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Inferring hypothesis-based transitions in clade-specific models of chromosome number evolution in sedges (Cyperaceae)

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ABSTRACT

Large-scale changes in chromosome number have been associated with diversification rate shifts in many lineages of plants. For instance, several ancient rounds of polyploidization events have been inferred to promote genomic differentiation and/or isolation and, consequently, angiosperm diversification. Dysploidy, although less studied, has been suggested to also play 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. Our null hypothesis is that the mode and tempo of chromosome evolution are to be homogeneous across the complete phylogeny. 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 a complex, heterogeneous model composed of different clade-specific chromosome evolution transitions are significantly supported against the null hypothesis of a model with no chromosome number model transition events along the phylogeny. This could suggest a link between diversification and changes in chromosome number evolution although other possibilities are not discarded. Our methodological approach may allow identifying different patterns of chromosome evolution, as found for Cyperaceae, for other lineages at different evolutionary levels.

1. Introduction

Chromosomal rearrangements are frequent in eukaryotes and are in many cases correlated with 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 of genes (Butlin, 2005), others could affect directly the 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; Smith et al., 2018; Soltis et al., 2009; Soltis and Soltis, 2016). This has led to an understanding of polyploidization as a possible driver for lineage radiation, despite a lack of direct evidence for a causal relationship (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 an evolutionary dead end (Escudero et al., 2014).

Probabilistic models have been recently formulated for chromosome evolution (ChromEvol 2.0 software, Glick and Mayrose, 2014; Mayrose

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et al., 2010). 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 can identify a 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 (Glick and Mayrose, 2014; Mayrose et al., 2010) with the ChromoSSE package in revBayes (Höhna et al., 2014). This software allows not only detecting shifts in the mode of chromosome evolution during anagenetic processes but also during cladogenesis, which can be associated with diversification rate shifts. Moreover, BiChroM type models (correlated rates of phenotype and chromosome evolution; Zenil-Ferguson et al., 2017, 2018) can be integrated with the classic ChromEvol models. Here, we expand these studies by applying different models of karyotypic evolution to different clades. Although it is possible to run this kind of analysis in revBayes with BiChrom functions, it has not been yet empirically tested. 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). 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; Spalink et al., 2018). This is especially true of the genus *Carex*, which alone displays a wide variation of chromosome number (2n = 12–124; Hipp et al, 2009; Roalson, 2008). Variation in the number of chromosomes and changes in the mode of evolution have been suggested as possible drivers 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 (Hipp et al., 2013; Melters et al., 2012; Mola and Papeschi, 2006). In lineages with holocentric chromosomes (see review in Márquez-Corro et al., 2018), fusions and fissions (termed 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) that allows more or less constant genomic content (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 C_4 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 to 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 (e.g. adaptive mutation perpetuated by fusion events) 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). However, diversification rates shifts within the family may be linked to phenotypic changes, changes in habitat, etc., rather than to the mode of chromosome number evolution.

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 number changes in the family at a constant rate, regardless of the diversification rate of independent clades.

2. Materials and methods

2.1. 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, Appendix A). This analysis included 1057 species out of the ca. 5500 circumscribed to Cyperaceae (Govaerts et al., 2017), and was based on a supermatrix alignment of the nuclear ribosomal genes ETS and 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 v.2 (Lanfear et al., 2016). We converted the resulting maximum likelihood phylogeny to ultrametric using treePL (Smith and O'Meara, 2012; see Fig. 1, Appendix B). 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; Appendix C).

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 Appendix C). Chromosomes counts were downloaded for a total of 825 taxa that were included in the phylogeny (Appendix C).

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 Appendix C).

2.2. Selecting the best scenario of chromosome evolution

We used ChromEvol v.2.0 (Glick and Mayrose, 2014; Mayrose et al., 2010) to model the mode of chromosome evolution. This software determines the likelihood 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

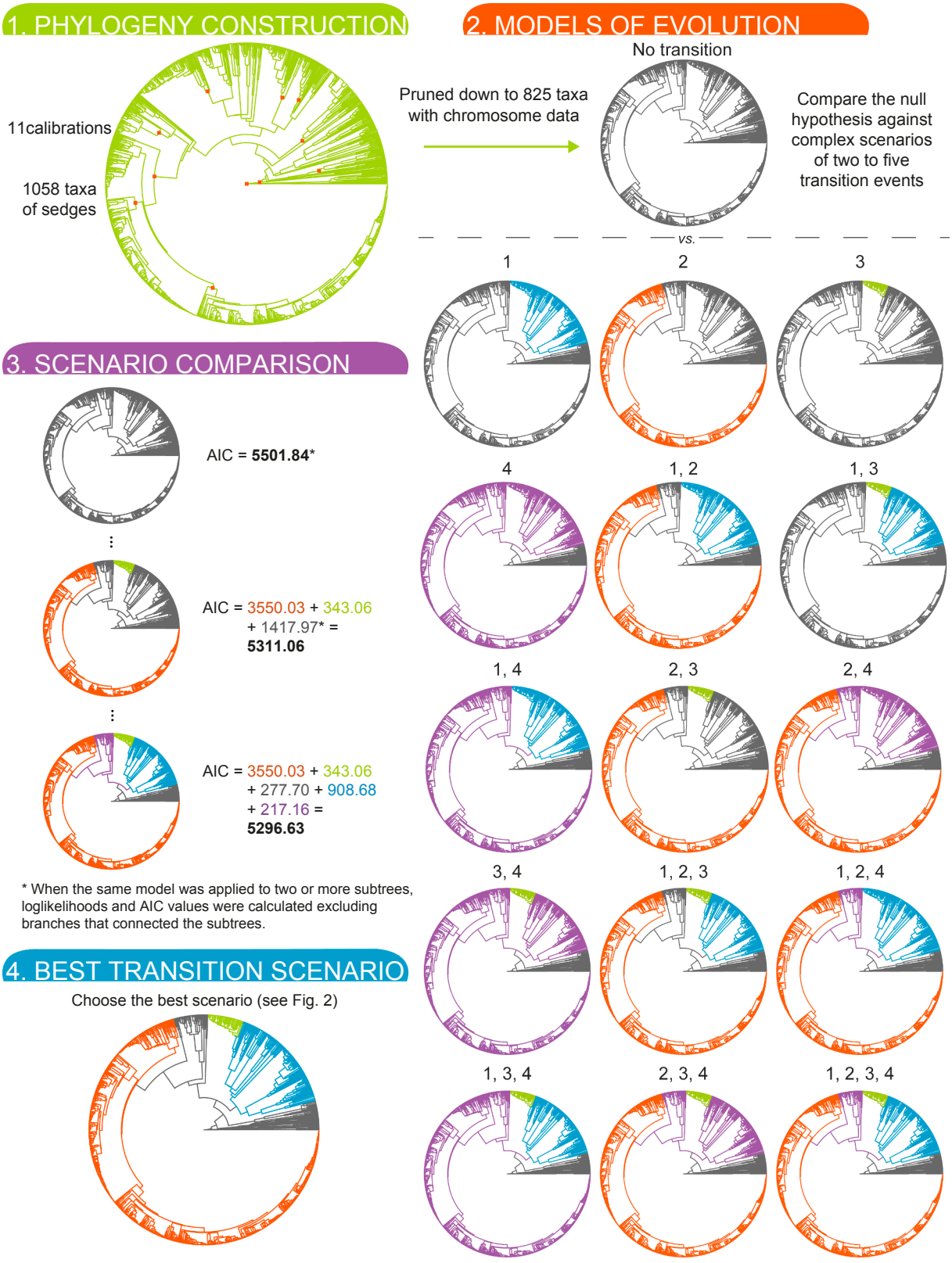

Fig. 1. Summarized infographic of the methodology followed in the study.

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-*Sideroscictae Carex* and C_4 *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

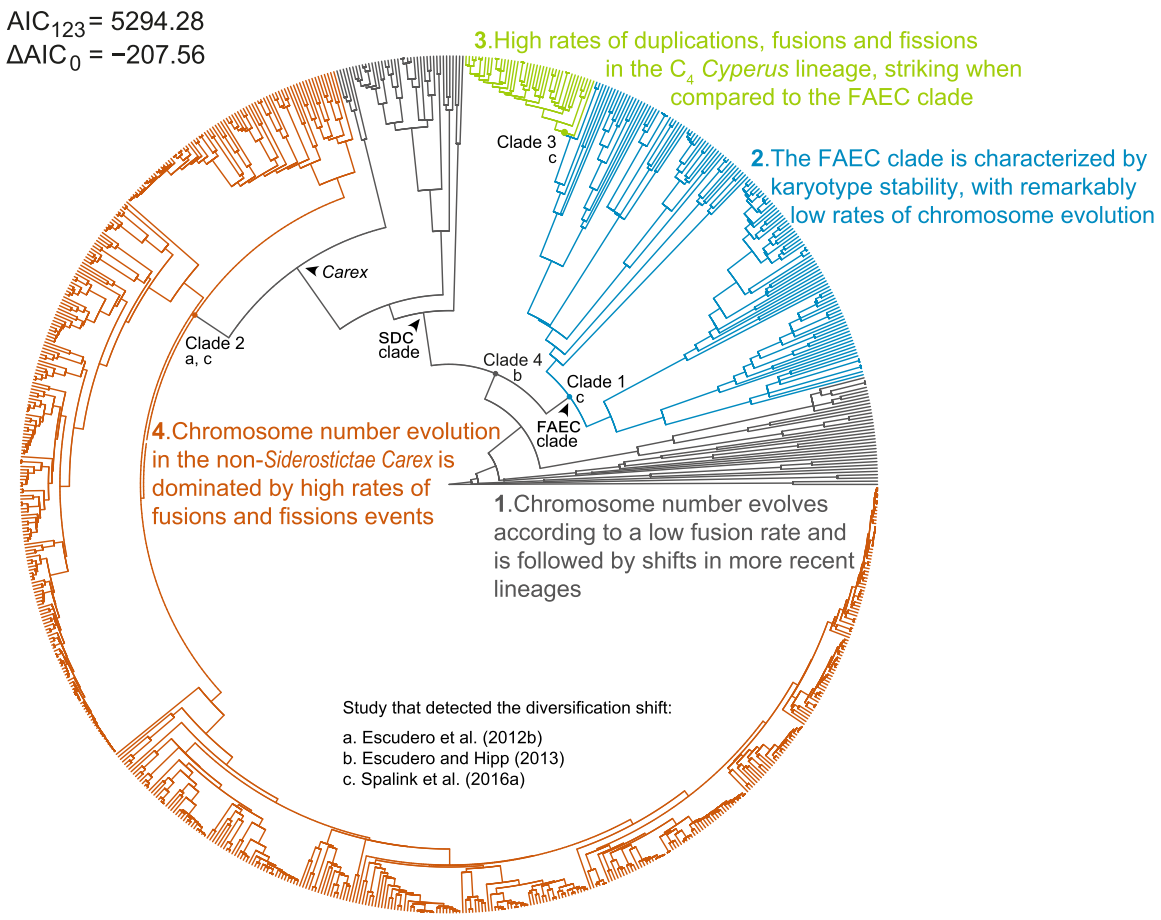

Fig. 2. Best-fitting scenario of chromosome evolution for the Cyperaceae phylogeny. Numbered clades correspond to those in which a shift in diversification rate have been detected (1, FAEC clade; 2, *Carex* lineage; 3, C_4 *Cyperus* lineage; 4, SDC + FAEC clade). Akaike information criterion (AIC) value of the best-fitting scenario (AIC_{123}) appears next to the phylogeny, compared (ΔAIC) to the null hypothesis AIC score (AIC_0).

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 subtrees and the branches that connect the subtrees are excluded from the analyses. The main advantage of this approach is that assumptions 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 the most complex (five models) scenario, 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 the two to five model cases. AIC weights (Wagenmakers and 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 C_4 *Cyperus*; and (iv) 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).

3. Results

Phylogenetic relationships among species are consistent with previous phylogenetic studies. This suggests that missing data does not interfere with the macroevolutionary relationships which are useful for this study.

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, Appendices D-E). 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 (C_4 *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

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 together with brief comments on the right side of the table.

Transition scenarios[†]	AIC	ΔAIC	AIC weight	Conclusions
Null	5501.84	0.00	$6.41e^{-46}$	No transition events
1	5382.08	−119.76	$6.51e^{-20}$	A single transition event, either in FAEC clade (1), non-*Siderostictae Carex* (2), C_4 *Cyperus* (3) or SDC + FAEC clade (4)
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	$9.20e^{-09}$	Scenarios of two transition events
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***	***$7.55e^{-01}$***	Scenarios of three transition events. The best scenario (1,2,3) suggests a sole mode of chromosome number evolution through sedges, with exception of clades 1, 2 and 3
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	$2.33e^{-01}$	Most complex scenario, with four transition events. This case is not much worse than the scenario 1,2,3 (ΔAIC = 2.35), and would support transition events in lineages 1, 2, 3 and 4

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.

each subtree (see Appendix F).

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 rate 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 C_4 *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 rate of −0.15 fission events/iMyr and 0.75 fusion events/iMyr (linear rate of −0.90 to −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 rate 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 Appendix E, with the best-fitting scenario depicted in Fig. 2. Analysis output files with all the inferred chromosome rate transitions of every model studied are available online at zenodo.org/record/2553838.

4. Discussion

4.1. 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 as previous analyses (Hinchliff and Roalson, 2013; Spalink et al., 2016b). This phylogeny allows studying evolutionary processes more thoroughly in Cyperaceae. We also use a new approach 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 sedge phylogeny is consistently rejected by the analyses (Table 1). This 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 heterogeneous modes of evolution.

The best-fitting scenario of karyological evolution in Cyperaceae suggests multiple model transitions throughout the family phylogeny. These include distinct modes of evolution in the C_4 *Cyperus* clade, in non-*Siderostictae Carex* clade, and the FAEC clade excluding C_4 *Cyperus*). We found no support for a distinct mode of chromosome evolution at the origin of the SDC + FAEC clade.

Chromosome numbers seem to have evolved primarily by fusion (Fig. 2, Appendices E-G) 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 (Davies, 1956; Hipp et al., 2009; Hoshino, 1981; Wahl, 1940). Accordingly, non-*Siderostictae Carex* shows here the lowest polyploidy rates of all subtrees with the exception of the remaining SDC clade and early divergent lineages (from Rhynchosporeae to Mapania clades, see Fig. 2) that show the lowest (in the transition to non-*Siderostictae Carex* 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* (Davies, 1956; Hipp et al., 2009; Hoshino, 1981; Wahl, 1940), but it has never been statistically tested at the genus level. *Carex* along constitutes ca. 40% of the species in the sedge family (Govaerts et al., 2017). Therefore, understanding whether diversification rate shifts are related to karyotypic change is key to comprehending chromosome

Table 2
Importance AIC weights for each clade and for the null scenario with no transitions. Sums with the highest probability of a chromosome number transition to occur are marked in bold.

Transition scenarios by clades	AIC weight sum
Null	$6.41e^{-46}$
1	**0.988**
2	**1.000**
3	**1.000**
4	0.245

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 the mode of karyological evolution corresponds to the FAEC clade excluding C_4 *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 slight increase of fission events as chromosome number grows (Fig. 2, Appendices E-G). 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*, see Appendix G). 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 C_4 *Cyperus* clade contrast remarkably with the karyotype stability of the FAEC clade (Fig. 2, Appendices E-G). 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 to other innovative mechanisms of the lineage, such as the evolution of the C_4 photosynthetic pathway (Larridon et al., 2013). Therefore, genome duplications and shifts in the photosynthetic pathway could have acted in concert.

Although a causal relationship between chromosome number model 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 another evolutionary process such as the development of C_4 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.

4.2. Final remarks

Summing up, this study proposes (i) the use of simple model vs. complex scenarios (i.e. including 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 C_4 *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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Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ympev.2019.03.006.

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