



Noise does not equal bias in assessing the evolutionary history of the angiosperm flora of China: A response to Qian (2019)

Abstract

In response to our paper on the evolutionary history of the Chinese flora, Qian suggests that certain features of the divergence time estimation employed might have led to biased conclusions in Lu et al (2018). Here, we consider Qian's specific criticisms, explore the extent of uncertainty in the data and demonstrate that (i) no systematic bias toward dates that are too young or too old is detected in Lu et al.; (ii) constraint of the crown age of angiosperms does not bias the generic ages estimated by Lu et al.; and (iii) ages derived from the Chinese regional phylogeny do not bias the conclusions reported by Lu et al. All these analyses confirm that the conclusions reported previously are robust. We argue that, like many large-scale biodiversity analyses, sources of noise in divergence time estimation are to be expected, but these should not be confused with bias.

In response to our paper on the evolutionary history of the flora of China, Qian (2019) suggests that the molecular-based estimates of divergence times may have substantially biased our conclusions (Lu et al., 2018). Although Qian (2019) notes some issues in divergence time estimation that the community also has raised (e.g. discordance between molecular estimates and the fossil record; the influence of incomplete phylogeny on divergence time estimation), some of his statements are misleading, and there is no evidence supporting his statement that the conclusions in Lu et al. (2018) are biased. Here, we consider Qian's specific criticisms, explore the potential uncertainty in our data, reanalyse the data with different constraints and address Qian's concerns on three major aspects below.

1 | DISCREPANCY BETWEEN MOLECULAR DATING AND THE FOSSIL RECORD REMAINS A CHALLENGE THAT MERITS FURTHER EXPLORATION

Qian (2019) notes that ages for some angiosperm genera inferred by Lu et al. (2018) were younger than the fossil record indicates. Of the 61 genera in Qian's table S1 (2.3% of the 2,665 genera included in our analysis), in at least 37 cases, the incongruence may derive

from the use of different taxonomies or uncertainty in generic circumscription (Table S1). For instance, two to 17 genera have been recognized for Magnoliaceae, a family that Qian (2019) raises as a particular concern, based on different taxonomic systems (Figlar & Nooteboom, 2004; Frodin & Govaerts, 1996; Xia, Liu, & Nooteboom, 2008). In the *Flora of China* treatment followed by Lu et al. (2018), *Magnolia* contains 20 species (Xia et al., 2008), whereas, in contrast, the genus includes 128 species in Azuma, García-Franco, Rico-Gray, and Thien (2001), the source used by Qian. Furthermore, at least 32 of the 61 genera to which Qian refers are actually non-monophyletic (Table S1) and deserve further taxonomic revision. When updated generic circumscriptions are employed, the fossils previously attributed to those genera (fossils upon which Qian relied) are no longer appropriate for use. In addition, there might be many fossils that are misidentified or assigned incorrect ages in fossil databases, considering the difficulty in determination of fossil species based on fragmentary organs (Parham et al., 2012; Xing et al., 2016). Therefore, errors in geological age and/or phylogenetic assignment of fossils might be other sources that contribute to the discrepancy between molecular dating and the fossil record. But these issues are well known. In contrast to Qian, we used only carefully vetted fossils, as in other large-scale studies (e.g. Magallón, Gómez-Acevedo, Sánchez-Reyes, & Hernández-Hernández, 2015; Zanne et al., 2014).

Qian (2019) asserts that insufficient use of the fossil record for calibrating node ages in Lu et al. (2018) is responsible for the discrepancy between generic ages inferred by Lu et al. (2018) and those indicated by the fossil record. There is no standard, however, for how many fossils are sufficient for divergence time estimation. Lee and Ho (2016) indicate that 'incorporating as much calibrating information as possible can severely constrain the possible range of inferred timescales. On the other hand, using a smaller subset of temporal information allows the molecules more latitude to speak for themselves'. In particular, both biologists and palaeontologists have emphasized the importance of explicit justifications of the age and phylogenetic position of fossils used for calibration (Parham et al., 2012). Divergence times in Lu et al. (2018) are based on 138 well-vetted fossils or secondary calibrations (for discussion of limitations of secondary calibrations, see dos Reis et al. (2018)) that cover the major lineages of angiosperms and are widely accepted by the botanical community (see supplementary information in Lu et al., 2018). We herein stress that explicit justifications of age, proper assignment of phylogenetic position of fossils and critical



evaluation of conflict among calibrations are all crucial for molecular dating—and all of these factors were carefully considered in Lu et al. (2018).

2 | CONSTRAINT OF CROWN AGE OF ANGIOSPERMS DOES NOT BIAS THE GENERIC AGES ESTIMATED BY LU ET AL

Qian (2019) speculates that another source for the discrepancy is the relatively young age of the constraint used by Lu et al. (2018) for the crown age of the angiosperms. We suggest that Qian (2019) over-emphasizes molecular estimates and largely ignores palaeobotanical evidence. The origin and rapid diversification of the angiosperms has been referred to as an 'abominable mystery' by Darwin (1903), and this question has puzzled generations of palaeobotanists (Axelrod, 1952; Doyle, 1969; Friis, Crane, & Pedersen, 2011; Scott, Barghoorn, & Leopold, 1960).

Despite advances in molecular dating and increased effort in palaeobotanical investigations, the discordance between molecular and fossil evidence regarding the age of angiosperms remains controversial (Barba-Montoya, dos Reis, Schneider, Donoghue, & Yang, 2018; Beaulieu, O'Meara, Crane, & Donoghue, 2015; Coiro, Doyle, & Hilton, 2019; Doyle, 2012; Herendeen, Friis, Pedersen, & Crane, 2017; Magallón et al., 2015). Indeed, numerous molecular studies have estimated the crown age of angiosperms to the Jurassic or even Triassic (e.g. Bell, Soltis, & Soltis, 2010; Foster et al., 2017; Li, Yi, et al., 2019; Zeng et al., 2014). Nevertheless, the earliest unequivocal fossils of angiosperms indicate a rapid diversification and possible origin of angiosperms in the early Cretaceous (see Coiro et al., 2019; Herendeen et al., 2017).

Some pre-Cretaceous fossils have been reported; however, critical assessment of these reports demonstrates that these fossils either represent other plant groups or lack features needed to be confidently assigned to the angiosperms (Coiro et al., 2019; Herendeen et al., 2017; Sokoloff, Remizowa, El, Rudall, & Bateman, 2020). Lu et al. (2018) constrained the crown node of angiosperms with a minimum age of 136 million years ago (Ma) based on the earliest pollen fossils of the angiosperm crown group (Brenner, 1996; Hughes & McDougall, 1987; Hughes, McDougall, & Chapman, 1991) and a maximum age of 140 Ma following the molecular estimation of Magallón et al. (2015). This does not mean that we reject the possibility of a late Jurassic origin of crown-group angiosperms, but we echo previous studies that early angiosperms might have had low diversity and were geographically restricted (Coiro et al., 2019; Feild & Arens, 2007; Feild, Arens, Doyle, Dawson, & Donoghue, 2004). Furthermore, as noted below, this constraint on the age of the angiosperm crown group may not substantively affect our estimation of generic ages.

Qian (2019) suggests that if we constrained the crown age of angiosperms to be older, the ages of many genera would increase substantially, which may lead to a much higher proportion of angiosperm genera that originated before the Miocene. To test this hypothesis,

we constrained the crown age of angiosperms to 198.1 Ma (in Lu et al., 2018, the node connecting Nymphaeales to all remaining angiosperms sampled represents the node defining the crown group), based on a recent plastid phylogenomic estimation (Li, Yi, et al., 2019). Although ages for some nodes (2.04%, 239 of 11,726; variation >5 Ma) and some genera (6.30%, 168 of 2,665; variation >5 Ma) were inferred to be older in the new analysis (Figure S1), the newly estimated generic ages are significantly correlated ($r = 0.996$, $p < 0.001$; Figure S1b) with those in Lu et al. (2018). Furthermore, the pattern of mean divergence times (MDT, Figure 1a) is congruent with that we originally reported. Significantly, the new analysis supports the finding that approximately 36% of the angiosperm genera in China might have originated before the Miocene (Table 1), which further confirms our earlier conclusion that approximately two thirds of the angiosperm genera in China did not originate until the early Miocene. Independent analysis from published molecular phylogenetic and biogeographical studies also supports the result that most clades of the East Asian flora originated since the Miocene (Chen, Deng, Zhou, & Sun, 2018). We thus note that the age of the constraint used for the crown age of the angiosperms does not significantly affect the estimates of generic ages, perhaps because the earliest lineages of extant angiosperms (i.e. *Amborella*, Nymphaeales, and Austrobaileyales) are much less diverse than the remaining clades and our calibrations have thoroughly covered the major lineages of angiosperms.

3 | AGES DERIVED FROM THE CHINESE REGIONAL PHYLOGENY DO NOT BIAS THE CONCLUSIONS REPORTED BY LU ET AL

Qian (2019) also asserts that some ages are 'too old', given that they were derived from an incomplete phylogeny. Indeed, incomplete sampling may lead to under- (particularly when early-diverged taxa within a clade are missing) or over-estimation of ages (when close relatives of a clade are missing). This is a valid concern, particularly in a poorly sampled tree. However, our phylogeny of the Chinese flora samples overall angiosperm diversity relatively well, including ca. 22% (2,909/13,164) of the angiosperm genera of the world (Christenhusz & Byng, 2016), to negate large-scale under- or over-estimation of generic ages. Most importantly, significant correlation ($p < 0.001$) between the ages of 2,222 genera shared by the phylogeny of the Chinese flora (Lu et al., 2018) and a global phylogeny (Zanne et al., 2014) indicates no systematic bias toward dates that are too young or too old in our study (see Qian's figure S1). Furthermore, the phylogeny was constructed with a focus on angiosperms in China, which included 1,803 newly generated sequences for taxa not yet represented in public databases (Chen et al., 2016) and had a higher proportion of sampling for the Chinese native angiosperm genera (92%) than the available global trees (e.g. 69%, Zanne et al., 2014; 81%, Smith & Brown, 2018). It should be noted that Chinese genera in Lu et al. (2018) do not necessarily represent clades that originated in China. The stem age of a genus was used as

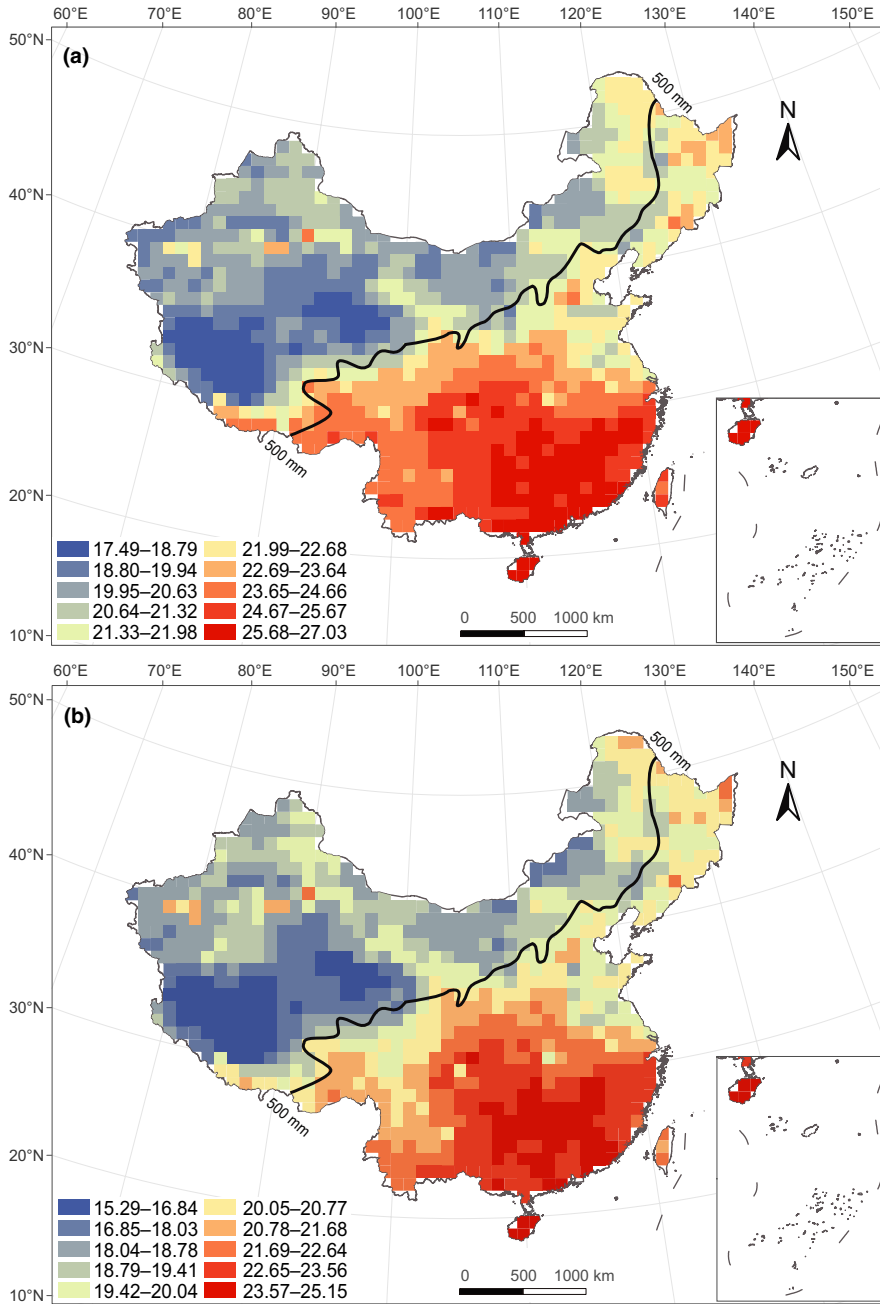


FIGURE 1 (a) Pattern of mean divergence time (MDT) when the crown age of angiosperms was constrained to the early Jurassic (i.e. 198.1 Ma) based on Li, Yi, et al. (2019). (b) MDT pattern when the 110 genera for which Qian (2019) expressed concern were excluded

an approximation of generic age to decrease the influence of missing taxa within a genus.

We agree with Qian that the age of a given genus tends to be estimated as older if close relatives of that genus are not sampled. However, the hypothetical case shown in Qian's figure 2 represents an extreme condition in our dataset in which a family has two or more genera in the world, but only one genus in China. Importantly, however, only a very small proportion of the genera (1.88%, 50 of 2,665 genera) in Lu et al. (2018) are potentially impacted by this problem (see our Figure S2 for more hypothetical cases). Hence, this potential problem raised by Qian, while of interest, is a non-issue for Lu et al. (2018). In addition, when the phylogeny includes two or three

genera in a family, the average divergence time of these genera in Lu et al. (2018) is much closer to that estimated by Smith and Brown (2018) for the global tree, despite different sampling strategies, calibration constraints and phylogeny construction methods between the two studies, suggesting that the results of Lu et al. (2018) are robust to sampling only plants distributed in China. We also test the robustness of our conclusions by excluding the 111 genera of particular concern to Qian (i.e. the 50 genera whose ages may have been over-estimated because of limited occurrence of confamilial genera in China and the 61 genera that we dated to be younger than indicated by the fossil record in Qian's table S1). The new analysis shows that approximately 66% of the angiosperm genera in China may have



TABLE 1 Number and percentage of angiosperm genera that diverged during geological timespans. Excluding noise: excluding the 110 genera for which Qian (2019) expressed concern. Early Jurassic constraint: constraining the crown age of angiosperms to 198.1 Ma following the divergence time estimates in Li, Yi, et al. (2019)

Geologic stratum	Lu et al. (2018), n (%)	Excluding noise, n (%)	Early Jurassic constraint, n (%)
Jurassic	0 (0%)	0 (0%)	7 (0%)
Cretaceous	141 (5%)	100 (4%)	164 (6%)
Palaeocene	83 (3%)	81 (3%)	72 (3%)
Eocene	315 (12%)	311 (12%)	341 (13%)
Oligocene	371 (14%)	371 (15%)	374 (14%)
Miocene	1,273 (48%)	1,239 (48%)	1,263 (47%)
Pliocene	290 (11%)	270 (11%)	261 (10%)
Pleistocene	192 (7%)	183 (7%)	183 (7%)
Total	2,665 (100%)	2,555 (100%)	2,665 (100%)

originated after the Miocene (Table 1), and the MDT pattern is consistent with that reported in Lu et al. (2018) (Figure 1b).

Qian (2019) claims that it is inappropriate to use ages derived from a regional phylogeny because of the impact on age estimation of gaps in the tree. Indeed, phylogenetic data for biodiversity analyses can be derived from either a purpose-built regional tree or a pruned synthetic tree (e.g. Phylomatic, Webb & Donoghue, 2005; the Open Tree of Life, Hinchliff et al., 2015). However, both approaches have limitations: taxon sampling in a purpose-built tree may still be limited and a major concern despite extensive global collecting efforts and broad international collaboration in material exchange, whereas a synthetic global tree may be comprehensive but poorly resolved given limitations in resolution due to the use of taxonomy to place many species. For papers published in the *Journal of Biogeography* from 2017 to 2019 (vols. 44–46) on subjects of biodiversity or biogeography, the proportion of taxon sampling for plant lineages with more than 500 species ranges from 3% to 37%; some studies aim to examine historical biogeography of major clades of a plant group (e.g. Luebert et al., 2017), while some focus on reconstructing the origin and diversification of species of a specific region (e.g. Veranso-Libalah, Kadereit, Stone, & Couvreur, 2018). To date, no study has explicitly examined the ages derived from a pruned synthetic global tree versus those from a purpose-built regional tree. However, case studies have demonstrated that mode of phylogenetic inference has little influence on phylodiversity metrics. In other words, equivalent results have been obtained from purpose-built and synthetic trees (Allen et al., 2019; Jantzen et al., 2019; Li, Trotta, et al., 2019). Nevertheless, the impact of limited sampling in a regional phylogeny on divergence times, using either a purpose-built or pruned tree, compared to a global phylogeny remains to be assessed directly. However, the close correlation of ages estimated in Lu et al. (2018) with those from Zanne et al. (2014) and Smith and Brown (2018), as noted above, suggests that ages inferred in a regional phylogeny may be reasonable estimates.

4 | CONCLUSION

All phylogenetic analyses include uncertainty. Large-scale biodiversity analyses are particularly prone to uncertainty resulting from noise

in both large datasets and analyses. Qian (2019) has indicated some of the issues that require consideration. However, while there is noise in our data, noise is not necessarily bias, and the results we reported originally are robust to noise in divergence time estimation. By reanalysing our data (Figure 1, Table 1) and reviewing related literature, we argue that it is inappropriate to attribute the incongruence between fossil and molecular ages to the use of an insufficient number of fossil calibrations or an inappropriate constraint of the crown age of the angiosperms. Discrepancies between molecular dates and the fossil record remain a challenge that merits extensive future study (Wilf & Escapa, 2015). We believe that close collaboration among biologists, palaeontologists and geochronologists, and improvement in dating methodologies will minimize the gap between ages inferred from the fossil record and those based on molecular dating. We also highlight that global collection and collaboration are required to facilitate a nearly complete global phylogeny of angiosperms, which can help verify the diversity patterns retrieved by regional phylogenies. However, we believe that regional phylogenies remain useful in advancing our knowledge of the diversity and diversification of lineages and biotas and are crucial for conservation (Allen et al., 2019; Kling, Mishler, Thornhill, Baldwin, & Ackerly, 2018).

KEYWORDS


cradle, crown age of angiosperms, divergence time, evolutionary history, flora of China, fossils, museum, phylogeny

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DATA AVAILABILITY STATEMENT

All data are available from Lu et al. (2018).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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