**Original article**

**Inferring hypothesis-based transitions in clade-specific models of chromosome number evolution along the sedges’ (Cyperaceae) phylogeny**

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**Abstract**

Chromosomal rearrangements have been shown to trigger diversification. For instance, several ancient rounds of polyploidization events have been inferred to promote angiosperm diversification. Dysploidy, although less studied, have been suggested to play also an important role in angiosperm diversification. In this article, we aim to elucidate the role of chromosomal rearrangements on lineage diversification by analyzing the two most recent and comprehensive sedge’s (Cyperaceae) phylogenetic trees. Mode and tempo of chromosome evolution were inferred for both phylogenies as null hypothesis. In order to discern patterns of diversification shifts and chromosome number changes within the family tree, we tested clade-specific chromosome evolution models for several clades/subtrees according to previously reported increments of diversification rates. Results show that alternative hypotheses of clade-specific models of chromosome evolution are significantly supported against the null hypothesis of a single model, which could suggest a link between diversification and changes in chromosome number evolution. Our methodological approach may allow identifying different patterns of chromosome evolution, as found for Cyperaceae, for other lineages at different evolutionary levels.

**Keywords**

ChromEvol, chromosome evolution, Cyperaceae, dysploidy, diversification rates, holocentric chromosomes, polyploidy

**1. Introduction**

Chromosomal rearrangements are frequent in eukaryotes and have been proved to drive differentiation and speciation (Coghlan et al., 2005). These rearrangements can be produced by a sole mechanism or a combination of translocations, inversions, duplications, deletions, dysploidy (fusions and fissions) and polyploidy (whole genome duplication –WGD–) (Coghlan et al., 2005). Whereas some of these events could produce changes in the genome structure and linkage disequilibrium of genes (Butlin, 2005), others could affect directly to the amount of gene content either erasing (i.e. deletions) or increasing it (i.e. duplications and polyploidies) (Coghlan et al., 2005). These events may promote speciation by provoking changes in species fitness, adaptability to new habitats, reproductive isolation and/or shifts in recombination rates (Butlin, 2005; Coghlan et al., 2005; Coyne and Orr, 2004; Navarro and Barton, 2003a, 2003b; Otto and Whitton, 2000; Rieseberg, 2001; Soltis et al., 2009).

In angiosperms, the role of polyploidy and its consequences on speciation has been intensely discussed, with a remarkable interest in ancient polyploid events in some of the species-richest lineages (Debodt et al., 2005; Smith et al., 2017; Soltis et al., 2009; Soltis and Soltis, 2016), which has led to understand polyploidization as a possible driver for lineage radiation (Comai, 2005; Hegarty and Hiscock, 2007, 2008; Levin, 1983; Otto, 2007; Otto and Whitton, 2000; Soltis and Soltis, 2016, 2000; Van de Peer, 2011). On the other hand, although dysploidy (fusions and fissions of chromosomes) is more frequent than polyploidy and specially aneuploidy (duplication or deletion of a chromosome) in angiosperms (Grant, 1981), its consequences in diversification have been disregarded, despite some authors have pointed out dysploidy as an important driver of species diversification (Gitaí et al., 2014; Lee and Namai, 1993, 1992; Orellana et al., 2007; Vallès et al., 2012; Vickery, 1995; Weiss‐Schneeweiss et al., 2009). Nonetheless, its role has been recently suggested to be neutral in terms of lineage diversification (Escudero et al., 2014).

The cosmopolitan family of sedges (Cyperaceae, ca. 5500 species; Govaerts et al., 2017) is the tenth species-richest angiosperm family and it is mainly diversified on the tropics, with the exception of genus *Carex* L., the most diversified genus of the family (ca. 2200 spp., 40% of species richness; Govaerts et al. 2017), that is distributed mostly along the temperate regions (Reznicek, 1990). Moreover, sedges are the angiosperm family with the highest known chromosome number variation (2n=4–224; Roalson, 2008). Because of its high species richness and wide range of chromosome numbers, Cyperaceae constitutes a model taxon for implementing studies on biodiversity, evolution and systematics, especially on the genus *Carex* (e.g. Hipp, 2007). This genus alone displays a wide variation of chromosome number (2n=12–124; Roalson, 2008) which has encourage important works on the aforementioned fields of study (e.g. Hipp, 2007; Roalson, 2008b). Variation in the number of chromosomes and changes in the mode of evolution have been suggested as a possible driver of species richness increment in *Carex* (Escudero et al., 2012b, 2014).

Four main shifts in diversification rate have been detected in Cyperaceae. Escudero et al. (2012b) found an increment in diversification rates in the non-*Siderostictae* clade (that comprises Core *Carex*, Caricoid *Carex* and *Carex* subgenus *Vignea*), which has been confirmed in a recent study by Spalink et al. (2016). Escudero and Hipp (2013) used Hinchliff and Roalson's (2013) phylogeny to infer an additional shift in diversification rates in the clade including the tribes Scirpeae, Dulichieae, and Cariceae plus *Khaosokia* *caricoides* (SDC clade) and the tribes Fuireneae, Abildgaardieae, Eleocharideae, and Cypereae (FAEC clade). Spalink et al. (2016) showed instead shifts in three different lineages inside the clade reported by Escudero and Hipp (2013; SDC+FAEC). This, in addition to the shift in the non-*Siderostictae* clade (as in Escudero et al. 2012b), Spalink et al. (2016) also found a shift in the FAEC clade and in the represented taxa of the C4 photosynthetic pathway *Cyperus* within Cypereae 2 clade (within FAEC).

The huge continuous variation in chromosome number of this family is explained by the presence of holocentric chromosomes, which means that the kinetochoric activity is present along the chromosomes. On the contrary, monocentric chromosomes presents a clear primary constriction in which kinetochoric activity is concentrated (Hipp et al., 2013; Melters et al., 2012; Mola and Papeschi, 2006). In lineages that present holocentric chromosomes (see review in Márquez-Corro et al. 2017), fusions and fissions (named symploidy and agmatoploidy, respectively; Escudero et al. 2014) are more common (Grant, 1981). This occurs even within species level, due to the characteristics of the kinetochoric plate (Hipp et al., 2013; Melters et al., 2012; Mola and Papeschi, 2006) and the neutral balance in DNA content (Escudero et al., 2014).

Cyperaceae family present lineages has been suggested to present different modes of chromosomal evolution (e.g. *Carex* karyotype evolves mainly via agmatoploidy and symploidy; Heilborn 1924; Davies 1956). Thus, this hyperdiverse family and its wide range of karyotypic variation constitute an ideal lineage to study shifts in chromosome evolution model and how they could be related with changes in diversification rates. We hypothesize that some shifts in lineage diversification could be related, at least in part, with changes in the mode of chromosome evolution. This could be explained by the fact that chromosome evolution may probably lead to different mechanism of adaptation and/or reproductive isolation that could drive differentiation and speciation (Butlin, 2005; Coghlan et al., 2005; Coyne and Orr, 2004; Navarro and Barton, 2003a, 2003b; Otto and Whitton, 2000; Rieseberg, 2001; Soltis et al., 2009).

Probabilistic models of chromosome number evolution have been recently formulated (Glick and Mayrose, 2014; Mayrose et al., 2010). These models include different parameters, with the simplest ones calculating the rate of gains, losses and ploidy level augments in chromosome number along a phylogeny. Complexes models allow identifying linear dependency between the starting number of chromosomes and the rate of ascending and decreasing chromosome gains and losses. Lineages within Cyperaceae have been studied by modeling chromosome number evolution (Escudero et al., 2014, 2013, 2010). Here, we applied these models not only to the latest sedges phylogenies (Hinchliff and Roalson, 2013; Spalink et al., 2016) but to different clades/subtrees related with diversification increment events. The implementation of the abovementioned methodology in this manner is crucial to shed light in the karyotype evolution of the family clades of study and might suggest links between lineage splits and chromosomes changes.

The null hypothesis is that chromosome number changes along the family at a constant rate, independent of specific clades. On the other hand, the alternative hypothesis implies the existence of transitions in the mode of chromosome evolution in specific clades (somewhat followed by or as a consequence of a shift in diversification rates). The aims of this study are (i) to elucidate the role of chromosome evolution in the diversification of the sedge family by the implementation of probabilistic models in an unprecedented manner, and (ii) to evaluate the potential utility of the nested models in studies of chromosome evolution for high species richness lineages in order to discern different evolution patterns within a phylogeny.

**2. Materials** **and** **methods**

**2.1. Family tree and chromosome counts**

Two comprehensive, recently published phylogenies of Cyperaceae, with somewhat different samplings (Hinchliff and Roalson, 2013; Spalink et al., 2016), were used for the analyses. Species haploid number were collected from online databases IPCN (Index to Plant Chromosome Numbers, Goldblatt and Johnson 2017) and CCDB (Chromosome Counts Database, Rice et al. 2015), and some chromosome number reports (see Appendix 1).

Chromosomes counts were downloaded for a total of 255 taxa (Appendix 1), of which 72 taxa were represented in both phylogenies. A total of 207 and 120 chromosome data were obtained for Hinchliff and Roalson (2013; ca. 45% of the species represented in the phylogeny –435 species–) and Spalink et al. (2016; ca. 35% –345 species–), respectively (Appendix 2).

Due to the holocentric characteristic of sedges’ chromosomes, counts could vary even within single species (Roalson, 2008). Because we aimed to detect shifts in chromosome number evolution along the Cyperaceae family tree, we assigned to the tips the most frequent number in the species dominated by symploidy/agmatoploidy series, and the record with the lowest chromosome number for the taxa presenting polyploidy (see Appendix 1).

**2.2. Implementation of the analyses**

Latest Cyperaceae phylogenies (Hinchliff and Roalson, 2013; Spalink et al., 2016) were analyzed with chromosome number information using ChromEvol v.2.0 (Glick and Mayrose, 2014; Mayrose et al., 2010) in order to elucidate the mode of chromosome evolution. This software allows determining the probability of a certain model to explain the given data along the phylogeny, based on the combination of the two first or more of the following parameters: (i) gain or (ii) loss of a single chromosome, (iii) polyploidization, (iv) half increment of the chromosome number (demi-polyploidization) and (v) increment of the base number with regard of a rate of multiplication different from a regular duplication. Furthermore, two additional parameters permit to detect linear dependency between the starting haploid number and the rate of (vi) gain and (vii) loss of chromosomes. Because we aim to elucidate clade-specific shifts of chromosome evolution, we discard those models regarding linear parameters.

As stated above, shifts in diversification have been detected in four main nodes of Cyperaceae (SDC+FAEC, FAEC, non-*Siderostictae* *Carex* and C4 *Cyperus*; Escudero et al., 2012b; Escudero and Hipp, 2013; Spalink et al., 2016), so the analyses were carried out not only for the complete phylogenies but for several clades/subtrees as well. The analyses were implemented on the entire phylogenies, clades that have been proved to exhibit diversification rates shifts, background of each analyzed particular clade (i.e. pruned tree without the corresponding clade), and further combinations of clades and backgrounds. A similar methodology, but not with models of chromosome number evolution, has been previously used to infer transitions in continuous character evolution using Brownian and Ornstein-Uhlenbeck models (see Escudero et al., 2012a, 2010; Hipp, 2007; O’Meara et al., 2006). We started covering from simplest to most complex scenarios, analyzing and comparing the models that best fit the data by calculating the Akaike information criterion score with ChromEvol (AIC, Mayrose et al. 2010). Therefore, if the model of chromosome evolution of the entire phylogeny presents less explanatory statistical power (higher AIC) than the models of chromosome evolution of the respective combinations of subtrees (lower AIC summation), a transition in the mode of chromosome evolution may be inferred on the pertinent node. Moreover, AIC weights (Wagenmakers and Farrell, 2004) were also calculated and summed in order to infer the importance weights of a transition occurring on each specific clade.

**3. RESULTS**

Best-fitting models for the complete trees were Const\_Rate\_Demi\_Est for Hinchliff and Roalson (2013) and Const\_Rate\_Demi for Spalink et al. (2016) phylogenies, with AIC values of 1489.68 and 893.625, respectively (see Table 1). The Const\_Rate\_Demi model implies a constant rate of single chromosome increment, decrement and a constant and equal rate of polyploidy and demi-polyploidy (Mayrose et al., 2010). In contrast, Const\_Rate\_Demi\_Est calculates independent rates of polyploidy and demi-polyploidy (Mayrose et al., 2010). The analysis of separate pruned trees and clades showed a significant decrement of the AIC score in both family phylogenies: ΔAIC = −24.88 and ΔAIC = −32.34 for Hinchliff and Roalson (2013) and Spalink et al. (2016), respectively (see Table 1).

The best scenario for Spalink et al.’s (2016) phylogeny showed a Constant\_Rate background with 0.32 gain events/Ma, 0.22 loss events/Ma and 0.02 duplication (i.e. polyploid) events/Ma along the phylogeny (Fig. 1a). Two shifts in the mode of chromosome evolution were detected. The first at the node 2 (non-*Siderostictae* clade), in which gains and losses increased (4.19 and 3.03 events/Ma, respectively), and no duplication was found (Constant\_Rate\_No\_Dupli model). The second shift (to Constant\_Rate\_Demi model) is inferred at the node 3, with 0 gain events/Ma, 3.36 loss events/Ma and 0.04 duplication events/Ma (equal rates of demi-ploidy and polyploidy), similarly to the corresponding clade of Hinchliff and Roalson (2013; Fig. 1b).

On the other hand, best chromosome evolution modeling on Hinchliff and Roalson (2013; Figure 1b, Appendix 3) was a background model (Constant\_Rate) of evolution based on gains (0.52 events/Ma), losses (0.46 events/Ma) and duplications (0.01 events/Ma). At the node 4 (SDC+FAEC clade), a transition to the Base\_Num model is inferred, with 1.36 fission events/Ma, 1.95 fusion events/Ma and a rate of base-number multiplication of 7.5e-4 events/Ma with a base haploid number x = 17. Further transitions are inferred for nodes 1 (FAEC clade) and 3 (C4 *Cyperus* lineage). On FAEC clade, the mode of evolution changed to the Constant\_Rate\_Demi model, with 0.16 events/Ma of gain, 0.08 events/Ma of loss and 0.03 events/Ma of duplication (either demi-polyploidization or WGD). Finally, the node 3 retained the Constant\_Rate\_Demi model, but experienced a change in the parameters. There are no fissions events (0 events/Ma), duplication augmented (demi-ploidy = polyploidy, 0.04 events/Ma), whereas fusions augmented remarkably (2.72 events/Ma). Interestingly, there is another chromosome evolution scenario supported (ΔAIC < 1) for this phylogeny (AIC = 1461.18 vs. 1461.71, Table 1). This latter implies a transition in every studied clade (SDC+FAEC, FAEC, non-*Siderostictae* *Carex* and the C4 *Cyperus* lineage).

The results of the remaining model combinations are included in Appendix 3, with the three best-fitting models depicted in Figure 1. Analysis output files with all the chromosome rate transitions of every model studied are available online at [github.com/jimarcor/ChromEvolCyp](https://github.com/jimarcor/ChromEvolCyp)

**4. Discussion**

**4.1. Chromosome evolution modes on Cyperaceae**

Implementing the methodology of studying full trees and subtrees separately has led to a significant increment in the adjusting (ca. >30 AIC score decrement) of the chromosome data to the distribution of different models of chromosome evolution along the phylogeny. Thus, the null hypothesis of a sole mode of chromosome evolution on the sedges’ family is consistently rejected by both phylogenies: ΔAIC = −28.50 and ΔAIC = −32.34 for Hinchliff and Roalson (2013) and Spalink et al. (2016), respectively (Table 1). Thus, the methodology is proved as favorable in order to study evolutionary transitions such as chromosome evolution model shifts at higher taxonomic levels, and could be used at finer evolutionary levels as well (e.g. analyzing close group of species). Moreover, this is also relevant in the study of organisms with holocentric chromosomes, whose labile karyotype could evolve differently throughout the phylogeny of the lineages, as it has been perceived in this study. Nonetheless, based on the results yielded comparing both phylogenies, further phylogenetic sampling and chromosome data must be gathered in order to obtain clear patterns of chromosome evolution transitions (see high incongruent weights for nodes 1 and 4 on Table 2).

Although the models vary slightly among the best scenarios of the two family trees used, this dissimilarity could be explained mainly by the different sampling between the phylogenies, which only share 72 species. Despite the samplings do not mostly overlap, congruency in the results was found when implementing the analyses in both phylogenies regarding mode of chromosome evolution, as resulting model’s parameters are similar (Figure 1, Appendix 3). Events per million years of fissions, fusions and duplication of chromosomes are alike when comparing between models of each clade or subtree (see Figure 1). On the other hand, the plausibility reflected by the importance weights for each node (Table 2) shows a highly supported and significant transition event of karyological evolution on the C4 *Cyperus* clade (node 3), significant and moderate support for transition on non-*Siderostictae* *Carex* clade (node 2), significant and low support for transition on FAEC clade (node 1), and marginally significant and low support for the SDC+FAEC clade (node 4) for analyses based on Hinchliff and Roalson (2013) and Spalink et al. (2016) phylogenies, respectively.

A clear transition related with the evolution of the represented C4 *Cyperus* species is showed by the results (Table 2), mainly by genome duplication and fusions (Figure 1, Appendix 3). This lineage includes the former genera *Alinula*, *Ascolepis*, *Lipocarpha*, *Kyllinga*, *Pycreus*, *Queenslandiella*, *Remirea*, *Sphaerocyperus* and *Volkiella* (Larridon et al., 2013). Lowest haploid numbers in this clade correspond to polyploid series. *Cyperus brevifolius* (=*Kyllinga* *brevifolia*), for instance, also presents high chromosome number range due to duplication (n = 9–86; Roalson, 2008). Accordingly, polyploidy has been suggested previously for *Cyperus* *esculentus* (Arias et al., 2011; De Castro et al., 2015), and has been reported as frequent in this lineage (see Roalson, 2008). Despite neo-polyploids have been argued not to feature higher diversification rates (Mayrose et al., 2011), this *Cyperus* lineage (ca. 760 species; Larridon et al., 2013) would constitute a counterexample of that trend. In this clade, lineage diversification could suggest a link with the mode of chromosome evolution towards an evolutionary scenario dominated by fusions and genome duplication. Alternatively, this increment of the diversification rate could be related with other innovative mechanisms of the lineage, such as the evolution to the C4 photosynthetic pathway (Larridon et al., 2013), or these three phenomena could have acted in concert. This case is very remarkable and should be studied in detail.

The second transition (with moderate and significant support in analyses based on Hinchliff and Roalson (2013) and Spalink et al. (2016) phylogenies, respectively) is the one corresponding to the genus *Carex* (Table 2). This genus now comprises former genera *Kobresia*, *Schoenoxiphium*, *Uncinia* and *Cymophyllus* (Global *Carex* Group, 2015), in which no or few genome duplications are inferred (Davies, 1956; Hipp et al., 2009; Hoshino, 1981; Wahl, 1940), contrary to the background tree. Models regarding this clade imply the evolution of chromosomes by events of agmatoploidy (fission) and symploidy (fusion). This phenomenon have been historically suggested (Davies, 1956; Hipp et al., 2009; Hoshino, 1981; Wahl, 1940), but it has never been statistically tested at genus level. *Carex* constitutes ca. 40% of the Cyperaceae species (Govaerts et al., 2017), so understanding whether diversification rates shifts are related to karyotypic change is key to comprehend chromosome evolution as output, trigger or part of the speciation process, as well as to elucidate whether this change is mediated by intrinsic (e.g. linkage disequilibrium), extrinsic (e.g. reinforcing ecological speciation) or the interplay of both factors. In this regard, ecological conditions have been stated to play an important role in *Carex* karyotype, as extreme and unstable habitats correlates with low chromosome number and, thus, with low recombination events (Escudero et al., 2012a).

The third transition (with significant and low support in analyses based on Hinchliff and Roalson (2013) and Spalink et al. (2016) phylogenies, respectively) corresponds to the FAEC clade (Table 2). In this case we have found incongruent results between both data sets (probably as result of different sampled species), and accordingly we consider that additional research would be necessary to support this shift in chromosome evolution. In this clade, a shift in the mode of chromosome evolution is dominated by a decrement of the fusion and fission events (Figure 1). Thus, karyotype is likely to remain stable within sampled lineages (e.g. *Fimbristylis*, *Eleocharis*) except for some instances (e.g. *Schoenoplectus*, *Schoenoplectiella*). The low importance weight given by Spalink et al’s (2016) analyses (Table 2) to the model shift for this clade is probably due to the poor sampling of some of the above-mentioned lineages, such as *Eleocharis*. This could have led to an inability to identify a different transition between sister lineages and this clade. In order to discern whether transition on the karyotype evolution in this lineage occurred, further phylogenetic and cytological studies are required.

Finally, SDC+FAEC clade presents marginally significant and low support for transitions in analyses based on Hinchliff and Roalson (2013) and Spalink et al. (2016) phylogenies, respectively (Table 2). The lack of clear support for this clade model transition might be due to the detection of the shift on diversification rate itself. Escudero and Hipp (2013) detected this deep phylogenetic shift. However, they did not find three other further shifts on diversification rates, which could be suggesting a result biased by a family tree with fewer representative species sampling. In fact, Escudero and Hipp (2013) focused their study on macroevolutionary patterns of diversification rather than events of speciation on finer scales. Interestingly, this node is marginally supported by Hinchliff and Roalson’s (2013) phylogeny alone (Table 2), that was the one used by Escudero and Hipp (2013).

Although a clear correspondence between chromosomes number transitions and diversification rates shifts cannot be inferred in this study, strong evidence is found in shifts in chromosome evolution modes through the family tree that somewhat might suggest a link. Nevertheless, as exemplified by the *Cyperus* lineage, this relationship could also be related to other evolutionary process such as the development of C4 photosynthetic pathway. In any case, further researches are required to accurately test the relationship between chromosome model evolution transitions and shifts in diversification rates.

**4.2. Final remarks**

Summing up, this study proposes (i) the use of separate pruned trees and clades vs. complete phylogenies as a feasible approach to the study of chromosome evolution in relation to other evolutionary processes; (ii) that, for Cyperaceae, the statistical support for a complex model was much higher than a simple model of chromosome number evolution; (iii) a clear pattern of fusions and duplications as the main mean of chromosome evolution for, at least, part of the lineage of C4 *Cyperus* species, (iv) agmatoploidy and symploidy in genus *Carex* (except *Siderostictae* clade), (v) karyotype stability trough most FAEC clade lineages. Further studies destined to improve phylogenetic sampling completeness and karyological data of the family are required. Then, the role of chromosomal rearrangements on lineage diversification could be more clearly elucidated.

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**Figure captions:**

**Fig. 1.** Three best-fitting scenarios of chromosome evolution for (a) Spalink et al. (2016) and (b) Hinchliff and Roalson (2013) Cyperaceae phylogenies. Numbered nodes correspond to those in which a shift in diversification rate have been detected (1, FAEC clade; 2, *Carex* lineage; 3, C4 *Cyperus* lineage; 4, SDC+FAEC clade). Gains, losses, duplication (“Dupli”), demiploidization (“Demi”) and base number rates (“Base Num R”) are expressed in events per million years. “Base num” is the haploid base number inferred for the respective node. BN: Base\_Num; CR: Constant\_Rate.

**Table 1. Akaike information criterion (AIC) values, difference (ΔAIC) from the null scenario (no transitions) and AIC weights for each scenario.**

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| Transition scenarios\* | **Hinchliff and Roalson (2013)** | | | **Spalink et al. (2016)** | | |
| **AIC** | **ΔAIC** | **AIC weight** | **AIC** | **ΔAIC** | **AIC weight** |
| Null | 1489.68 | 0 | 3.14e−07 | 893.62 | 0 | 5.75e−08 |
| 1 | 1475.69 | −13.99 | 3.42e−04 | 888.30 | −5.32 | 8.24e−07 |
| 2 | 1482.08 | −7.60 | 1.40e−05 | 868.56 | −25.06 | 1.59e−02 |
| 3 | 1476.05 | −13.63 | 2.85e−04 | 890.50 | −3.12 | 2.74e−07 |
| 4 | 1490.14 | 0.46 | 2.49e−07 | 891.35 | −2.27 | 1.80e−07 |
| 1,2 | 1476.63 | −13.05 | 2.14e−04 | 867.78 | −25.84 | 2.36e−02 |
| 1,3 | 1464.80 | −24.88 | 7.92e−02 | 884.64 | −8.98 | 5.15e−06 |
| 1,4 | 1472.07 | −17.61 | 2.10e−03 | 883.46 | −10.16 | 9.28e−06 |
| 2,3 | 1469.97 | −19.71 | 5.98e−03 | ***861.28*** | ***−32.34*** | ***6.07e−01*** |
| 2,4 | 1483.22 | −6.46 | 7.95e−06 | 870.72 | −22.90 | 5.42e−03 |
| 3,4 | 1475.37 | −14.31 | 4.02e−04 | 889.07 | −4.55 | 5.60e−07 |
| 1,2,3 | 1465.74 | −23.94 | 4.96e−02 | 864.11 | −29.51 | 1.48e−01 |
| 1,2,4 | 1472.60 | −17.08 | 1.60e−03 | 870.88 | −22.74 | 4.99e−03 |
| 1,3,4 | ***1461.18*** | ***−28.50*** | ***4.85e−01*** | 879.79 | −13.83 | 5.80e−05 |
| 2,3,4 | 1470.86 | −18.82 | 3.82e−03 | 863.89 | −29.73 | 1.64e−01 |
| 1,2,3,4 | **1461.71** | **−27.97** | **3.71e−01** | 867.22 | −26.40 | 3.12e−02 |

The best scoring scenario is indicated with bold italics. AIC score within 2 units of the best scoring scenario is in bold.

\*Each number corresponds to a transition in the mode of chromosome evolution for the respective clade.

|  |  |  |
| --- | --- | --- |
| Node | **Hinchliff and Roalson (2013)** | **Spalink et al. (2016)** |
| Null | 5.75e-8 | 3.14e-7 |
| 1 | **0.989** | 0.207 |
| 2 | 0.432 | **1.000** |
| 3 | **0.996** | **0.950** |
| 4 | **0.864** | 0.206 |

**Table 2. Importance weights for no transition scenario and for each node.**