters and number of taxa studied in the analysis ranged from 0.736 to 2.089 (Table 1). In bryophyte systematics, morphology has been usually represented by discrete characters and data conflict is frequently discussed regarding this type of morphological characters (e.g., Crandall-Stotler et al., 2005). Consequently, continuous characters were discarded for this study if present. The datasets contain from 1 to 11 genes, mostly from chloroplasts; thus resulting in 1,234 to 10,977 aligned bases. The ratio between morphological characters and molecules varies from 0.006 to 0.057 (average 0.021, median 0.012). Altogether, the proportion of inapplicable, polymorphic and missing cells varied from 0.042 to 0.394 (Table 1). In some of the original studies, missing data was not scored distinctly from inapplicable characters (e.g., Crandall-Stotler et al., 2005). Moreover, other authors did not discriminate clearly between missing and polymorphic characters (e.g., Pedersen and Hedenäs, 2002). While we are aware that scoring polymorphic data as missing data may conceal the contribution of the former data type (Nixon and Davis, 1991), solving such scoring issue in the original matrices is unfeasible and out of scope for the present study. Subsequently, we did not differentiate among these data types. All of these types of data are collectively referred to as “non-fixed” characters.

2.2. *Data analyses*

In the following evaluations, *topological congruence between data types*, as well as *changes in average support and resolution* (number of supported groups) in the combined data, were plotted against both the number of morphological characters (N_c/T ratio; where T is the number of taxa and N_c the number of characters) and the proportion of non-fixed cells. *Clade stability* values retrieved from the molecular data were plotted against the values from the combined data, and the N_c/T ratio and proportion of non-fixed cells were highlighted in each replicate. In these graphics (Fig. 4), replicates above or under the diagonal indicate a better performance of either the molecular or the combined data, respectively. In evaluations involving tree comparisons, topological congruence was assessed on the basis of two different measures. The similarity between topologies under comparison was calculated by the SPR distance. SPR distance is the minimum number of SPR moves needed to convert a given tree into another divided by the $T - 2$ (Goloboff, 2008). Besides the topological similarity, another aspect of topological congruence is the proportion of common groups (= *clades*) between trees. The number of common groups between trees is calculated as the number of shared nodes divided by $T-2$. Both measures return values from 0 (maximum incongruence) to 1 (maximum congruence). Searches and evaluations were implemented in TNT scripts and batch files available upon request.

2.2.1. *Topological congruence between data types*

The conflict between data types was first assessed as the topological congruence between the trees derived from the morphological and molecular partitions. This evaluation allows exploring congruence between independent hypotheses where inconsistencies are exclusively due to conflict between partitions. In order to evaluate the influence of the N_c/T ratio and non-fixed cells, the topological congruence was evaluated by the SPR similarity and the proportion of common groups. The evaluation was performed by, first, inferring the most parsimonious tree(s) (MPTs) from the molecular partition. Subsequently, a random number of morphological character were activated and the MPTs were estimated. In each iteration, the N_c/T ratio and the proportion of non-fixed cells were calculated and the congruence between the molecular and the morphological trees was measured. Note that, in our datasets, the proportion of non-fixed cells diminishes with the number of cells (N_c x T). In this character sampling protocol, non-fixed data could reach proportions above, below or equal to its actual value when the N_c sampled is lower than the final N_c/T. This procedure was repeated 200 times per dataset and weighting scheme (ew and iw), leading to 4000 compared replicates.

2.2.2. *Change in average support and resolution in the combined data*

Another approach to assess the conflict between data sources, and their relative contribution, is by estimating the effect of a given data type on the support values rendered by the complementary data (Gatesy et al., 1999b). In order to conduct a global assessment on the impact of morphology, the changes in average support and resolution (i.e., number of supported groups) after combining data were employed as estimators of data conflict. Changes were calculated as the ratio between those support values retrieved by the combined data and the molecular partition during symmetric resampling (see above). Therefore, indicating a net increase (above 1), a net decrease (below 1) or no change (equal 1) after combining morphological and molecular data. It has been argued that mutually exclusive groups recovered with high support values may be indicative of extensive data conflict whereas groups with low values might be a consequence of stochastic error (Bull et al., 1993; de Queiroz, 1993; Wiens, 1998b). Consequently, during the assessment of changes in both the average support and resolution, resampling was conducted considering the three cut-off frequencies: 90, 75 and 50. Note that while calculating the number of shared groups supported by the individual data partitions might provide a contrast between independent data types, it ignores any outcome from character interaction. On the contrary, measuring support and resolution changes after combining data allows considering the impact of such interaction and revealing potential cases of hidden support (Gatesy et al., 1999b; Gatesy and Arctander, 2000). This procedure was repeated 10 times per dataset, weighting scheme (ew and iw) and cut-off frequency; resulting in 600 assessments of support change.

2.2.3. *Group stability*

Stability, support values are also not optimality criteria, has always been of particular interest to systematists. To evaluate the influence of morphology on the stability of groups, datasets were assessed for their capability to retain the original groups when taxa were randomly removed from the dataset. Taxon removal has been previously used to address group stability to the addition of data (e.g., Goloboff et al., 2008; Ramírez, 2003). The logic of those evaluations is that the higher the stability, the more capable the data (or method) is at explaining the information yet to be added. In our case, the rationale of this analysis is to test whether the integration of morphology improves such capability relative to the molecular partition. Stability was then evaluated by randomly deactivating taxa in increasing proportions of the total taxon number (5%, 10%, 15%, 20% and 25%) and estimating the congruence with the results from the

unperturbed dataset. Topographical congruence between the two partitions was evaluated by comparing SPR similarity (see discussion above) and the proportion of common nodes. As before (*see above*), assessing the stability in individual partitions may provide an assessment between independent data though it may also disregard character interaction. Additionally, the volume of sequence-level data usually exceeds that of morphology; thus biasing such comparison against morphology (e.g., Dávalos et al., 2014). For each stability measure, 10 iterations were conducted per dataset, taxon removal proportion and weighting scheme; resulting in 2,000 total replicates.

3. Results

3.1. *Topological congruence between data types*

The topological congruence between data partitions was low, in general. In the comparisons utilizing the complete data partitions, the SPR similarity ranged from 0.023 (2.3%) to over 0.4 (40%) while the number of common groups fluctuated from 0.018 (1.8%) to 0.275 (27.5%, Table 2). Seven (D1-D5, D9 and D10; "ew", Fig. 1) or six (D1, D2, D4, D5, D9 and D10; "iw", Fig. 1) matrices responded positively to the N_c/T ratio under equal weighting or extended implied weighting, respectively (Fig. 1, Supplementary Fig. S1). According to the proportion of common groups, dataset D7 increased the congruence with the molecular data up to 7.3% or 5.3% of the total groups. However, SPR similarity depicted a negative response in D7 diminishing from 35%-40% to a minimum of 14.8%-9.3% in different weighting schemes (Fig. 1, Table 2; Supplementary Fig. S1). D3, D6 and D8 hardly responded to the N_c/T ratio and the SPR similarity between their complete partitions was reduced under extended implied weighting (Table 2; Supplementary Fig. S1).

In these comparisons between data partitions, the congruence was mainly driven by the N_c/T ratio. In six datasets (D2-3, D6-10), replicates showed no differences in congruence as the proportion of non-fixed data changed (*Y-axis*; Fig. 1). Only in four datasets (D1, D2, D4 and D5) the replicates having low N_c/T ratios (≤ 1.0; *X-axis*) showed congruence improvements as the proportion of non-fixed data changed (1.0 in *Y-axis*, Fig. 1). In these cases, congruence exceeded 15% or 30% when using the proportion of common groups or SPR similarity, respectively (Fig. 1). Finally, note that different datasets entailing dissimilar features (i.e., N_c/T ratio or proportion of non-fixed data) reached similar congruence values when the complete partitions were compared (e.g., D1 and D5; Table 2; Supplementary Fig. S1). Likewise, matrices wherein morphology had comparable features did not yield the same congruence values (e.g., D6 and D8; Table 2).

3.2. *Changes in average support and resolution*

After adding morphology to the molecular data, the average support and the resolution (number of supported groups) improved as compared to analyses of molecular data alone. Changes in both average support values and resolution behaved similarly across the evaluations conducted; consequently, only changes in average support are shown (*see changes in resolution in* Supplementary Fig. S2). Under the weakest cut-off level (50), six datasets showed higher estimates of support and resolution, and three matrices rendered no negative impact by addition of morphological characters ("cut50"; Fig. 2, Supplementary Fig. S2). The strictest cut-off level (90) ameliorated the contribution of morphology as seen from the four datasets with lower support and resolution ("cut90"; Fig. 2, Supplementary Fig. S2). Extended

implied weighting, especially when using the intermediate cut-off level (75), enhanced both the best and worst performed datasets as compared to equal weighting ("cut75"; Fig. 2, Supplementary Fig. S2). The maximum (1.48) and minimum (0.51) changes in both support estimates were seen under the intermediate cut-off frequency (75) under implied weighting (Fig. 2, Supplementary Fig. S2).

The data properties explored here (N_c/T ratio and proportion of non-fixed data) had opposite associations with the changes in support and resolution. The integration of morphology produced a negative association with both support estimates as the N_c/T ratio increased (Fig. 2A, Supplementary Fig. S2). Under extended implied weighting, support and resolution tended to drop faster with the N_c/T as compared with equal weighting; especially, under the intermediate cut-off frequency ("cut75"; Fig. 2A, Supplementary Fig. S2). The proportion of non-fixed cells, in contrast, correlated positively with changes in support and resolution in four (out of six) assessments (Fig. 2B, Supplementary Fig. S2). This positive association was seen under equal weighting when the intermediate and strictest cut-off frequencies (75, 90) were employed and under extended implied weighting when using the weakest and strictest cut-off frequencies (50, 90; Fig. 2B). Except for the weakest cut-off frequency ("cut50"), extended implied weighting diminished the positive trends between support and non-fixed data as compared to equal weighting (Fig. 2B, Supplementary Fig. S2). Finally, note that at least two datasets in each cut-off criterion improved their support values in similar magnitudes despite having different N_c/T ratios or proportions of non-fixed data (e.g., datasets with N_c/T ratios of 1.25 and over 2.0 in Fig. 2; Supplementary Fig. S3).

3.3. *Group stability*

During iterative taxon removal, adding morphology generally improved the stability of the inferred groups (replicates below the diagonal; Fig. 4). In the evaluations using SPR similarity, equal weighting resulted in better performance than the molecular data as the taxon removal increased (15-25%; "ew", Fig. 4A, B). Although replicates were more dispersed under implied weighting, combined data yielded more stable results as more taxa were removed ("iw", Fig. 4A, B). Regarding data properties, combined datasets with high N_c/T ratios ratio (> 1.5) rendered both stable and unstable results as compared to their molecular counterpart (Fig. 4A). In those matrices characterised by mid N_c/T ratios (1.0-1.5 ratios), the combined data performed poorer than their molecular partition (replicates above the diagonal; Fig. 4A). Combined datasets performed better than the molecular partition when morphology consisted of low N_c/T ratios (< 1.0; Fig. 4A). As for the non-fixed data, molecular data rendered more stable results when the complementary morphology consisted of a high proportion of non-fixed cells (20% of non-fixed data; Fig. 4B).

Comparisons using the proportion of common groups agreed with the previous analysis in that the combined data rendered more stable results, especially under extended implied weighting ("iw", Fig. 4C, D). In these evaluations, combined datasets with morphology entailing high N_c/T ratios (≥ 1.5) retrieved both the highest and lowest stability values (Fig. 4C). Matrices with mid and low N_c/T ratios (< 1.5; Fig. 4C) rendered intermediate stability values (Fig. 4C). In concordance with the previous evaluation using SPR similarity, the proportion of non-fixed cells corresponded inversely to the proportion of retained groups (Fig. 4D). While datasets with a low proportion of non-fixed data maximised stability, datasets with numerous non-fixed data recovered few original groups (20% of non-fixed data; Fig. 4D).

4. Discussion

The present paper aimed at reviewing the role of morphology in bryophyte phylogenetics in the context of partitioned and combined analyses. The results showed that increasing the volume of morphological data increases the congruence between independent data partitions. Non-fixed data, conversely, had a minor effect on congruence as compared to the N_c/T ratio. Among the datasets improving congruence, the morphological partitions had different numbers of either characters or non-fixed data. Therefore, suggesting that the role of morphological data in combined analyses is taxon-specific. Integrating both data types improved the phylogenetic inference by increasing group support and stability. In these combined data, N_c/T ratio affects more clearly on group support than on stability. In contrast, non-fixed data impact on stability is higher than in group support. Our results, while agreeing partly with previous studies (Flores et al., 2017b; Goloboff et al., 2008; Poe and Wiens, 2000; Watanabe, 2016; Wiens, 1995, 1998b), do not fully support the view that morphology might be problematic in phylogenetic inference of bryophytes (e.g., Holyoak and Pedersen, 2007; Liu et al., 2012; Yu et al., 2013). Ultimately, previous assumptions about the utility of morphological characters in the bryophyte systematics are challenged.

4.1. *Congruence between data types*

Comparisons of individual data partitions showed overall modest levels of congruence between data types as seen from both SPR moves and the proportion of common groups (Fig. 1; Table 2). At first sight, these low values agree with the statements about widespread character conflict in bryophytes (*for references see* Goffinet and Shaw, 2009). However, a different interpretation emerges when the congruence is evaluated regarding its association with data properties (Fig. 1; Supplementary Fig. S1). Despite the modest values of similarity, only dataset D7 showed a significant reduction of congruence as the N_c/T ratio increased: from 35% to 14.8% (i.e., a reduction of 20.2%; Fig. 1). In six to seven datasets, the congruence incrementally increased as the N_c/T ratio increased (Fig. 1; Supplementary Fig. S1). Previous simulations and empirical studies have shown that increasing the number of characters leads to improved levels of accuracy and reduced levels of incongruence between data types (de Sá et al., 2014; Huelsenbeck and Hillis, 1993; Puttick et al., 2017; Wahlberg and Nylin, 2003; Wiens, 2001, 2003, 2004, 2006). Although not aiming at assessing data conflict, former studies on morphological data of plants have shown that increasing character sampling does not lead to higher homoplastic datasets (Sanderson and Donoghue, 1996, 1989). Our results, along with simulations and empirical studies, emphasise that sampling numerous characters may mitigate the conflict between data types.

The N_c/T ratio had a stronger impact on topological congruence than the proportion of non-fixed data (Fig. 1); agreeing with previous findings that non-fixed data has a minor impact on phylogenetic inference as compared to the number of characters (Guillerme and Cooper, 2016; Wiens, 1995). Replicates having both low Nc/T ratios and low proportions of non-fixed cells were only found to have congruence exceeding 15% in four datasets (1.0 in *Y-axis*, Fig. 1; Supplementary Fig 1). In this regard, authors reported positive effects on simulated data (Poe and Wiens, 2000; Wiens, 2003, 1998a, 1995; Wiens and Servedio, 1997) and negative impacts on empirical matrices (Gauthier et al., 1988; Prevosti and Chemisquy, 2010; Wiens, 1995). From our results is not possible to conclude whether non-fixed data improves or reduces congruence since replicates with both high and low proportions of non-fixed data improved congruence (Fig. 1). Instead, our results suggest that non-fixed data plays a minor role in character congruence. In contrast with other analyses (Prevosti and Chemisquy, 2010), our evaluation implies that the low congruence is caused by low N_c/T ratios (Fig. 1). Differences in homoplasy levels, the nature of the taxa under consideration, and the inability to discriminate between missing characters and inapplicable

characters might account for the discrepancies between the present study and those conducted on other taxa (Prevosti and Chemisquy, 2010).

It is widely recognised that data which are seemingly incongruent in partitioned analyses may be successful in recovering groups with enhanced support upon combination (Gatesy et al., 1999b; Gatesy and Arctander, 2000; Hughes and Vogler, 2004; Lee, 2009). Except for some specific cases (e.g., Boisselier-Dubayle et al., 2002; Crandall-Stotler et al., 2005), data types have rarely been compared in a total-evidence framework in bryophyte phylogenetics. Data types are rather compared in light of discrepancies between morphology-based classification and molecular trees (e.g., Holyoak and Pedersen, 2007; Rubasinghe et al., 2011; Gallego et al., 2014). Our partitioned analyses are congruent with this latter practice in that comparing morphology and molecules does not entail any dependency in the data. In this sense, the results from the partitioned analyses suggest that improving character sampling may commonly lead to the enhanced congruence between morphology and molecular data. Nevertheless, a more conservative approach considering character interaction may be required to explore the contribution of morphology to bryophyte phylogenetics.

4.2. *Support and resolution in the combined data*

Upon merging morphological and molecular data, the average support and resolution (number of supported groups) improved in the datasets evaluated (Fig. 2). As the cut-off criterion was relaxed to include groups with lower support, morphology contribution increased such that only one dataset reduced its average support after combining data ("cut50"; Fig. 2). However, when compared with data properties, changes in average support and resolution are negatively correlated with the N_c/T ratio (Fig. 2A). These negative trends contrast with the results of Bremer et al. (1999) showing higher support values as more characters were sampled. However, in Bremer et al.'s (1999) study, differences in support values were also seen among datasets involving the same N_c/T ratio (*see Fig. 1 and Table 2* in Bremer et al. 1999). For both outcomes (Bremer et al.'s and ours), a perfect tie between the N_c/T ratio and group support is hardly to be expected since other factors might be related to support (e.g., character change rate). Both studies found that combined analyses have frequently improved support as compared to results recovered when analysing the individual data types. Moreover, in agreement with a recent study (Flores et al., 2017a), our combined datasets usually recovered higher support values when analysed using extended implied weighting at all cut off frequencies ("iw"; Fig. 2A). Therefore, our results agree with previous studies that found that combining data and weighting against homoplasy improves group support in bryophytes.

The proportion of non-fixed cells showed no negative impact on changes in the average support value and resolution (Fig. 2B, Supplementary Fig. S2). Moreover, a positive trend was seen in four out of six conditions (Fig. 2B, Supplementary Fig. S2). This pattern contrasts with previous studies claiming that morphological variability within species can hinder the recognition of groups at a given taxonomic level (e.g., Crum and Anderson, 1981; Bischler, 1998; Shaw and Allen, 2000; Draper et al., 2007; Karlin and Robinson, 2017). A possible explanation for the positive effect of non-fixed data is that this data type commonly displays less homoplasy than fixed data (Goloboff, 2014). Therefore, in empirical matrices that are have higher levels of homoplasy than simulated data (Prevosti and Chemisquy, 2010), non-fixed data can artificially increase character congruence. In our evaluations, the positive trend is diminished in two cut-off frequencies when the homoplasy of non-fixed cells is taken into account ("cut75" and "cut90"; "iw", Fig. 2B). This incremental association when data are analysed using extended implied weighting stresses the utility of considering the homoplasy of non-observed data.

4.3. *Individual responses and hidden support*

The analysis performed on both the individual partitions and the combined data called attention into two complementary patterns. On the one hand, datasets expected to perform similarly based on their N_c/T ratios proved to be highly contrasting regarding their congruence between data types. For instance, datasets with mid N_c/T ratios retrieved low and high SPR values (e.g., D1 and D5; Table 2). Conversely, datasets having different N_c/T ratios showed comparable values of congruence (D6 and D8; Table 2). Although these can be the result of stochastic factors (e.g., sampled characters), they could suggest taxon-specific responses as well. Depending on the taxon, sampling numerous morphological characters can fail to recover groups in common with molecules whereas few characters can be successful in doing so. In this regard, taxonomists have stated that morphology either portrays poor information to recognise the same groups as the molecular data (e.g., *Mannia* Opiz.; Schill, 2006) or matches the groups of molecular trees (e.g., *Sphagnum* L.; Crum and Seppelt, 1999; Shaw, 2006). Both interpretations, the overall positive trend and the taxon-specific cases, are not exclusive. Our results support both views: while improvements are commonly reached as more data is sampled, some taxa may still respond distinctly to such sampling. In this sense, we should not ignore the fact that, even within bryophytes, taxa are *not* comparable between groups; i.e. we might be dealing with clades and lineages of different age and also the number of characters available as evidence of the past evolutionary changes (Mishler, 1985).

On the other hand, our combined datasets recovered higher support values despite the low congruence between individual partitions. Based on the amount and distribution of conflicting characters between partitions, groups can either improve or reduce their support (Gatesy et al., 1999b). Consider, for instance, the groups supported by the individual partitions and the combined data in Figure 3 and Supplementary Fig. S4. While combining data can improve resolution, only a small proportion of the supported groups are shared between both partitions: four in Marchantiidae (D2; Fig. 3; Table S1) and six in Polytrichales (D1; Supplementary Fig. S4, Table S1). In the scenario where conflict is due exclusively to *between-partition* inconsistency, the combined data resolves a given group in favour of the data partition with higher support. In this case, the group in question should be recovered with similar support to the difference between those from the individual partitions (i.e., without hidden support; *see examples in* Gatesy et al., 1999b). In our analyses, however, the support values of such groups are sometimes improved relative to the individual partitions (blue groups, Fig. 3). Rather than indicating a conflict between data partitions alone, this suggests the existence of character conflict within partitions. In that scenario, the net amount of characters supporting a given group overpasses the number of contradicting characters. Thus, revealing hidden support after combination (Gatesy et al., 1999b). In other words, even in cases of character conflict, morphology can still contain information supporting the same groups from the molecular data. This outcome underlines the need for explicitly considering both data types when assessing their relative contribution to the phylogenetic inference (Gatesy et al., 1999b; Gatesy and Arctander, 2000; Lee, 2009); an approach rarely followed in current bryophyte systematics.

4.4. *Group stability*

The combined data was often more stable as compared to the molecular partition; however, group stability was equal to that of the combined dataset or greater for the molecular partition at higher levels of taxon removal (> 15%; Fig. 4). A puzzling outcome from the analyses using both SPR similarity and the proportion of common groups is that datasets with high N_c/T ratios can retrieve stable or unstable trees (Fig. 4A, C). Giribet (2003) argued that group stability is usually – but not always – proportional to the net

amount of data supporting its monophyly. Following this reasoning, the stability should correlate with the N_c/T ratio if characters were congruent upon combination. In our comparisons, the poor performance of those datasets with high N_c/T ratio implies that character conflict increases in these matrices as compared to other datasets. A tempting explanation is that the more morphological characters are sampled, the higher the conflict between characters (Scotland et al., 2003). However, this is contradicted by other datasets with the same N_c/T ratio that retrieved stable results. Additional sources of conflict should be contemplated as well. Errors in taxon scoring and character definition - likely to be common in large matrices (Simões et al., 2016) – could conceal the phylogenetic signal of congruent characters.

The proportion of non-fixed cells responded negatively to group stability: replicates with a low proportion of non-fixed cells performed better than those with a high proportion of non-fixed data (Fig. 4B, D). As opposed to previous works (Wiens, 2004, 1998a, 1998c; Wiens and Servedio, 1997), our evaluations on empirical matrices showed that non-fixed data affects the accuracy of the phylogenetic inference. When the homoplasy of non-fixed data is down-weighted, the poor performance of these combined matrices with a high proportion of non-fixed cells becomes clearer ("iw"; Fig. 4B, D). In these cases, molecular data outran combined matrices by rendering more stable– or "predictable" – results (replicates above the diagonal; Fig. 4B, D). A plausible source of disagreement with previous works (Guillerme and Cooper, 2016; Wiens, 1995) is that our evaluations employ empirical matrices that are prone to higher levels of homoplasy (Prevosti and Chemisquy, 2010). It is seen from our evaluations on both partitioned and combined data that non-fixed data is more relevant to the stability of the inferred groups rather than group support or congruence between data types in bryophytes.

A concern that follows from these results is whether non-fixed data (or more specifically polymorphism) hinders the inference of stable phylogenetic hypotheses. In simulating the effect of polymorphic data, Wiens (1995) showed that intraspecific variability leads to increased levels of polymorphism. It could be argued that higher species richness could then give place to unstable inferences by promoting polymorphism. However, note that polymorphism is not caused by species richness but morphological variability among populations (e.g., Draper et al., 2007; Wiens, 1995). Similarly, species richness does not account for homoplasy (Supplementary Fig. S5). As documented by Wiens (1995, 2004), adding more characters is a sensible strategy to counterbalance the effect of polymorphism or missing data on accuracy. Likewise, increasing the sampling effort of morphological data is likely to improve stability regardless of the species richness within different groups of bryophytes.

5. Concluding remarks

We conducted the first assessment of the impact of the number of morphological characters and the proportion of non-fixed data on the phylogenetic inference in various groups of bryophytes. Our analyses reveal that combining morphology and molecular data is superior to other approaches. Although topological congruence between individual partitions was low in general, group support, resolution and stability improved after the integration of both data types. N_c/T ratio influences support values while non-fixed data limits group stability. The magnitude of the response to morphology depended on the taxonomic group as well. Therefore, suggesting that excluding morphology based on previous assumptions of putative data conflict, may lead to the underestimation of support values in specific taxonomic groups. Our findings support a recent study showing that decreasing the number of morphological characters for extant taxa

impacts on the accuracy of the phylogenetic inference (Guillerme and Cooper, 2016). Our results, thus, expand on those focused on other taxonomic groups (Gatesy et al., 1999a; Lee, 2009; Sanderson and Donoghue, 1989; Wahlberg et al., 2005; Wiens, 1998d, 2004) and rejects the common view that morphology is problematic in phylogenetic analyses of bryophytes (Cox, 2018; Goffinet and Shaw, 2009).

The present assessment of character conflict differs considerably from those usually conducted in other bryological studies. Previously, authors have sometimes combined data types depending on the results of congruence tests (e.g., Boisselier-Dubayle et al., 2002; Schill, 2006). More often, however, morphology is discussed in light of the molecular data without being included in the analysis (e.g., Holyoak and Pedersen, 2007; Rubasinghe et al., 2011; Gallego et al., 2014). Comparing molecular phylogenies with morphology-based classifications presuppose that the latter was based on the results of phylogenetic analyses (Wiens, 2004); however, that is hardly the case in bryophytes (Crandall-Stotler et al., 2009; Goffinet et al., 2009; *see discussion in* Flores et al., 2017a). Our analyses, as well as those by Gatesy et al. (1999b) and Lee (2009), indicate that comparing morphology-based and molecular-based hypotheses obtained from independent analyses may oversimplify estimations of character conflict.

An alternative to the above strategies is the "integrative approach", whereby morphological characters of interest are mapped onto a molecular phylogeny and either diagnosis or an evolutionary trend is obtained (e.g., Coudert et al., 2017). The main argument for mapping morphology, instead of including it in a simultaneous analysis, relies on that both data sources are independent. However, this approach dismisses character interaction (*see review in* Assis, 2017). In their combined phylogeny of liverworts, Flores et al. (2017a) showed that including morphology – rather than just mapping it – improved the diagnosis of the inferred groups. Moreover, it was seen that characters previously suggested as diagnostic were not synapomorphies for the respective groups (Flores et al., 2017a). Although the current analyses did not focus on comparing the relative performance of the "integrative approach" with the total-evidence strategy, it is evident that the former is not proper for assessing the conflict between data types after the lack of interaction between morphology and molecules.

Even though the *Nc/T* ratio correlated negatively with support changes between datasets, it was also evident that morphology improved support and stability. Given that the congruence between independent data types does not seem to be related to the number of genes (Table 2), there is no reason to propose that the number of genes affects character conflict. However, most of the datasets explored herein were published over a decade ago. As commented by other authors (Cox, 2018; Crandall-Stotler et al., 2009; Goffinet and Shaw, 2009), homology concepts in bryophyte morphology have undergone significant changes after the advent of molecular phylogenetics. It is tempting to consider that additional factors other than homoplasy should be related to data conflict (Supplementary Fig. S5). Errors in character definition and assessment of primary homology may play a key role in character conflict. In vascular plants, for instance, it was shown that modern morphological datasets render congruent results regarding molecular phylogenies (Coiro et al., 2018). Conversely, earlier datasets portrayed scarce information to recover the same groups as the molecular data (Coiro et al., 2018). Our outcomes indicate that improving morphological sampling is necessary for achieving congruent results. Nonetheless, the dominance of molecular phylogenies seems to have restricted the compilation of novel and comprehensive morphological datasets to isolated cases (e.g., Bippus et al., 2018; Flores et al., 2017b; Juarez-Martínez et al., 2016). To better comprehend the causes underpinning putative conflict between data types, future studies should focus on reliable hypotheses of homology and character definition. By incorporating novel concepts of homology, modern morphological datasets could enhance congruence between data types and

lead to amended diagnosis (Flores et al., 2017a). The present work provides useful insights for delineating future total-evidence studies in bryophyte phylogenetics. The construction of large and quality-reliable morphological matrices, and integrating these matrices with fossils and genomic data, will facilitate addressing deep nodes relationships within embryophytes.

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Table 1. Datasets employed in the present study. The ratio between sampled characters and taxa considers only morphological characters. The proportion of non-fixed cells includes the number of polymorphic and missing cells relative to the total number of cells in the morphological matrices.

Table 2. Topological congruence between the complete data partitions measured by SPR similarity ("SPRSIM") and proportion of common nodes, under equal weighting ("ew") and extended implied weighting ("iw"). Maximum and minimum values are highlighted in ***bold italics***.

Fig 1. Topological congruence between data partitions as the number of morphological characters is randomly activated. The proportion of non-fixed cells (*Y-axis*) is rescaled to 1.0 and the number of morphological characters relative to the taxon number (N_c/T ratio; *X-axis*) is rescaled to 2.0. Replicates above or below the dashed line had a higher or lower proportion of non-fixed cells than the complete partition, respectively. In each replicate, the topological congruence is highlighted as the SPR similarity (colour code) and the proportion of common groups (size code). Evaluations were performed under equal weighting ("ew") and extended implied weighting ("iw").

Fig. 2. Changes in support values after adding morphology to the respective molecular data partition. Changes relative to the molecular data are plotted against the N_c/T ratio (A) and the proportion of non-fixed cells (B). Values above or below 1 indicate increment or decrement relative to the molecular data (dashed line). The magnitude of the changes after considering groups above 50, 75 and 90 are reported ("cut50", "cut75" and "cut90", respectively). "iw" = extended implied weighting, "ew" = equal weighting.

Fig. 3. The number of supported groups (>50) by the combined data and the individual partitions in Marchantiidae under equal weighting. Support values above branches correspond to Symmetric Resampling by calculating the difference in raw frequencies between the groups and their most frequent contradictory group (GC). Common groups between individual partitions are highlighted in red, conflicting groups in blue. Nodes collapsed within each

common group are denoted with dashed lines. Note the support value in the conflicting groups (blue) across the three datasets.

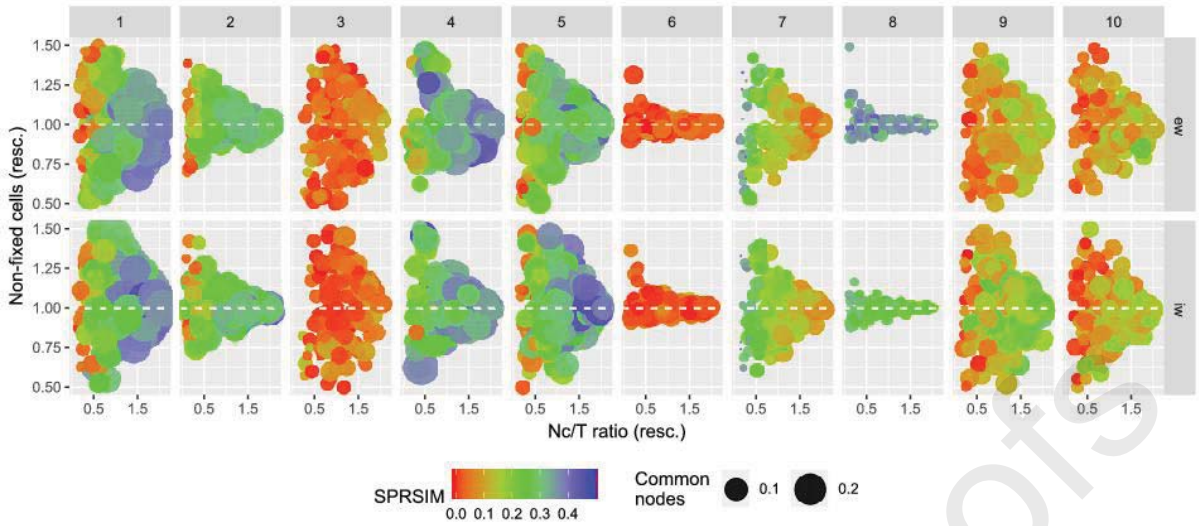
Fig. 4. Group stability under taxon removal. The performance of the molecular data (*Y-axis*) is plotted against the combined data (*X-axis*) in five taxon removal intensities (5%-25%). Stability is measured as the SPR similarity (A, B) and the proportion of common groups (C, D). The diagonal represents a perfect tie between both datasets. The position of the replicates above or below the diagonal represents a better performance by the molecular or the combined data, respectively. The SPR similarity and the proportion of common groups indicate stability: maximum stability (1.0) or low stability (< 1.0). The N_c/T ratio (A, C) and the proportion of non-fixed cells (B, D) in each replicate are highlighted. “iw” = extended implied weighting, “ew” = equal weighting.

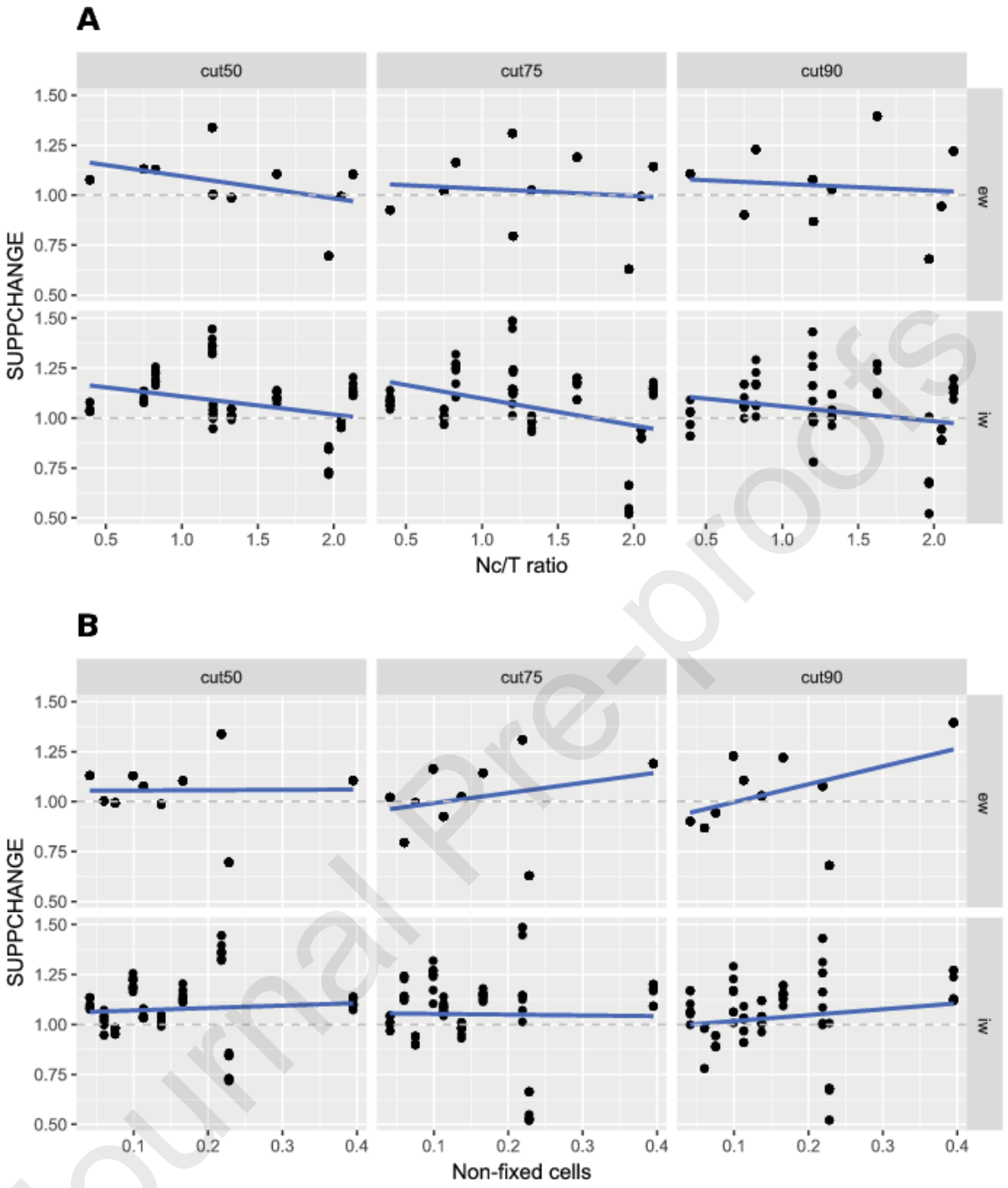
Table 1. Datasets employed in the present study. The ratio between sampled characters and taxa considers only morphological characters. The proportion of non-fixed cells includes the number of polymorphic and missing cells relative to the total number of cells in the morphological matrices.

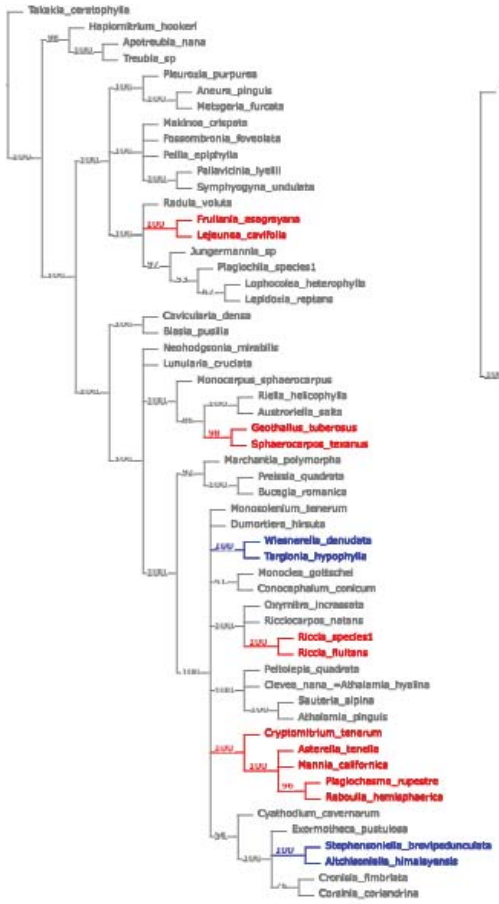
Dataset	Authors	Taxonomic group	N_c/T ratio	Proportion of non-fixed cells	Gene number
D1	Hyvönen et al., (2004)	Acrocarpous mosses (Polytrichopsida)	0.827	0.099	5
D2	Flores et al. (2017,a)	Complex thalloid liverworts (Marchantiidae)	2.127	0.166	11
D3	Pedersen and Hedenäs (2003)	Acrocarpous mosses (Bryaceae)	0.750	0.042	7
D4	Shaw et al. (2008)	Pleurocarpous mosses (Hypopterygiaceae)	2.048	0.075	6
D5	Crandall-Stotler et al. (2005)	Simple thalloid liverworts (Metzgeriidae)	1.327	0.137	8
D6	Kruijer and Blöcher (2007)	Pleurocarpous mosses (Hypopterygiaceae)	1.966	0.229	3
D7	Huttunen et al. (2004)	Pleurocarpous mosses (Brachytheciaceae, Meteoriaceae and Lembophyllaceae)	0.395	0.112	3
D8	De Luna et al., (1999); Newton and De Luna (1999)	Acrocarpous and Pleurocarpous mosses	1.625	0.394	1
D9	Pedersen and Hedenäs (2002)	Pleurocarpous mosses (Plagiotheciaceae)	1.205	0.059	3
D10	Pedersen et al. (2007)	Acrocarpous mosses (Bryaceae)	1.200	0.212	5

Table 2. Topological congruence between the complete data partitions measured by SPR similarity ("SPRSIM") and proportion of common nodes, under equal weighting ("ew") and extended implied weighting ("iw"). Maximum and minimum values are highlighted in ***bold italics***.

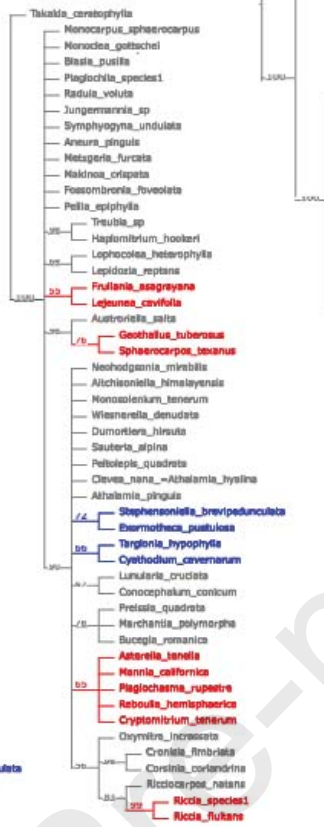
Dataset	N_c/T ratio	Proportion of non-fixed cells	SPRSIM (iw; ew)	Proportion of common nodes (iw; ew)
D1	0.827	0.099	***0.4***; 0.397	***0.275***; 0.216
D2	2.127	0.166	0.315; 0.297	0.019; 0.148
D3	0.750	0.042	0.047; 0.136	0.059; 0.039
D4	2.048	0.075	0.352; 0.372	0.1; 0.150
D5	1.327	0.137	***0.4***; 0.311	0.125; 0.125
D6	1.966	0.229	***0.023***; 0.051	0.036; 0.071
D7	0.395	0.112	0.148; 0.093	0.073; 0.053
D8	1.625	0.394	0.226; 0.324	***0.018; 0.018***
D9	1.205	0.059	0.285; 0.188	0.116; 0.093
D10	1.200	0.212	0.197; 0.131	0.029; 0.059



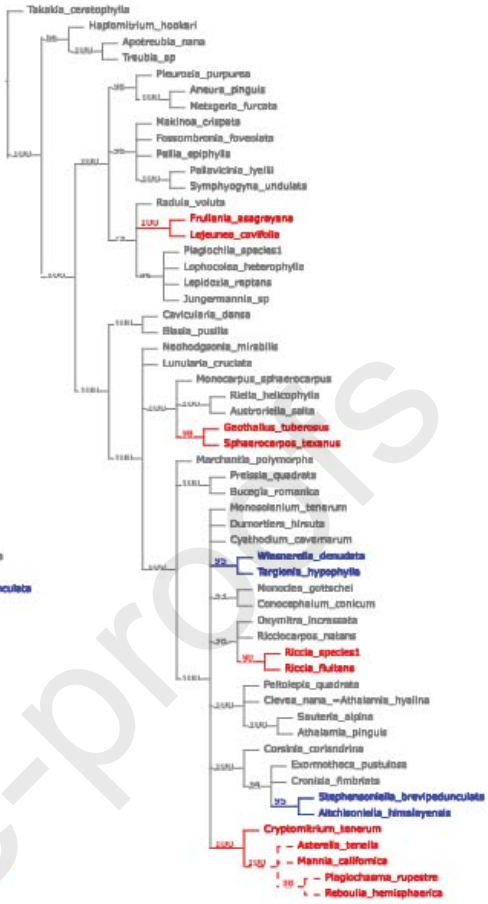




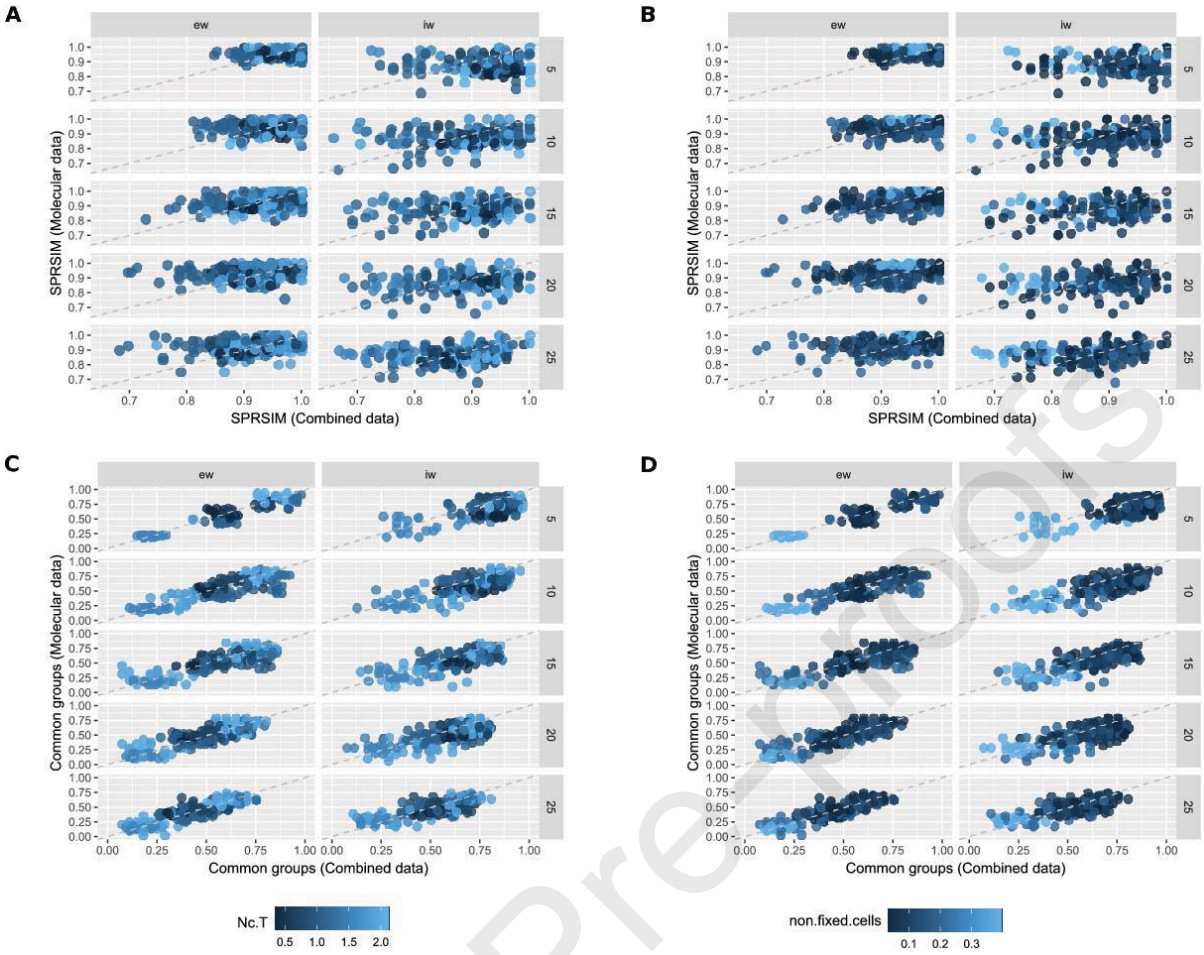
Combined data - nodes supported: 38



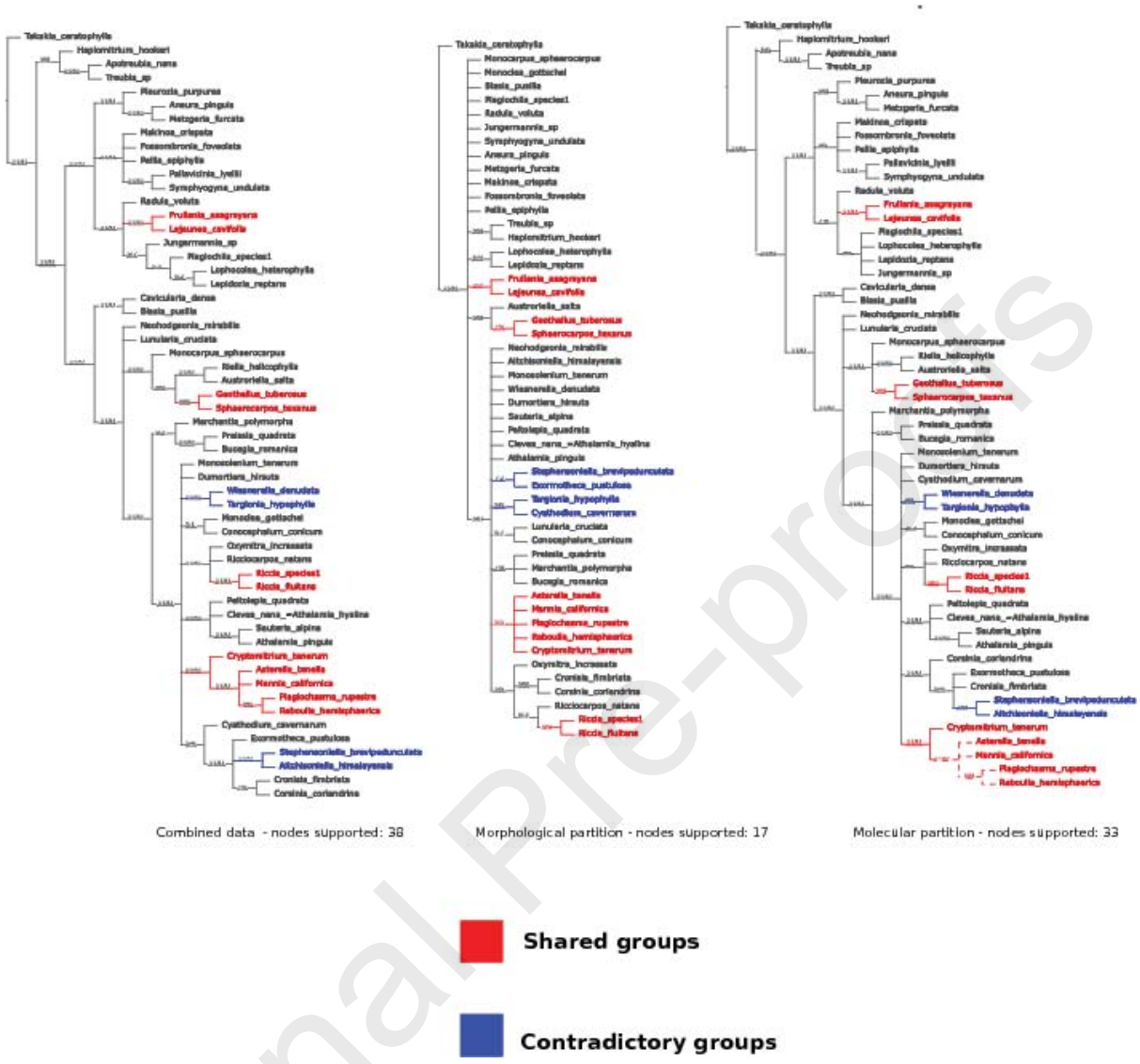
Morphological partition - nodes supported: 17



Molecular partition - nodes supported: 33



Graphical abstract



Combined data - nodes supported: 38 | Morphological partition - nodes supported: 17 | Molecular partition - nodes supported: 33

Shared groups

Contradictory groups

Highlights

- A detailed evaluation on character conflict is conducted across different groups of bryophytes.
- Congruence between data types improves as the number of characters increases.
- Combined analyses showed that morphology contributes to support and stability.
- While non-fixed data has little impact on congruence and support, it influences group stability.
- Responses to the addition of morphology may depend on the taxonomic group.