Reconstruction of evolutionary trajectories of coffee chromosomes

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Abstract

Background Polyploidization is a widespread phenomenon in plants, especially in angiosperms. Because of the rearrangement of chromosomes and the loss of genes, the number of plant chromosomes will reduce. Studies have shown that core dicotyledons are derived from ancestors with seven proto-chromosomes, which triplicated in a core-eudicot-common hexaploidization. Therefore, dicotyledon with different chromosome numbers have evolved on the basis of 21 chromosomes. On this basis, we selected grape as the intermediate reference species to infer the karyotype evolutionary process of coffee. Results We found that all the chromosome fusion forms in grape were end-end joining, and 7 (70.0%) chromosome fusion forms in coffee were end-end joining. In the process of grape forming 19 chromosomes, there were three chromosome fusions and one chromosome fission. In the process of coffee 11 chromosomes formation, 10 chromosome fusions occurred. During the process, we inferred that satellite chromosomes formed by telomeres from the same or different chromosomes were produced; and the lost of them resulted in chromosome number reduction Conclusions Notably, we found that the major fusion mode of chromosomes in coffee is end-end joining, which is well explained by telomere-centric model, shared by grape and possibly by many other eudicots. This is contrastively different from the observation of monocot plants like grasses, in which nested chromosome fusions often occurred. The present work will help to understand the structural and functional innovations of plant chromosomes.

Background

Polyploidization is an important mechanism driving plant evolution [1, 2]. Polyploidy leads to rapid structural and functional evolution of plant genomes, loss of a large number of genes, and increase structural variations [3, 4]. The chromosomes was doubled or tripled in an affected genome, thereafter, the number of chromosomes usually decreases [5]. Actually, the common ancestor of dicotyledons experienced core-eudicot-common hexaploidization (ECH) around 115 and 130 million years ago, and the ancestor of dicotyledons was inferred to have seven proto-chromosomes [6, 7]. The structure of the ancestral genome of dicotyledon is better preserved in extant grape (*Vitis vinifera*) genome, helping understand the formation of ancestral eudicot genome and even other angiosperm genomes [8], and provide a reference to decipher the process of karyotype evolution of angiosperms in millions of years.

However, due to the occurrence of chromosome fission and fusion, the numbers of chromosomes among different plants in modern dicotyledons are different, sometimes due to extra polyploidization [9, 10]. Durian (*Durio zibethinus*) experienced hexaploidization event 19-21 million years ago after ECH, the number of chromosomes was 2n=60 [11]. Kiwifruit (*Actinidia chinensis*) experienced two tetraploidization events after ECH, and the number of chromosomes was 2n=58 [1, 7]. The paleogenomics analysis of watermelon (*Citrullus lanatus*) revealed that seven chromosomes of the ancestral genome of dicotyledon underwent 81 division and 91 fusion to form 11 chromosomes of the existing watermelon[12]. This indicated that chromosomes experienced a lot of rearrangements after polyploidization.

Chromosome reduction is largely due to chromosome fusion, and the biological mechanism has been studied [13-16]. Studies have suggested that chromosome reduction tends to combine two chromosomes into one larger chromosome and one smaller chromosome, while smaller chromosomes are lost during meiosis [17, 18]. Modern chromosomes were reported often produced by centromere fusion of ancestral chromosomes[19, 20]. Recently, based on a previously raised telomere-centric chromosome rearrangement model, it was inferred that wheat and Brachypodium chromosomes have experienced independent evolutionary trajectories[9].

Genome alignment analysis can help reconstruct the ancestral genome of modern species. Evolution history from ancestral genome to existing karyotype can be inferred based on the number of events such as insertion, deletion, fusion, splitting and translocation [21, 22]. Previously, based on the analysis of the evolutionary pattern of the ancestral genome of flowering plants, it was inferred that the ancestral karyotypes of grass plants consisted of 7 chromosomes [23], dicotyledons consisting of 7 chromosomes, monocotyledons of 5 chromosomes and the recent common ancestral karyotypes of flowering plants of 15 chromosomes [13].

Here, by performing comparative genomics analysis with gene colinearity within a genome and between genomes with grape as a reference[24, 25], we inferred the evolutionary trajectories of coffee chromosomes, and in addition, those of grape chromosomes.

Methods

Plant genome data sets

The whole genome sequence of grape (2n=38) was downloaded from a public database Phytozome version12 (https://phytozome.jgi.doe.gov/pz/portal.html). The whole genome sequence of coffee (2n=22) was downloaded from the coffee genome database (http://coffee-genome.org/).

Inferring collinear homologs

Therefore, in order to analyze gene collinearity, we first used BLASTP [26] to analyze homologous sequences within a genome and between genomes, and then characterized the homoeology relationship between grape and coffee chromosomes. The is E-value < 1 E-10 and the output file format is TABULAR format (outfmt-6). Then, homologous fragments between genomes were inferred by MCScan [2], which are often used in genome collinearity analysis. Maximal gap length between genes in colinearity along a chromosome sequence was set to be 50 genes apart.

Dot-plot generation

According to the gene CDS sequence information of plants, BLASTN was used to make homologous alignment between genomes. The best, second best, and other matched DNA segments with E-value >1e-10 were displayed in different colors, to help distinguish orthology from paralogy, or layers of paralogy as a result of recursive whole-genome duplication (WGD) events[27].

Results

Inference of grape karyotype evolution

In order to understand the evolutionary trajectories of coffee chromosomes, we first reconstructed those of grape chromosomes. According to gene collinearity in the grape genome (Additional file 1: Figure S1), the ancestors of dicotyledons had 7 proto-chromosomes, tripled to 21 chromosomes after the ECH. In extant grape genome, there are 19 chromosomes. Here, by searching homologous genes within grape genome, we drew a homologous gene dotplot and by revealing gene colinearity, we inferred the tripled homoeologous regions due to the ECH.

The proto-chromosomes of dicotyledons were named G1, G2, G3, G4, G5, G6, and G7. During the ECH, G1 tripled to produce three extant homoeologous chromosomes named A1, B1 and C1. So were the other 6 proto-chromosomes. If ignoring intra-chromosome inversion and translocation, nearly to its full length, grape chromosome 1 (Vv1) can be viewed to be homoeologous to chromosome 14 (Vv14B) and chromosome 17 of grape (Vv17), respectively. Therefore, we can infer that Vv1, Vv14B and Vv17 originate from an ancestral chromosome, here named G5 (Fig 1a). Likewise, Vv2, Vv15 and Vv16 are homoeologous chromosomes, produced by G1 (Fig 1b). Like this, another two groups of homoeologous chromosomes are inferred to originate from two respective ancestral chromosomes, with Vv6, Vv8, Vv13 originated from G6 (Fig 1c) and Vv10, Vv12 and Vv19 originated from G7 (Fig 1d). However, Vv3 is homoeologous to posterior part of chromosome 4 (Vv4B), and posterior part of chromosome 7 (Vv7B) and Vv18. We inferred that Vv4B and Vv7B were originated from the fission of the same ancestral chromosome. Therefore, we inferred that Vv3, Vv18, Vv4B and Vv7B were originated from another ancestral chromosome, namely, G4 (Fig 1e). The anterior segment of Vv7 (Vv7A) is homoeologous to the complete Vv5 and anterior segment of Vv14 (Vv14A). We named their ancestors as G3. (Fig 1f). The anterior segment of Vv4 (Vv4A) is homologous to the complete Vv9 and Vv11. Therefore, Vv4A, Vv9 and Vv11 were originated from another ancestral chromosome, namely, G2 (Fig 1g). We infer that the ancestral chromosomes G2 and G4 might have fused by end-end joining (EEJ), then fused with G3 by end-end joining, and then divided, finally forming Vv4 and Vv7. Vv14A and Vv14B are derived from ancestral chromosomes G3 and G5, respectively, thus it can be inferred that another chromosome fusion occurred during the formation of Vv14. This chromosome fusion is also through end-end joining. After three chromosome fusions and one chromosome fission, eventually 19 extant chromosomes formed in grape (Fig 4).

Inference of coffee karyotype evolution

In order to clarify the karyotype evolution process of coffee chromosomes, we characterized homologous collinear fragments and chromosome rearrangements between coffee and grape chromosomes, and inferred the karyotype evolution process from 7 chromosomes of dicotyledon ancestors to 11 chromosomes of coffee. By searching homologous genes within or between grape and coffee genomes, we drew homologous gene dotplots, showing homologous regions between two genomes and in each genome.

Coffee chromosome 1 (Cc1) formed by the end-end joining of chromosome Vv6 and chromosome Vv7A, i.e., originating from the fusion of ancestral chromosomes (A6 and B3) (Fig 2a). Different regions of Cc4 are orthologous to the Vv9 and Vv17, suggesting that B2 and C5 fused by end-end joining (Fig 2b). Cc3 is orthlogous to grape chromosome 5, and therefore inferred to be directly originated from the ancestral chromosome (A3) (Fig 2c). Similarly, the homologous fragment of Cc10 can only be found on grape chromosome 18, so we infer that it was originated from the ancestor chromosome 4 (Fig 2d). In addition, the formation of Cc6 involved the merge of Vv11 (C2) and Vv8 (B6), with the former one inserted directly into the middle part of the latter. This type of chromosome fusion is called nested chromosome fusion (NCF) (Fig 2e). The nested fusion process can occur as follows: Vv11 crossed-over to form a circular chromosome near its two telomeres, and solution of the crossing-over produced a free-end chromosome and a satellite chromosome formed by two telomeres; then the free-end chromosome was then inserted into the centromeric regions of Vv8, while the satellite chromosome may be lost. Inversions might have occurred within the neo-chromosome to form the extant Cc6. Cc8 is homologous to Vv2 (A1) and the anterior segment of Vv4 (A2), which indicates that the fusion of A1 and A2 of ancestral chromosome (Fig 2f). The fusion may be an EEJ (Fig 5).

Comparatively, the formation of chromosomes 2, 5, 7, 9 and 11 in coffee is complex, involving the fusion and rearrangement of several ancestral chromosomes. We infer that the B7 (Vv12) and B4 (Vv4p+Vv7p) of the ancestor chromosome fused first by an EEJ, and then fused again with B5, forming a chromosome 7 (B4 + B5) and a chromosome B7 and B4 fused later in coffee. We infer that the B7 and B4 fused first, resulting in two intermediates (B4' and B7/B4) and one satellite chromosome, and the satellite chromosome lost. Then the B4'and B5 fused again, and the chromosome rearrangement resulted in the formation of Cc7 (Fig 3a). The intermediate B7/B4 continues to cross with chromosome A5, fusing into a new intermediates B7/B4/A5 and forming Cc11 (Fig 3b). Intermediate B7/B4/A5 then crossed with A7, fused into two new intermediates, and eventually fused with C7 and A4 to form Cc5 (Fig 3c) and Cc9 (Fig 3d), and A4/B7/A4'. On the other hand, C3 fuses with B1 and C6 to form the intermediate C3/B1/C6, and the two intermediates fused with C1 to form Cc2 (Fig 3e). To sum up, the chromosome of coffee has undergone 6 chromosome fusion and complex rearrangement after triploidization 7 chromosomes of the ancestor of dicotyledon to form chromosome 2 in coffee. The 11 chromosomes in the coffee genome have undergone 10 fusions, only 3 of which are nested chromosome fusion (NCF) (Fig 6). During the formation of coffee chromosomes, 10 satellite chromosomes might have formed and then were all lost, and reduced the chromosome number from 21 to 11 in it genome. Besides, Vv5 (A3), Vv7A (B3), Vv14A (C3), Vv9 (B2), Vv11 (C2), Vv17 (C5), Vv18 (C4), Vv19 (C7), the seven homoeologous chromosomes

tripled by the ancestor chromosomes of dicotyledons remained intact in the coffee chromosomes, with almost no structural changes. (Fig 5 and 6).

Discussion

Through analyzing gene collinearity, we can find homologous gene pairs produced by ECH events within coffee or grape genome and between genomes. The chromosomes of grape and coffee in dicotyledon were compared with those of seven ancestors. It can be found that the collinear genes of ancestor chromosomes are retained in grape chromosomes. It can also be seen that the ancestor genes of dicotyledon on 11 chromosomes of coffee are preserved. These two representations help to identify homologous regions between genomes and show evolutionary redistribution (Fig 7).

Taking the dicotyledon grape as a reference for studying karyotype evolution, we want to know whether it mediates the karyotype evolution process from 7 chromosomes of dicotyledon ancestor to 11 chromosomes of coffee. Actually, we found that the two lineages evolved their chromosomes in totally independent manner. All fusions in coffee are specific to its own lineage, but were not shared with grape.

By deducing the evolution process of existing chromosome karyotypes in grape and coffee, we found that all the chromosome fusions formed in grape were EEJ, and 7 (70.0%) chromosome fusion forms in coffee were EEJ, while only 30.0% of changes were nested chromosome fusion. In fact, all chromosome fusions to form the Arabidopsis thaliana karyotype from that of A. lyrata are EEJ type. Therefore, we inferred the end-end joining chromosome fusion may be the main mode of chromosome fusion in dicotyledon. This is contrastively different from the findings in grasses. In the study of the chromosome karyotypes evolution process of grasses, we found that most chromosome fusions are NCF [27]. Specifically, in the formation of extant sorghum, foxtail millet, Brachypodium chromosomes involved only NCF; while for maize and wheat chromosomes, most fusions are NCF[9].

The karyotype evolution of coffee and grape was well explained by telomere-centric model[27]. During the process of chromosome fusions, satellite chromosomes may be produced; if the not counting them or with them being lost, chromosome numbers reduce. During the formation of extant grape (n = 19) and coffee (n = 11) chromosomes, originated from the 21 proto-chromosomes after the ECH, we inferred that there have been 2 and 10 satellite chromosomes formed, and the lost of them resulted in chromosome number reduction.

Conclusions:

Grapes are used as intermediate links between different major dicotyledons and a model plant. We take it as a reference and want to know the karyotype evolution process from dicotyledon ancestors to coffee. Notably, we found that the major fusion mode of chromosomes in coffee is end-end joining, which is well explained by telomere-centric model, shared by grape and possibly by many other eudicots. This is contrastively different from the observation of monocot plants like grasses, in which nested chromosome

fusions often occurred. The present work will help to understand the structural and functional innovations of plant chromosomes.

Abbreviations

WGD: whole-genome duplication; ECH: core-eudicot-common hexaploidization; NCF: nested chromosomal fusion; EEJ: end–end joining

Declarations

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Availability of data and materials:

All data generated or analyzed during this study were included in this published article and the Additional files.

Authors' contributions:

The study was conceived by XW and JW. JL, FM, JY, YZ, CL, ZZ, HG, YX, XL and YH contributed to data collection and bioinformatics analysis. XW and JL participated in preparing and writing the manuscript. All authors contributed to revising the manuscript. All authors had read and approved the final manuscript.

Ethics approval and consent to participate:

Not applicable

Consent for publication:

Not applicable

Competing interests:

The authors declare that they have no competing interests.

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Additional File Legend

Additional file 1: Fig S1. Dotplot between grape and coffee. *Vitis vinifera* and *Coffea canephora* chromosomes are respectively, aligned horizontally and vertically. Red dots show homologous grape genes best matching coffee genes, and blue dots show other matches.

Figures

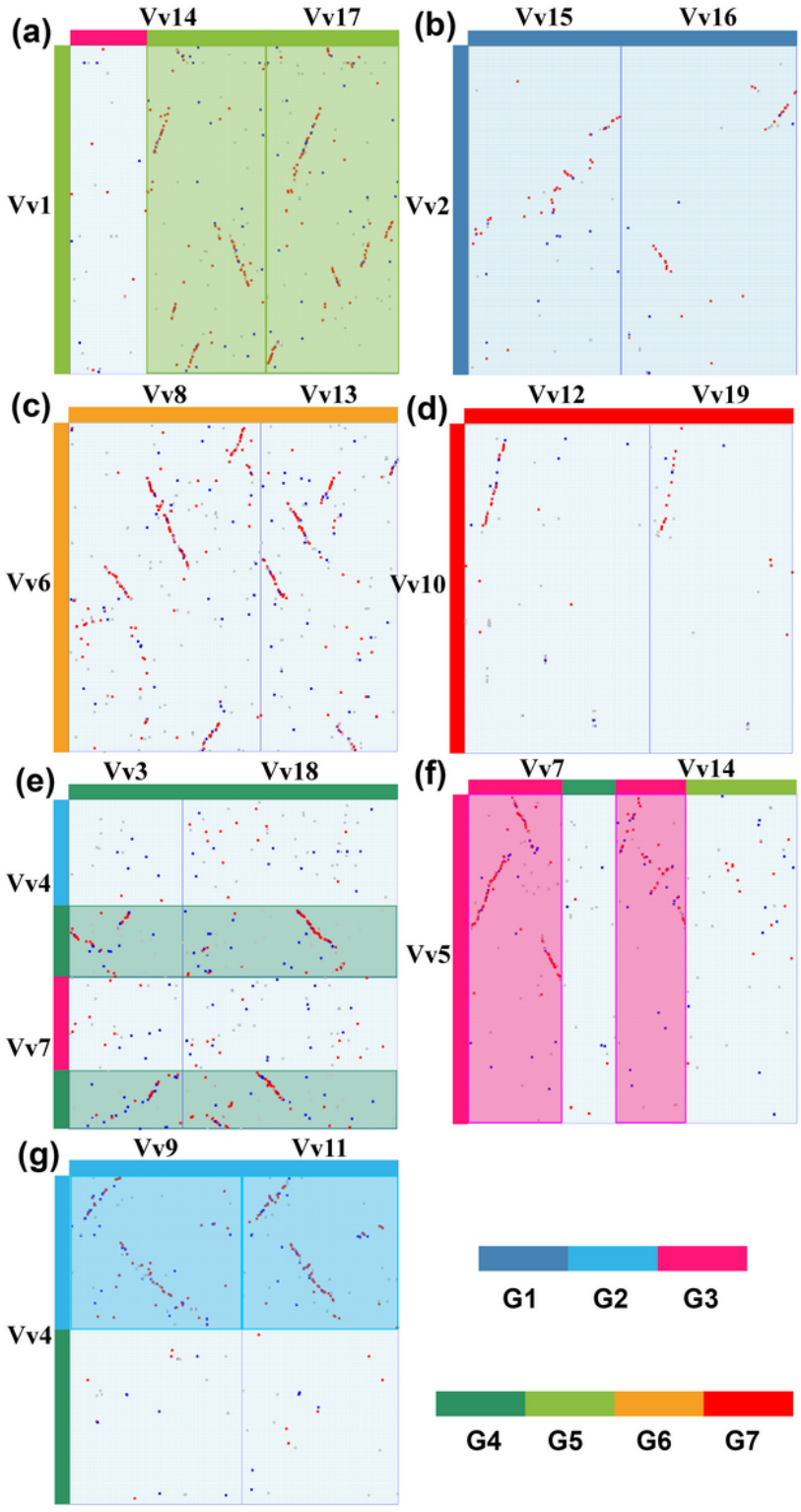

Figure 1

Chromosome fusions during the evolution of grape. Chromosomes, shown as rectangular blocks, are arranged horizontally and vertically to the dotplot. According to the color matching scheme of seven ancestral chromosomes G1-G7 in dicotyledons, different regions of grape chromosomes were colored separately. Homologous blocks can be classified as best, resulting from chromosomal orthology, and second best, resulting from paralogy from ancestral polyploidy. Vv, Vitis vinifera. a Vv1 (A5), Vv14B (B5),

Vv17 (C5) from the same ancestor G5 chromosome; b Vv2 (A1), Vv15 (B1), Vv16 (C1) from the same ancestor G1 chromosome; c Vv6 (A6), Vv8 (B6), Vv13 (C6) from the same ancestor G6 chromosome; d Vv10 (A7), Vv12 (B7), Vv19 (C7) from the same ancestor G7 chromosome; e Vv3 (A4), Vv4B+Vv7B (B4), Vv18 (C4) from the same ancestor G4 chromosome; f Vv5 (A3), Vv7A (B3), Vv14A (C3) from the same ancestor G3 chromosome; g Vv4A (A2), Vv9 (B2), Vv19 (C2) from the same ancestor G2 chromosome.

Figure 2

Chromosome fusions during the evolution of coffee. Chromosomes, shown as rectangular blocks, are arranged horizontally and vertically to the dotplot. According to the color matching scheme of seven ancestral chromosomes G1-G7 in dicotyledons, different regions of coffee chromosomes were colored separately. Homologous blocks can be classified as best, resulting from chromosomal orthology, and second best, resulting from paralogy from ancestral polyploidy. Vv, Vitis vinifera; Cc, Coffea canephora. a Formation of chromosome Cc1; b Formation of chromosome Cc4; c Formation of chromosome Cc3; d Formation of chromosome Cc10; e Formation of chromosome Cc6; f Formation of chromosome Cc8.

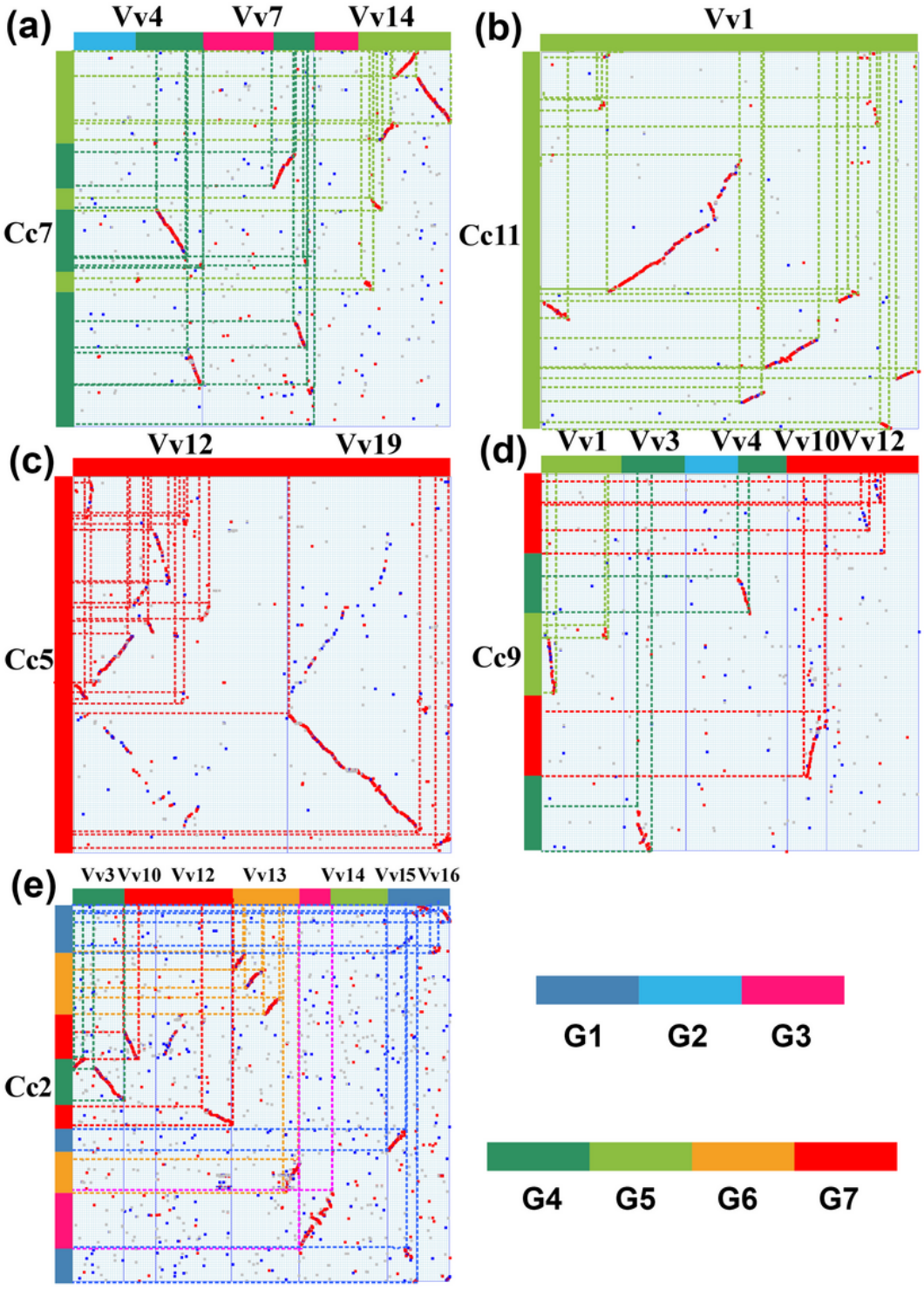

Figure 3

Chromosome fusions during the evolution of coffee. Chromosomes, shown as rectangular blocks, are arranged horizontally and vertically to the dotplot. According to the color matching scheme of seven ancestral chromosomes G1-G7 in dicotyledons, different regions of coffee chromosomes were colored separately. Homologous blocks can be classified as best, resulting from chromosomal orthology, and second best, resulting from paralogy from ancestral polyploidy. Vv, Vitis vinifera; Cc, Coffea canephora. a

Formation of chromosome Cc7; b Formation of chromosome Cc11; c Formation of chromosome Cc5; d Formation of chromosome Cc9; e Formation of chromosome Cc2.

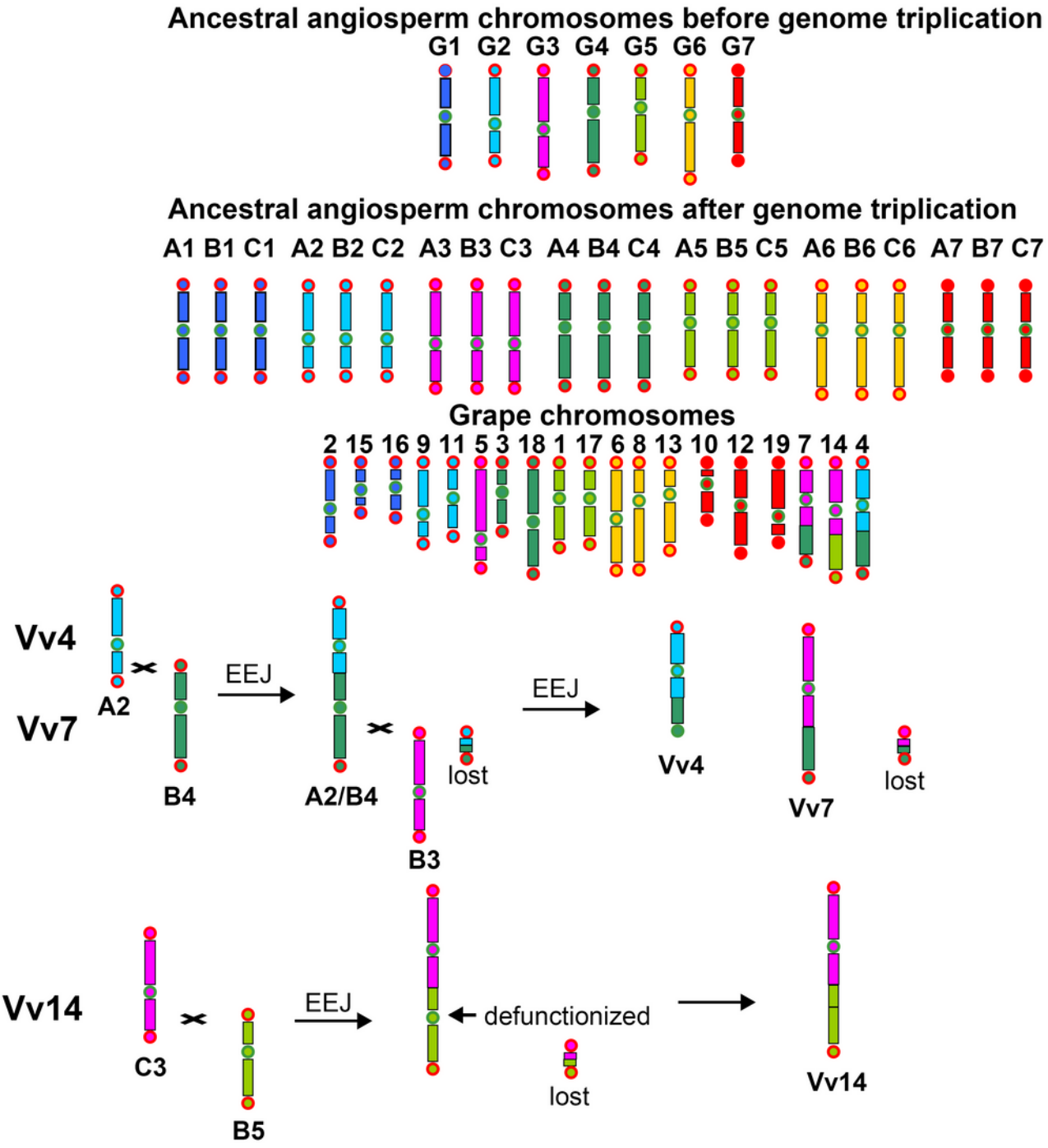

Figure 4

The evolution process of grape (Vv) chromosomes. The picture shows the karyotypic evolution of the grape chromosome with the ancestor chromosome. Chromosomes with almost the same structure as ancestral chromosomes are not displayed.

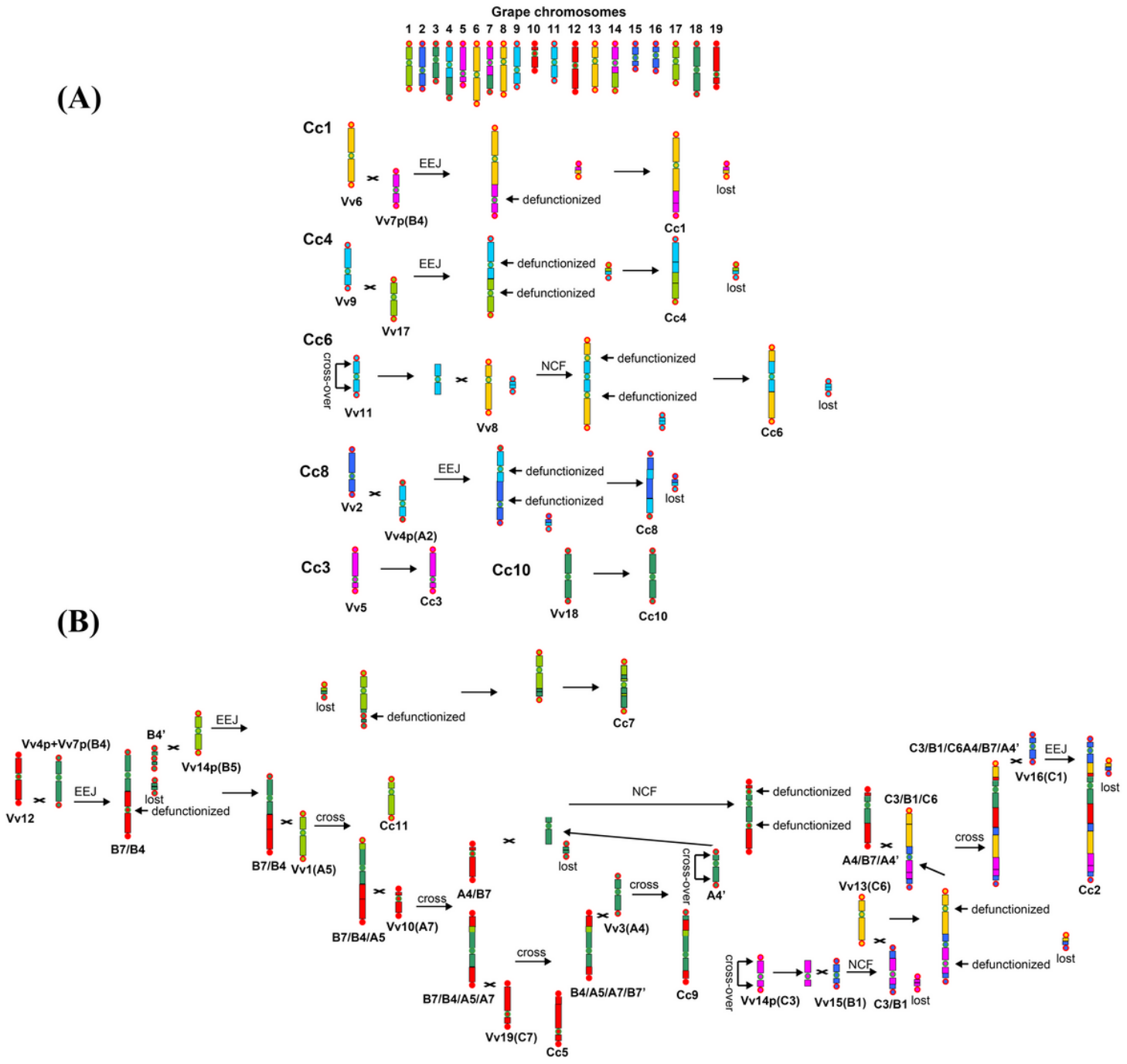

Figure 5

The evolution process of part of coffee (Cc) chromosomes. The karyotype evolution of chromosome 1,3,4,6,8,10 in coffee is shown in the picture.

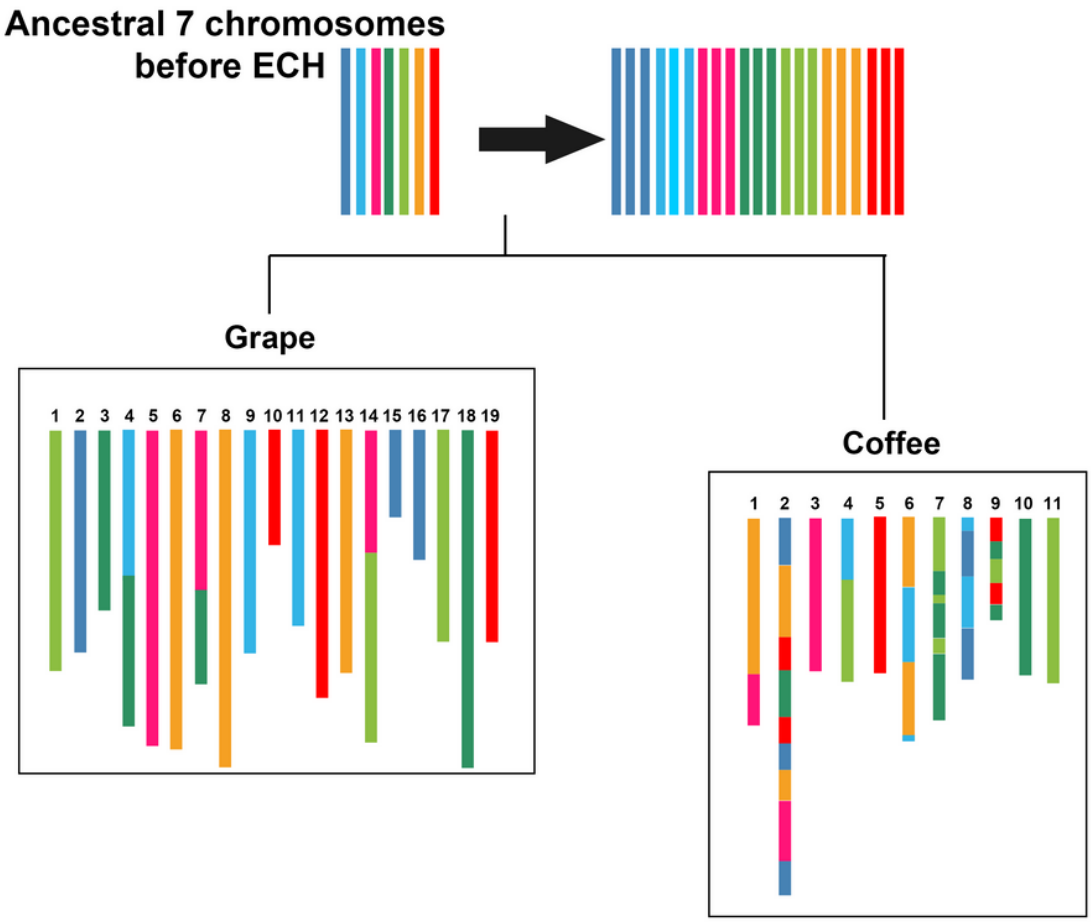

Figure 6

The evolution process of part of coffee (Cc) chromosomes. The karyotype evolution of chromosome 2,5,7,9,11 in coffee is shown in the picture.

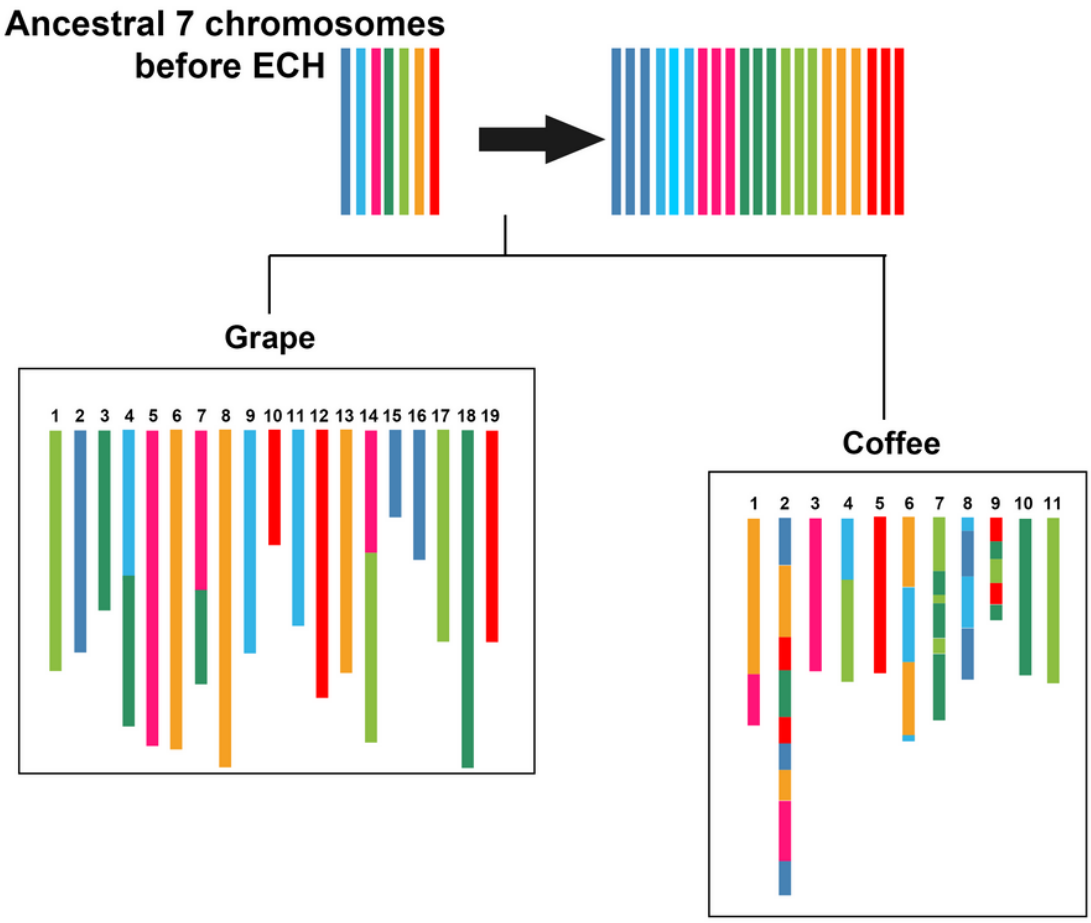

Figure 7

Schematic representation of homologous regions in grape and coffee genomess with ancestral genome. Seven ancestral chromosomes are used as references, and each color block in the existing genome corresponds to a homologous region in the reference genome.

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- FigureS1.png