**Original article**

**Inferring Hypothesis-based Transitions in Clade-specific Models of Chromosome Number Evolution along Phylogenies**

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**Summary**

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, has 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 a new comprehensive sedge (Cyperaceae) phylogenetic tree.

Mode and tempo of chromosome evolution were inferred for the complete phylogeny 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 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.

This 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.

**Key words**

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

**Introduction**

Chromosomal rearrangements are frequent in eukaryotes and are related to differentiation and speciation (Coghlan *et al.*, 2005). These rearrangements can be produced by a sole mechanism or a combination of translocations, aneuploidy, dysploidy 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 the amount of gene content through either deletions or duplications of DNA (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 have been intensely studied, with a particular interest in ancient polyploid events in some of the most species-rich lineages (Debodt *et al.*, 2005; Soltis *et al.*, 2009; Soltis & Soltis, 2016; Smith *et al.*, 2017). This has led to an understanding of 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 (translocations, fusions and fissions that lead to changes in chromosome number) is more frequent than polyploidy and especially aneuploidy (duplication or deletion of an entire chromosome) in angiosperms (Grant, 1981), its consequences in diversification have been largely unexamined (though, see Gitaí *et al*., 2014; Lee and Namai, 1993, 1992; Orellana *et al*., 2007; Vallès *et al*., 2012; Vickery, 1995; Weiss‐Schneeweiss *et al*., 2009). Dysploidy has recently been suggested to not represent a dead end through evolutionary time (Escudero *et al.*, 2014).

Probabilistic models of chromosome number evolution have been recently formulated and implemented on ChromEvol 2.0 software (Mayrose *et al.*, 2010; Glick & Mayrose, 2014). These models vary in their complexity, with the simplest ones calculating the rate of gains and losses of chromosomes and changes in ploidy level along a phylogeny. More complex models allow identifying linear dependency between the current number of chromosomes and the rate of increasing and decreasing chromosome numbers. More recently, Freyman and Höhna (2018) expanded ChromEvol functions with the ChromoSSE package in revBayes (Höhna *et al.*, 2014). This software allows detecting shifts in the mode of chromosome evolution during cladogenesis associated with diversification rate shifts or binary phenotypic character evolution (BiChroM; Zenil-Ferguson *et al*. 2017, 2018). However, none of these new approaches considers the possibility of more than one model of chromosome evolution throughout the phylogeny. Here, we expand these studies by applying different models of karyotypic evolution to different clades. This approach is crucial to identify changes in the mode of chromosomal evolution as innovations that may be related to shifts in diversification rates.

The cosmopolitan family of sedges (Cyperaceae, ca. 5500 species; Govaerts *et al*., 2017) is the tenth most species-rich angiosperm family. It has mainly diversified in the tropics, although genus *Carex* L., the most diversified genus of the family (ca. 2200 spp., 40% of species richness; Govaerts *et al*. 2017), and several other lineages are distributed mostly in temperate regions (Reznicek, 1990). Remarkably, Cyperaceae has the highest known chromosome number variation among all angiosperm families (2n=4–224; Roalson, 2008). Because of its high species richness and wide range of chromosome numbers, Cyperaceae constitutes a model taxon for incorporating studies of biodiversity with evolution and systematics (e.g. Hipp, 2007). This is especially true of the genus *Carex*, which alone displays a wide variation of chromosome number (2n=12–124; Hipp, 2007; Roalson, 2008). Variation in the number of chromosomes and changes in the mode of evolution have been suggested as a possible driver of diversification in *Carex* (Escudero *et al*., 2012b, 2014). 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. By contrast, monocentric chromosomes have a clear primary constriction in which kinetochoric activity is concentrated (Mola & Papeschi, 2006; Melters *et al.*, 2012; Hipp *et al.*, 2013). In lineages with 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 (Mola & Papeschi, 2006; Melters *et al.*, 2012; Hipp *et al.*, 2013) that allows more or less constant C-values despite chromosome number variation (Escudero *et al.*, 2014).

Four main shifts in diversification rate have been detected in Cyperaceae. Escudero *et al*. (2012b) found an increase 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*. (2016b). 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*. (2016b) showed instead shifts in three different lineages inside the SDC+FAEC clade reported by Escudero and Hipp (2013). Thus, in addition to the shift in the non-*Siderostictae* clade (as in Escudero *et al*. 2012b), Spalink *et al*. (2016b) 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).

Different modes of chromosomal evolution are present in Cyperaceae. For example, *Carex* karyotype evolves mainly via agmatoploidy and symploidy (Heilborn 1924; Davies 1956), whereas polyploidy is more common in the rest of sedges (Escudero *et al.*, 2012b). Thus, this hyperdiverse family and its wide range of karyotypic variation constitute an ideal lineage to study shifts in chromosome evolution 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 lead to different mechanisms 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).

The aims of this study are (i) to elucidate the role of chromosome evolution in the diversification of the sedge family using probabilistic models, and (ii) to evaluate the utility of nested models for studying chromosome evolution in diverse lineages. We hypothesize that transitions in the mode of chromosome evolution are closely preceded or followed by a shift in diversification rates in Cyperaceae. Our null hypothesis, by contrast, is that chromosome numbers change in the family at a constant rate, regardless of the diversification rate of independent clades.

**Materials and Methods**

*Family Tree and Chromosome Counts*

A new comprehensive phylogeny of Cyperaceae was created from NCBI GenBank database sequences of previous studies (e.g. Hinchliff and Roalson, 2013; Spalink *et al*., 2016b; Jiménez-Mejías *et al*. 2016a). This analysis included 1058 species out of the ca. 5500 circumscribed to Cyperaceae (Govaerts *et al*. 2017; see Fig.1, Supporting Information S1), and was based on a supermatrix alignment of the nuclear ribosomal genes ETSand ITS, the plastid genes *mat*K, *ndh*F, *rbc*L, *ycf*6, and the chloroplast spacer region *trn*C-*ycf*6. Though we used the GTRCAT model in RAxML (Stamatakis, 2006) for computational purposes, the model parameters were individually calculated for five different partitions identified using PartitionFinder v2 (Lanfear *et al*., 2016). We converted the resulting maximum likelihood phylogeny to ultrametric using treePL (Smith & O’Meara, 2012). A total of eleven calibrations were placed on key nodes throughout the phylogeny based on fossil evidence (Jiménez-Mejías *et al*. 2016b; Spalink *et al*. 2016a, 2016b; Supporting Information S2). We have included the treePL configuration file in Dryad.

Species haploid numbers were collected from online databases IPCN (Index to Plant Chromosome Numbers, Goldblatt and Johnson 2017), CCDB (Chromosome Counts Database, Rice *et al*. 2015), and some chromosome number reports (see Supporting Information S2). Chromosomes counts were downloaded for a total of 825 taxa that were included in the phylogeny (Supporting Information S2).

Due to the holocentric characteristic of sedge chromosomes, counts can vary within single species (Roalson, 2008). Because we aimed to detect shifts in chromosome number evolution along the 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 species presenting polyploidy (see Supporting Information S2).

*Selecting the Best Scenario of Chromosome Evolution*

We used ChromEvol v.2.0 (Mayrose *et al.*, 2010; Glick & Mayrose, 2014) to model the mode of chromosome evolution. This software determines the probability of a model to explain the given data along the phylogeny, based on the combination of two or more of the following parameters: (i) gain or (ii) loss of a single chromosome, (iii) polyploidization, (iv) demi-polyploidization (half increment of the chromosome number) and (v) incremental changes to the base number with regard to a rate of multiplication that is different from a regular duplication. Two additional parameters detect linear dependency between the current haploid number and the rate of (vi) gain and (vii) loss of chromosomes.

Shifts in diversification have been previously detected in four main nodes (1-4; Fig. 2) of Cyperaceae (SDC+FAEC, FAEC, non-*Siderostictae* *Carex* and C4 *Cyperus*; Escudero *et al*., 2012b; Escudero and Hipp, 2013; Spalink *et al*., 2016b), so analyses were conducted independently not only for the complete phylogeny but also for the same phylogeny split in several combinations of subtrees (see below). These included clades that exhibit diversification rates shifts, the background phylogeny of these clades (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). Specifically, we used the censored approach described by O’Meara *et al*. (2006). This approach breaks up the original tree in several subtress and the branches that connect the subtrees are excluded from the analyses. The main advantage of this approach is that asumptions are not made about when and how the trait shift occurs in the missing branch. We developed models ranging from the simplest (one model) to most complex (five models) scenarios, identifying the models that best fit the data by calculating the Akaike information criterion score with ChromEvol (AIC, Mayrose *et al*. 2010). In order to compare the simplest (one model) with the more complex scenarios (two to five models), the branches connecting the subtrees were removed in both the single model and two to five model cases. AIC weights (Wagenmakers & Farrell, 2004) were calculated and summed to infer the importance weights of a transition occurring on each specific clade.

In our specific study case, we defined four main clades (where shift in diversification rates were previously detected): (i) clade 1 is FAEC clade; (ii) clade 2 corresponds to non-*Siderostictae* *Carex* clade; (iii) clade 3 is C4 *Cyperus*; and clade 4 conforms SDC+FAEC clade. Our chromosome modeling analyses were performed in up to five different subtrees: (i) subtree 1 is clade 1 after excluding clade 3; (ii) subtree 2 corresponds to clade 2; (iii) subtree 3 conforms clade 3; (iv) subtree 4 corresponds to clade 4 after excluding subtrees 1, 2, and 3; and (v) subtree 5 corresponds to the remaining phylogeny after excluding clade 4 (see Fig. 2).

**Results**

The best-fitting null model for the complete tree was Linear\_Rate\_Demi\_Est, with an AIC score of 5501.84 (see Table 1). The Linear\_Rate\_Demi\_Est model implies a constant rate of incremental/decremental change in chromosome number, polyploidy, and demi-polyploidy, and a linear relationship between the rate of incremental/decremental change and chromosome number (Mayrose *et al.*, 2010).

The analysis of separate subtrees showed a significant decrease in AIC scores (see Table 1). In the best-fitting model (ΔAIC = −207.56), a transition in the model of karyotype evolution was observed in each of the analyzed subtrees except for the subtree 4 (clade 4, SDC+FAEC; Fig. 2, Supporting Information S3-S4). In this case, subtree 4 and 5 displayed the same model, a Base\_Num model, with 0.07 fission events/Myr, 0.70 fusion events/Myr and a rate of base-number multiplication of 0.2e-3 events/Myr with a base haploid number x = 13. Further transitions are inferred for subtrees 1 (FAEC clade excluding subtree 3), 2 (non-*Siderostictae Carex*) and 3 (C4 *Cyperus* lineage). Because these transitions include linear rates parameters, we specify the events per chromosome number and million years (hereafter iMyr) and the range of fission and fusion rates using the minimum and maximum chromosome number in each subtree (see Supporting Information S5).

On the subtree 1 (FAEC clade excluding subtree 3), the mode of evolution changed to the Linear\_Rate\_Demi model, with negligible constant rates of fusion or fission (0 events/Myr), 0.03 duplication events/Myr (either demi-polyploidization or WGD), and a linear relationship of 8.2e-3 fission events/iMyr and 5.2e-3 losses events/iMyr (linear and net rates of 0.02–0.45 fission events/Myr and 0.02–0.29 fusion events/Myr). The C4 *Cyperus* lineage retained the Linear\_Rate\_Demi\_Est model, with 13.68 fission events/Myr, 9.98 fusion events/Myr, 0.22 duplication events/Myr, 1.59 demi-polyploid events/Myr, and a relationship of -0.15 fission events/iMyr and 0.75 fusion events/iMyr (linear rate of -0.90–-12.30 fission events/Myr and 4.50–61.50 fusion events/Myr, and net rate of 12.78–1.38 fission events/Myr and 14.48–71.48 fusion events/Myr). Finally, the non-*Siderostictae Carex* best model was Linear\_Rate\_Demi\_Est, with a constant rate of 2.50 fission events/Myr, 2.13 fusion events/Myr, 2.7e-3 duplications events/Myr, 0.01 demi-polyploidy events/Myr, and a linear relationship of 0.02 fission events/iMyr and 0.07 fusion events/iMyr (linear rate of 0.14–1.30 fission events/iMyr and 0.49–4.55 fusion events/iMyr, and net rate of 2.64–3.80 fission events/Myr and 2.62–6.68 fusion events/Myr).

The results of the remaining AIC scores of model selection and combination are included in Supporting Information S4, with the best-fitting models depicted in Figure 2. Analysis output files with all the inferred chromosome rate transitions of every model studied are available online at [github.com/jimarcor/ChromEvolCyp](https://www.github.com/jimarcor/ChromEvolCyp).

**Discussion**

*Chromosome Evolution Modes on Cyperaceae*

The sedge phylogeny presented here is the most comprehensive family tree published to date, with more than twice as many taxa than previous analyses (Hinchliff & Roalson, 2013; Spalink *et al.*, 2016b). This phylogeny allows studying evolutionary processes more thoroughly in Cyperaceae. We also present a new methodology for inferring modes of chromosomal evolution across this phylogeny. By separately analyzing the full tree and subtrees, we have clarified our understanding of chromosome evolution along the Cyperaceae phylogeny.

The null hypothesis of a single mode of chromosome evolution on the sedges’ family is consistently rejected by the analyses (Table 1). Thus, our approach appears to be useful for studying transitions in chromosome evolution at higher taxonomic levels and could be used at finer evolutionary levels as well (e.g., analyzing groups of close species). Our results are particularly relevant in the study of clades containing species with holocentric chromosomes, whose labile karyotypes could exhibit various modes of evolution.

The best-fitting model of karyological evolution in Cyperaceae suggests multiple model transitions throughout the family phylogeny. These include distinct modes of evolution in the C4 *Cyperus* clade (clade 3), in non-*Siderostictae* *Carex* clade (clade 2), and the subtree 1 (FAEC clade excluding subtree 3). We found no support for a distinct mode of chromosome evolution at the origin of the SDC+FAEC clade (clade 4).

Chromosome numbers seem to have evolved primarily by fusion (Fig. 2, Supporting Information S5-S6) until diversification of the non-*Siderostictae* *Carex* and FAEC clades. The shift at the non-*Siderostictae* *Carex* (Table 1-2) is mainly related to a massive increase in the rate of chromosome fissions and fusions. This clade also includes the former genera *Kobresia*, *Schoenoxiphium*, *Uncinia* and *Cymophyllus* (Global Carex Group, 2015), in which no or few genome duplications have been inferred (Wahl, 1940; Davies, 1956; Hoshino, 1981; Hipp *et al.*, 2009). Accordingly, non-*Siderostictae* *Carex* shows here the lowest polyploidy rates of all subtrees with the exception of subtrees 4 and 5 that show the lowest (in the transition from subtrees 4 and 5 to subtree 2 a soft increase of polyploidy rates was detected). Models regarding this clade imply the evolution of chromosomes by events of agmatoploidy (fission) and symploidy (fusion). This phenomenon has been suggested to occur in *Carex* (Wahl, 1940; Davies, 1956; Hoshino, 1981; Hipp *et al.*, 2009), but it has never been statistically tested at the genus level. *Carex* along constitutes ca. 40% of the Cyperaceae species (Govaerts *et al.*, 2017). Therefore, understanding whether diversification rate shifts are related to karyotypic change is key to comprehending chromosome evolution as the result, trigger, or part of the speciation process and whether this change is mediated by intrinsic factors (e.g. linkage disequilibrium), extrinsic factors (e.g. reinforcing ecological speciation), or both.

A second transition in mode of karyological evolution corresponds to the subtree 1 (FAEC clade excluding C4 *Cyperus*; Table 1-2). This shift in the mode of chromosome evolution is dominated by a decrease of the rate of fusion events, and a slightly increase of fission events as chromosome number grows (Fig. 2, Supporting Information S5-S6). Chromosome duplication seems to have no large effect, and thus, karyotypes are likely to remain largely stable within this clade, particularly in lineages such as *Fimbristylis* and *Eleocharis* (though, some instances of duplication may be evident in *Schoenoplectus* and *Schoenoplectiella*). This pattern could suggest the possibility of constraints against chromosome number evolution in this clade, although the selection process that would cause such results remains obscure.

The high rates of fusions, fissions, demi-polyploidization and duplications in the C4 *Cyperus* clade contrast remarkably with the karyotype stability of the FAEC clade (Fig. 2, Supporting Information S5-S6). Lowest haploid numbers in this clade correspond to a polyploid series; *Cyperus brevifolius* (=*Kyllinga* *brevifolia*), for instance, also presents high chromosome number ranges due to duplication (n = 9–86; Roalson, 2008). Polyploidy has also been suggested previously for *Cyperus* *esculentus* (Arias *et al.*, 2011; De Castro *et al.*, 2015), and has been reported as frequent throughout the clade (see Roalson, 2008). Though neo-polyploids generally do not 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. Nevertheless, although high rates of fission and fusion have been detected, these parameters could be the byproduct of a biased chromosome dataset. Since there are few species represented in this clade and chromosome data depends on the current published reports, high fusion and fission rates can be due to the inability to detect further duplications and demi-polyploidization. In this case, lineage diversification could suggest a link with the mode of chromosome evolution towards an evolutionary scenario dominated by incremental changes to ploidy. Alternatively, this increase in the diversification rate could be related with other innovative mechanisms of the lineage, such as the evolution of the C4 photosynthetic pathway (Larridon *et al.*, 2013). Therefore, genome duplications and shifts in the photosynthetic pathway could have acted in concert.

Although a clear correspondence between chromosome number transitions and diversification rates shifts cannot be assured in this study, strong evidence is found in shifts in chromosome evolution modes through the family tree that 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. Further research is required to accurately test the relationship between chromosome model evolution transitions and shifts in diversification rates. The results of these studies could provide new insight into the macroevolutionary processes that explain these patterns.

*Methodological* *Caveats*

Hablar del posible impacto que puede tener el numero de cromosoma usado; esto ya se ha explicado un poco en Cyperus… explicar de Nuevo, indicando que, a este nivel tan grande, eso metería más ruido, pues a nivel de especies estamos supeditados a la información que hay disponible, especialmente en el caso de holocéntricos on tanta variabilidad. En este caso, también se cometería el sesgo por los números publicados. En cualquier caso, los valores forman series disploides, por lo que el resultado sería el mismo.

Hablando de limitaciones de software, tratar los diferentes métodos que se han usado, pero que todavía no hay uno específico para este tipo de análisis.

*Final Remarks*

Summing up, this study proposes (i) the use of single model vs. complex models (i.e. two to five different models) of chromosome evolution as a feasible approach to the study of chromosome evolution; (ii) that, for Cyperaceae, the statistical support for a complex transition scenario was much higher than a simple model of chromosome number evolution; (iii) a clear pattern of high rate of duplications, and possibly fusions and fissions, as the main mean of chromosome evolution for, at least, part of the lineage of C4 *Cyperus* species, (iv) very high rate of agmatoploidy and symploidy in genus *Carex* (except *Siderostictae* clade), (v) karyotype stability (low rates of chromosome evolution) through most FAEC clade lineages.

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**Author contributions**

M.E. planned and designed the research. J.I.M.-C. collected the data. J.I.M.-C., D.S. and M.E. performed analysis. J.I.M.-C., S.M.-B., D.S., M.L. and M.E. wrote the manuscript.

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**Figure captions:**

Figure 1. Summarize infographic of the methodology followed in the study.

Figure 2.Best-fitting scenarios of chromosome evolution for the Cyperaceae phylogeny. Numbered clades 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). Fissions/fusions (constant, CR), duplication (“Dupli”), demi-polyploidization (“Demi”) and base number rates (“Base Num R”) are expressed in events per million years. Linear rate fissions/fusions (LR) are expressed in events per chromosome number and million years (iMyr). “Base\_Num” is the haploid base number inferred for the respective clade. Akaike information criterion (AIC) of the best-fitting scenario (AIC1) appear next to the phylogeny, compared (ΔAIC) to the null hypothesis AIC score (AIC0).

Table 1. Akaike information criterion (AIC) values, difference (ΔAIC) from the null scenario (no transitions) and AIC weights for each scenario. Importance weights for no transition scenario and for each clade appear on the right side of the table.

|  |  |  |  |
| --- | --- | --- | --- |
| Transition scenarios\* | **AIC** | **ΔAIC** | **AIC weight** |
| Null | 5501.84 | 0.00 | 6.41e-46 |
| 1 | 5382.08 | −119.76 | 6.51e-20 |
| 2 | 5369.57 | −132.27 | 3.38e-17 |
| 3 | 5420.74 | −81.11 | 2.62e-28 |
| 4 | 5467.23 | −34.61 | 2.10e-38 |
| 1,2 | 5330.73 | −171.11 | 9.20e-09 |
| 1,3 | 5345.63 | −156.21 | 5.34e-12 |
| 1,4 | 5369.09 | −132.75 | 4.31e-17 |
| 2,3 | 5311.06 | −190.78 | 1.72e-04 |
| 2,4 | 5377.40 | −124.44 | 6.75e-19 |
| 3,4 | 5387.07 | −114.77 | 5.36e-21 |
| 1,2,3 | ***5294.28*** | ***−207.56*** | ***7.55e-01*** |
| 1,2,4 | 5333.07 | −168.77 | 2.84e-09 |
| 1,3,4 | 5332.64 | −169.20 | 3.53e-09 |
| 2,3,4 | 5302.58 | −199.26 | 1.19e-02 |
| 1,2,3,4 | 5296.63 | −205.21 | 2.33e-01 |

The best scoring scenario is indicated with bold italics.

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

Table 2. Importance weights for each clade and weight for the null scenario of no transitions.

|  |  |
| --- | --- |
| **Transition scenarios** | **AIC weight sum** |
| Null | 6.41e-46 |
| 1 | **0.988** |
| 2 | **1.000** |
| 3 | **1.000** |
| 4 | 0.245 |