

Supplementary File S2

Background information on recent dated trees for the Fagales

DATA BASIS

When comparing Fagaceae fossils to published dating estimates for Fagales one has to keep in mind that there are substantial issues with the data used. The commonly used plastid gene regions such as *trnK/matK*, *rbcL*, *atpB-rbcL*, *trnL/trnLF* (e.g. Li et al. 2004; Sauquet et al. 2012; Xiang et al. 2014; Xing et al. 2014; Larson-Johnson 2016) are hardly discriminative towards the leaves of the Fagales tree. To compensate for this insufficiency, the studies of Sauquet et al. (2012) and Xing et al. (2014) include data from the ITS region¹. The ITS is a mostly non-coding, typically divergent nuclear region that is part of the 35S rDNA – the cistron that encodes for the 35S pre-RNA and is organised as tandem-repeats in the terminal part of one, or several in case of studied Fagaceae, chromosomes (e.g. Volkov et al. 2007; Ribeiro et al. 2011). In the case of Fagaceae, the concatenation of ITS with plastid gene regions as done by Sauquet et al. (2012) and Xing et al. (2014) is highly problematic for two reasons: First, the signal in the nuclear gene regions, ITS but also the *Crabs Claw (CRC)* gene (Oh & Manos 2008) or 2nd intron of the *LEAFY* gene (Renner et al. 2016) is often in conflict with the signal from the included plastid markers (see also Larson-Johnson 2016, supplement, fig. S1) that are much less divergent (and can be close to zero between genera for commonly included plastid gene regions; see e.g. Simeone et al. 2016b). Forcing incongruent data, data preferring differing topologies, on the same tree invites topological artefacts (wrong branches) and inflates branch lengths (incompatible sequence patterns), hence, can distort dating estimates. Second, the substantial intra- and interspecific variation in the Fagaceae, together with *Nothofagus* (s.str.) the only Fagales lineage that has been relatively well studied using more than a single specimen per species (Manos et al. 2001; Mayol & Rosselló 2001; Muir et al. 2001; Denk et al. 2002; Cavender-Bares et al. 2004; Denk et al. 2005; Grimm et al. 2007; Denk & Grimm 2010), cannot be captured by placeholder sequences. Neither Sauquet et al. nor Xing et al. clarify how ITS placeholder accessions were selected for the concatenated matrix, which is problematic in the latter study as it aimed at a species-level sample. Because of intensive research in the past, gene banks include > 1000 ITS accessions for oaks (600+ alone from Denk & Grimm 2010) and > 150 ITS accessions for the c. 9 species of beech trees (Denk et al. 2002; Denk et al. 2005), the latter represented in the Xing et al. data set by

¹ Xing et al. included *Crabs Claw [CRC]* data, but forgot to note/include the accession numbers in their supplementary material.

several redundant, artificial taxa (*F. orientalis*, *F. sylvatica* subsp. *orientalis*, *F. sylvatica*, *F. taurica* etc.)

Because of the known issues with including ITS data in concatenated data sets comprising mainly plastid data, Grimm & Renner (2013) opted against using ITS in their re-dating of the Betulaceae. Another issue with ITS data for all-Fagales trees is that the non-coding parts, the internal transcribed spacers ITS1 and ITS2, are typically too divergent to be properly aligned between different families and sometimes within families. The latter is the case for *Fagus* when compared to all other Fagaceae. Hence, it was not included in the Fagaceae ITS tree by Denk & Grimm (2010), nor were any other Fagaceae included in the recent dating of *Fagus* that relied on ITS data and data from the 2nd intron of the nuclear *LEAFY* gene (Renner et al. 2016).

Possibly to avoid conflicting signal and accordingly (very) low branch support values, the dated trees by Xiang et al. (2014; species sample) and Larson-Johnson (2016; one placeholder per genus, some genera missing) rely exclusively on plastid data. This is also suboptimal in the case of a family that is well-known for its disparity between plastid signatures and taxonomy, systematics, and nuclear-based phylogenies; compare e.g. Manos et al. (1999); Li et al. (2004) vs Manos et al. (2001); Forest et al. (2005); Oh & Manos (2008); see also Manos et al. (2008); Acosta & Premoli (2010); Premoli et al. (2012); Simeone et al. (2016a) for further comparisons. Aware of the taxonomic decoupling of plastid signatures in oaks (and related Fagaceae), Hubert et al. (2014) based their chronogram for oaks exclusively on nuclear data, the latter producing molecular trees that are in good agreement with systematic concepts and conserved morphological traits (Manos et al. 2001; Denk & Grimm 2009a, 2010). Hubert et al. also made use of clade-consensus sequences as an experimental workaround to compensate for missing data (see supplementary information to Sauquet et al. 2012; Xing et al. 2014 for large data gaps in the used matrices) and to deal with the substantial intra-individual ITS variation.

Minor problems lie in the data harvesting strategy. All studies rely on data harvested from gene banks, but the authors overlooked labelling issues in the NCBI taxonomy tree. No information is given how the data were filtered for mislabelled accessions. In one case (*Engelhardia*), Sauquet et al. combined data from two different genera overlooking that junior synonyms of *Alfaropsis roxburghiana* are still recorded in gene bank under their old genus name (*Engelhardia*). The studies by Xiang et al. (2014) and Xing et al. (2014) took over the minimum age constraints from the earlier study by Sauquet et al. (2012), but use a species-

level data set rather than one placeholder per (selected) genus. Although this strategy is generally appreciable, particular with respect to our study (since we are interested in dating estimates for the Fagaceae subtree only), it can be error-prone. Both studies appear to have just used the taxonomy information associated with the NCBI GenBank flatfiles when harvesting the data for their matrices. NCBI GenBank explicitly gives no warranty for the information in the NCBI taxonomy tree, which can include errors and redundancies as in the case of Fagales. As consequence, they include several redundant, partly artificial taxa. *Fagus*, a genus with today c. 9 species, is represented in Xing et al.'s tree by 18 taxa, which partly refer to exactly the same biological entity but have been placed in different subtrees (possibly because of data overlap and intra-individual variability issues). Furthermore, neither Xing et al. nor Xiang et al. provide information how sequences were chosen in those cases where more than a single accession has been available for a given taxon in the NCBI taxonomy tree. For instance, gene banks can include dozens of plastid and ITS sequences per oak species, including such that are divergent from each other (cf. Simeone et al. 2016a). Apparently neither Xiang et al. nor Xing et al. tested for species coherence prior to data harvesting, otherwise they would have noticed the discrepancy between labels and sequences in the case of plastid data of Fagaceae.

In the placeholder studies that relied on one accession per included genus and gene region, some genera were generally excluded (Sauquet et al. 2012) or from some analyses (Larson-Johnson 2016). Selection of placeholders can be critical but is not detailed in either study. One observation is that Sauquet et al. preferred ≥ 15 year old data of partly problematic quality over newer data (G. Grimm, pers. obs., 2013) Particularly in Fagaceae, but also other Fagales, choosing a placeholder for a genus can be problematic. Sauquet et al. and Larson-Johnson include *Quercus rubra* (a North American red-oak) accessions as sole placeholder for *Quercus*; plastid signatures of North American oaks – in contrast to their Eurasian counterparts – are similar to those of the two North American monotypic Fagaceae *Chrysolepis* and *Notholithocarpus*; but only the latter can be considered a close relative of oaks (Manos et al. 2008; Oh & Manos 2008; Denk & Grimm 2010; Hubert et al. 2014; Simeone et al. 2016a). The ITS/CRC sequences of *Chrysolepis* are markedly different and associate the genus with the tropical-subtropical, mainly Malesian genus *Lithocarpus* (see also Fig. S2-1), the most distant living relative of oaks (Eurasian and North American) among the core Fagaceae (Castanoideae; Oh & Manos 2008; Denk & Grimm 2010).

Of the four studies, only Sauquet et al. (2012) provide full documentation of their used data. About a third of the characters in the original concatenated matrix (WG32MS) are either gaps

or missing data; the matrix includes several taxon pairs with no or limited sequential overlap. In three of the six partitions, more than one third of the taxa are completely missing, and 56–71% of the focus group or ingroup (Nothofagaceae). The most underrepresented lineage is the New Guinean-New Caledonian genus *Trisyngyne* (formerly *Nothofagus* subgenus *Brassospora*), with 23 accessions covering a maximum of three out of the six partitions, the *rbcL* gene (complete), the *atpB-rbcL* spacer (three missing), and the ITS (five missing, only old data used, including a contaminant or mis-labelled sequence of one species). Of the other families of the Fagales, the Betulaceae are the most under-represented, four of the six currently accepted genera are missing. The dataset used by Xing et al. (2014), stored with the Dryad repository, is still (per August 2016) under embargo², and cannot be investigated at this point. The non-embargoed supplementary material reveals huge data gaps and asymmetry in data coverage (no information given for the second included nuclear region, *CRC*). For instance, the Casuarinaceae are not represented by ITS data at all, the data which provides most of the intra-family divergence in other clades of the Fagales in that study. Xiang et al. (2014) and Larson-Johnson (2016) provide no links to their data sets.

METHODOLOGICAL SHORTCOMINGS

Two of the calibrations systems applied by Sauquet et al. (2012) are flawed for estimating divergences ages in Fagales, hence, the estimates for Fagaceae discussed here. The “safe” ingroup constraints are too young. The roots of all former subgenera, now genera (Heenan & Smissen 2013), of the Nothofagaceae can be traced back to the Paleogene or even late Cretaceous using the pollen record of the family (e.g. Dettmann 1994; Hill 2001). Although intergeneric plastome divergence in Nothofagaceae is comparable to that in other Fagales families (Heenan & Smissen 2013; Simeone et al. 2016b), and the same applies to ITS (compare data provided by Manos 1997 with that of other Fagales families), the overall level of divergence is much lower than the found within its (equally old) sister clade, which includes all remaining Fagales. As consequence, the relatively young, “safe” ingroup constraints must give much to young estimates for the rest of the Fagales trees (Sauquet et al. 2012; see also File S3 in this supplement). The “vicariance” calibration system implemented by Sauquet et al. is purely hypothetical. The according vicariance hypothesis for the unfolding of Nothofagaceae has long been rejected (Svenson et al. 2001; Knapp et al. 2005). Minimum ages of 55 Ma for divergences between Australia/New Zealand (*Fuscospora*, *Lophozonia*)

² Authors and journals can agree on not releasing the data upon publication; although this practise is not recommended by the Dryad Repository.

and New Caledonia/New Guinea (*Trisyngyne*) stand in stark contrast with the divergence patterns in these genera. Sequences of according species pairs show minimal differences (0–5 mutations per region in species of the same genus). Thus, only the estimates obtained with “safe” outgroup constraints or all constraints should be considered for further discussions.

Xing et al. (2014) used, among other constraints, three Fagaceae fossils to inform node heights within the Fagaceae subtree, essentially following the earlier study of Sauquet et al. (2012). The different samples (species-level in Xing et al., genus-level for outgroup, i.e. all non-Nothofagaceae in Sauquet et al.) trigger a multitude of topological differences towards the leaves of the preferred trees in both studies (intra-family relationships; see Fig. S2-1 for Fagaceae). For unknown reasons, Xing et al. linked some fossils to the nodes which they considered to correspond to the constrained nodes in Sauquet et al. rather than to their methodologically appropriate positions. In the case of Fagaceae, this is unproblematic for two of the three used constraints. In the case of the unnamed *Castanea* fossil (fossil F9 in Sauquet et al. 2012, appendix 2), which should be linked to the stem node of *Castanea* (i.e. the MRCA of *Castanea* and *Castanopsis* according Xing et al.’s tree; see argumentation in Sauquet et al., appendix 2), the fossil was instead used as minimum age prior to constrain the MRCA of all “quercoids”, i.e. MRCA of all Castanoideae and *Quercus*; i.e. four nodes deeper in the tree. In contrast, Xiang et al. (2014) used another of Sauquet et al.’s fossils (F10; linked to the stem of *Castanopsis*, thus equivalent to the unnamed *Castanea*) to correctly constrain the stem age of the MRCA of *Castanea* and *Castanopsis* to ≥ 43.8 Ma. The same fossil was also used by Sauquet et al. to constrain the stem age of *Castanea*, probably under the implicit assumption that *Castanea* and *Castanopsis*, the latter not included in Sauquet et al.’s study, are sister genera. Xiang et al. opted, however, against including *Castanopsoidea* and *Trigonobalanoidea* as additional constraints in contrast to Sauquet et al. and Xing et al.

A limitation of traditional node dating is that it can only provide minimum estimates for divergences: minimum ages for the ‘most recent common ancestor’ (MRCA) of a group of modern taxa. Such a set-up is prone to underestimate divergence ages (see Grimm et al. 2015 for a recent case study comparing node dating estimates with those from fossilised-birth-death dating). For example, the oldest known beech so far has been *Fagus langevinii* (c. 50 Ma; Manchester & Dillhoff 2004). In traditional node dating, this fossil can be used a prior to inform the minimum age of the MRCA of *Fagus* and its sister clade (remaining Fagaceae), i.e. the MRCA of all (extant) Fagaceae (Sauquet et al. 2012; Xiang et al. 2014; Xing et al. 2014). Likely an underestimation with respect to the morphology of *Fagus langevinii* and the genetic divergence between *Fagus* and other Fagaceae. *Fagus langevinii* is a modern-type

Fagus, but lacks clear affinity to one of the extant sublineages (Denk et al. 2005; Denk & Grimm 2009b), hence cannot be used to constrain the MRCA of extant *Fagus*. The substantial genetic distance between *Fagus* and the other Fagaceae in all gene regions sequenced so far is comparable to that e.g. between Betulaceae and Juglandaceae (main-text Fig. 1; Simeone et al. 2016b). Fusing both lines of evidence, *F. langevinii* is a stem fossil with respect to contemporary *Fagus*, but probably much closer to the MRCA (latest common ancestor) of all extant *Fagus* than the first members of the Fagoideae/*Fagus* lineage (Denk & Grimm 2009b; see also Renner et al. 2016; main-text Fig. 4). In case of the MRCA of Fagaceae, hence, the *Fagus* root age, the node dating estimates are still relatively old, because only slightly younger fossils are used to constrain minimum age deep within the core Fagaceae tree, i.e. constrain nodes much higher up in the Fagales tree to a minimum age of c. 40 Ma (Fig. S2-1). Furthermore the next deeper nodes (MRCA of Fagaceae and core Fagales; MRCA of all Fagales) were constrained to be at least of Cretaceous age (≥ 83.5 Ma; see main-text Fig. 1 for the effective genetic distance between these nodes).

In contrast to node dating, total evidence dating (Ronquist et al. 2012) makes explicit use of the age of a fossil and its putative phylogenetic position, optimised during the same run simultaneously with the node heights (i.e. the divergence age estimates). Its shortcoming is that the morphological partition that is used to place the fossil needs to have sufficient signal (Ronquist et al. 2012), if not, fossils are more or less randomly placed, often outside the modern clades. This can lead to too young or generally misleading dating estimates because the fossils inflict further topological ambiguity and/or unrepresentative branch-lengths (supplement to Grimm et al. 2015; Larson-Johnson 2016). Larson-Johnson subsequently excluded a portion of fossils from her analyses because of their ambiguous phylogenetic placement. For the included Fagaceae fossils, it can be noted that the best-supported position of *Trigonobalanoidea* (Larson-Johnson 2016, fig. S3) is not the one shown in the preferred tree (in-text fig. 1); a quick re-assessment of the signal in the morphological (and molecular) matrix is not feasible as no NEXUS files are provided. Table S3 in the supplement to Larson-Johnson (2016) reveals a high proportion of missing data in the morphological partition with little overlap between groups: 19 of the 89 characters are entirely missing for Betulaceae/Nothofagaceae/ Fagaceae (extant and extinct), 25 for Juglandaceae (extant and extinct), 50 for Myricaceae and Casuarinaceae (extant), and 53 for unplaced, ancient Fagales. Proportion of missing data for the fossils is $> 50\%$. The study has further methodological drawbacks regarding the diversification and trait analyses (insufficient sampling, use of outdated/inappropriate methods, S. Renner, pers. comm., 2016), but also with respect to the

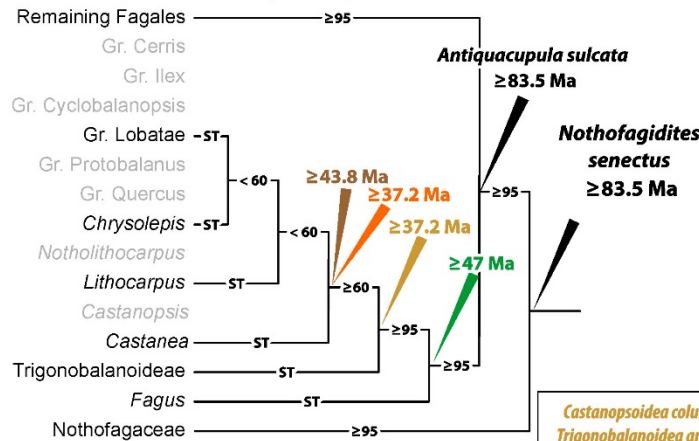
set-up of the dating analyses: (i) most nodes relate to ‘soft’ polytomies with low support (Larson-Johnson 2016, fig. S3) indicating a general lack of discriminating signal in the used matrix, the same problem applies to large portion of the Xiang et al. tree; (ii) the root was arbitrarily fixed to too young maximum age of 96.6 Ma (Larson-Johnson refers to “earliest records of fagalean fruit forms”; Xing et al. use, for example, a cut-off of 125 Ma); (iii) erroneous age priors for the node dating performed in addition to the total evidence dating. Regarding the Fagaceae subtree, the age of the MRCA of *Lithocarpus/Castanopsis* was constrained to (absolute, i.e. min-max) 44.1–43.5 Ma based on the age of *Castanopsis crepetii* (43.8 ± 0.3 Ma old fossil; Larson-Johnson 2016, tabs S7, S9) instead of informing a minimum (\geq) age of 43.8 Ma all other studies). According to Sauquet et al. (2012, appendix 2), this fossil can be linked to the stem of *Castanopsis*, hence, was linked by Larson-Johnson to one node deeper than should be, repeating the error of Xing et al. (2014). A second Fagaceae prior constrained a middle Eocene age of 48.6–37.2 Ma (correct: 47.8–37.8; Cohen et al. 2013, updated) for the split between *Fagus*/extinct *Pseudofagus* based on *Fagus langevinii* and ignoring the actual early Eocene age of the McAbee flora from which *F. langevinii* was described (c. 50 Ma; Denk & Dillhoff 2005; Dillhoff et al. 2005). At least two lineages of *Fagus* are established by the middle Eocene around the Arctic (Denk & Grimm 2009b; Renner et al. 2016). If *Pseudofagus* is a sister lineage, the divergence must have happened in the early Eocene or earlier. The selective, partly erroneous use of node age constraints (typically constraining maximum ages instead informing minimum ages) ensured the coherence of both approaches (S. Renner, pers. comm., 2016). Together with odd intra-family relationships (Fig. S2-1; see also Larson-Johnson 2016, figs S1–S3, in-text fig. 1) this lead to problematic divergence estimates.

TOPOLOGICAL DIFFERENCE BETWEEN DATED TREES

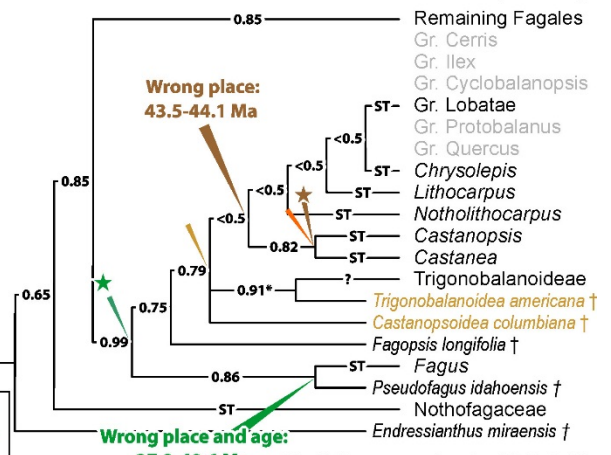
Relying on different sets of data, the four all-Fagales studies used here for discussion of our fossils (Sauquet et al. 2012; Xiang et al. 2014; Xing et al. 2014; Larson-Johnson 2016) differ not only in their age estimates for the Fagaceae subtree but more so in their optimised topologies (Fig. S2-1). Whereas the interfamily relationships are quite stable and follow largely the original phylogenetic study of Li et al. (2004), intra-family and intrageneric (as far as analysed) can be substantially different in all four studies and are typically in conflict with in-depth studies focussing on parts of the Fagales tree (e.g. Forest et al. 2005: Betulaceae; Oh & Manos 2008; Hubert et al. 2014: oaks). As consequence, the dated node representing the most recent common ancestor of one or more Fagaceae lineages as listed in is not necessarily

referring to the same clade(s). However, none of the recent all-Fagales studies discuss the topological instability of their reconstructions.

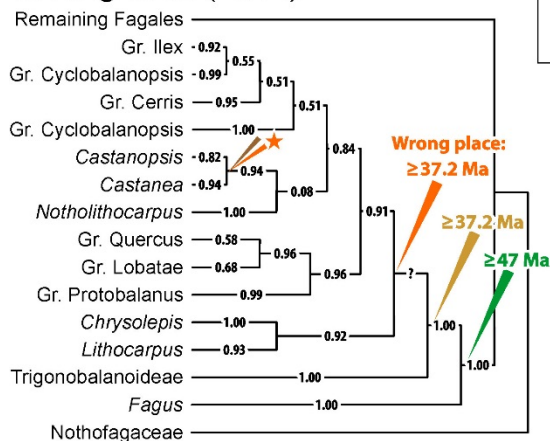
A. Sauquet et al. (2012)



B. Larson-Johnson (2016)



C. Xing et al. (2014)



D. Xiang et al. (2014)

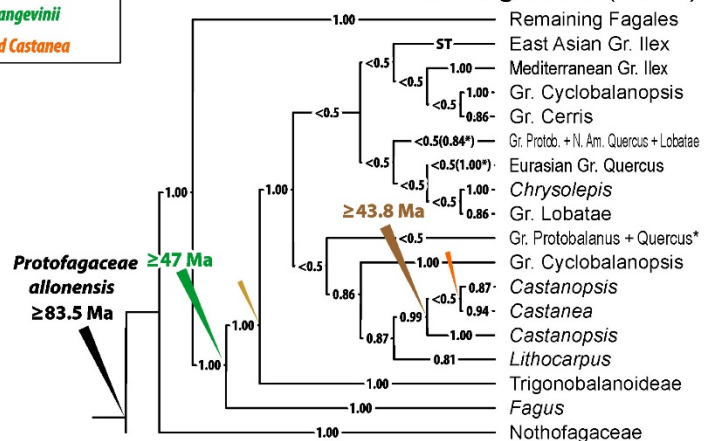


Figure S2-1. Relationships within Fagaceae seen in recent dated trees on Fagales. Numbers at branches refer to non-parametric bootstrap support under maximum likelihood (A) or Bayesian posterior probabilities (B–D). Used age priors for node dating are indicated; arrows without labels refer either to the correct (stars) position for used age priors or the potential position of age priors used in the other three studies. Note that the same age prior can constrain deep and flat nodes within the Fagaceae subtree, depending on the inferred Fagaceae phylogeny. All shown phylogenies contrast in parts more detailed studies with focus on the Fagaceae or their largest genus, *Quercus* (Manos et al. 2001; Manos et al. 2008; Oh & Manos 2008; Denk & Grimm 2010; Hipp et al. 2014; Hubert et al. 2014; Hipp et al. 2015). ST = singleton, lineage represented by a single representative; * The dated tree (Xiang et al. 2014, fig. S3) differs from the tree with the overall highest support (Xiang et al. 2014, fig. S2) by producing a clade comprising *Q. tomentella* (a North American golden-cup oak, *Quercus* Group Protobalanus) and *Q. polycarpa* (= *Q. petraea* subsp. *iberica*; a western Eurasian member of Group *Quercus*). In Xing et al.'s majority rule consensus tree (Xiang et al. 2014, fig. S1), both species are included in their respective clades (mixed N. American clade comprising members of Groups Protobalanus, *Quercus* and Lobatae and the Eurasian Group *Quercus* clade)

Regarding the inferred Fagaceae relationships the following deficits of the dated trees are apparent.

(i) The Fagaceae subtrees in the node dating chronogram of Sauquet et al. (2012, fig. 1; four genera missing) and total-evidence chronogram of Larson-Johnson (2016, fig. 3), recognising *Castanea(-Castanopsis)* as sister to the remaining Castanoideae (including the tropical, mainly Malesian *Lithocarpus* and the two endemic, monotypic genera of western North America) and *Quercus* are simply wrong (cf. Manos et al. 2008; Denk & Grimm 2010) and a likely artefact due to the problematic placeholder/gene sampling strategy in these studies. Notably, the critical branches within the core Fagaceae (Castanoideae+Quercoideae) received low support (Fig. S2-1). The estimated Miocene *Quercus* root ages in Sauquet et al.'s and Larson-Johnson's chronograms, defined by the age of the MRCA of *Chrysolepis* and *Quercus*, are at best estimates for the final isolation of the North American *Quercus* plastome from that of coexisting Fagaceae or simply representing the split between western North American and eastern North American core Fagaceae plastomes and, hence, fundamentally biased. The oak lineage to which *Quercus rubra* belongs, *Quercus* Group Lobatae, is much older (Hubert et al. 2014), and was diverged from its sister clades (*Quercus* Group Protobalanus, Group Quercus) at least by the middle Miocene (early Miocene with respect to the new, here presented data).

The two studies aiming at species-level samples failed to resolve the oaks as an clade (see also Manos et al. 2008); the 'New World' (or high-latitude) clade of oaks is placed as sister to a clade including most/all Castanoideae and the 'Old World' oaks. In these chronograms, the MRCA of all oaks hence coincides with the MRCA of most (Xing et al. 2014) or all (Xiang et al. 2014) Castanoideae and oaks (black dot in Fig. S2-1), and accordingly high estimates are obtained (main-text Tab. 2; File S3). Xing et al., including nuclear data from the ITS region and *CRC* gene succeeded in placing *Chrysolepis* + *Lithocarpus* as sister to the remaining Castanoideae + *Quercus*. *Notholithocarpus* is separated from the 'New World' oaks but its position within the 'Old World' oak + Castanoideae clade is unresolved. Overall, Xing et al.'s topology matches best what would be expected from a matrix combining nuclear and plastid gene regions (Manos et al. 2008) and comes closest to the phylogenetic synopsis on relationships within the Fagaceae in general (main-text Fig. 2; Manos et al. 2008; Oh & Manos 2008; Denk & Grimm 2010; Hubert et al. 2014; Hipp et al. 2015). In contrast, Xiang et al., who did not include nuclear data and no data on *Notholithocarpus*, find a (Eurasian) Castanoideae clade (*Lithocarpus*, *Castanea* + *Castanopsis*), nested within *Quercus* (intrageneric relationships essentially unresolved; Fig. S2-1). The position of *Chrysolepis* is

unresolved. In the Xing et al. tree, again, the nuclear data ensures recognition of most intrageneric groups of *Quercus* (cf. Denk & Grimm 2010), except for Group Cyclobalanopsis, which is dissolved into two clades (possibly a missing data artefact). Further intra-*Quercus* relationships contrast those based on a recent analyses of six new + two known (ITS, *CRC*) nuclear gene regions (Hubert et al. 2014) and currently assembled phylogenomic data (Hipp et al. 2015). The latter studies recognise two main clades, the ‘New World’ fide Manos et al. (2001) or high-latitude clade (Groups Protobalanus, *Quercus*, Lobatae) and ‘Old World’ fide Manos et al. (2001) or mid-latitude clade (Groups Cyclobalanopsis, *Cerris*, *Ilex*). Within the New World clade of oaks, Group Lobatae is resolved as sister to Groups Protobalanus + *Quercus*; in the Old World, Group Cyclobalanopsis is sister to a clade comprising Groups *Ilex* and *Cerris*, the latter possibly being a more recent (Miocene) offspring of Group *Ilex* (Hubert et al. 2014; Simeone et al. 2016a). This molecular -phylogenetic framework is in near-perfect agreement with the fossil record of the group (e.g. Grímsson et al. 2015). The *Fagus* subtrees in both studies (Xiang et al. 2014; Xing et al. 2014) can be entirely disregarded (cf. Denk et al. 2005; Denk & Grimm 2009b; Renner et al. 2016).

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