**On the estimation of species age from phylogenetic trees**

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**Abstract**

Estimating species age (the elapsed time since origination) can give an insight into how species longevity might influence eco-evolutionary dynamics. Traditionally, species ages have been measured in the fossil record; however, recently, researchers have estimated the ages of extant species from the branch lengths of time-calibrated phylogenies. This approach poses problems because phylogenetic trees typically do not contain information about speciation and extinction modes. When phylogenies do not include extinct lineages, the branch lengths of extant sister species are likely to appear longer than they truly are. Additionally, different speciation modes (e.g., bifurcating, budding, or anagenetic) cause different topological representations of phylogeny and, thus, affect the relationship between branch lengths and species age. Information about extinctions provided by fossils is incomplete for most clades, and the prevalent mode of speciation is largely unknown. Here we evaluate through simulations the effect of extinction and mode of speciation on phylogenetic estimation of species age. We found that extinction rate and speciation modes greatly influence the accuracy of branch length as an approximation of species age. Under the assumption of bifurcating speciation we measured a relatively low mismatch between true and phylogenetic age, which however increased with extinction rates. The erroring in estimated species age was substantially higher under budding speciation and further increased with the inclusion anagenetic speciation. An extinction sensitivity analysis showed many incorrect inferences when using the phylogenetic age. We propose an approach to partially correct phylogenetic ages under budding speciation. The geometric function was not accurate but presented a high confidence interval coverage. Altogether our results indicate that we should be cautious when inferences are made from the relationship between phylogenetic ages and eco-evolutionary variables, and, when possible, we should perform a critical evaluation of speciation modes, through spatial analysis and extinction events, through fossil calibrations.

Our analyses show that species ages cannot be confidently estimated from phylogenetic trees although broad confidence interval can be inferred.

**Key words:** Evolutionary history, Extinction rates, Simulations, Speciation modes.

**Introduction**

The estimation of species age, or the elapsed time since species origin, is important to evaluate mechanisms that link species longevity with eco-evolutionary processes (Benton 2013, Swenson 2019). For instance, age-dependent extinction hypotheses test the relationship between age and extinction probability, assessing whether different extinction rates affect young vs old species (Pearson 1995, Balmford 1996, Eldredge *et al.* 2005). Likewise, species age could be a measure of colonization time, especially in island systems or during biotic invasions triggered by geological events, such as the formation of the Central American Isthmus for the Great American Interchange (Carrillo *et al.* 2015, Tanentzap *et al.* 2015). Species age is measured in the fossil record through different statistical and probabilistic approaches based mostly on taxa’s stratigraphic duration (Foote 1996, Foote & Raup 1996). Several of these approaches consider the differences in fossil sampling and temporal resolution (Alroy *et al.* 2001, Silvestro *et al.* 2019). Species ages estimated from paleobiological data offer a reliable measure of species’ temporal duration which can be used in macroevolutionary studies (Van Valen 1973, Benton 2016, Silvestro *et al.* 2020). More recently, several studies have used the length of terminal branches in time-calibrated phylogenies as a proxy for the age of extant species (Gaston & Blackburn 1997, Johnson *et al.* 2002a, Verde Arregoitia *et al.* 2013, Tanentzap *et al.* 2020). However, this approximation, which we hereafter refer to as “phylogenetic age”, can lead to over or underestimations due to three non-exclusive shortfalls.

First, incomplete sampling of extant species reduces the accuracy of the tree topology and increases the uncertainty in any phylogenetic estimation (Heath *et al.* 2008, Mynard *et al.* 2023).

Second, extinction events will mask branching events in phylogenetic trees of extant species [cite Nee et al 90s]. Even in phylogenetic trees that include extinct taxa, the incompleteness of the fossil record will inevitably lead to missing lineages and uncertain topologies. Unsampled extant and extinct species from the phylogeny results in an inflation of the length of terminal branches leading to sampled species (i.e., the tips of the tree), thus altering phylogenetic species ages. For instance, if the extinct species of the *Homo* genus are not included in a phylogenetic tree, the phylogenetic age of *Homo sapiens* is approximately 10 million years, i.e., the age of the last common ancestor with its sister species, the chimpanzee (Rivas-Gonzáles et al. 2023). This estimate exceeds the age of the oldest known fossil of modern humans by two orders of magnitude (Figure 1; Callaway 2017).

The third, and perhaps most challenging shortfall in phylogenetic species ages, is that the tree alone does not contain information about the underlying speciation mode and does not include species labels across its branches, such that only the tips can be unequivocally assigned to a species [ref]. Alternative speciation modes are generally discussed in the literature reflecting different biological processes and species concepts, including bifurcating, budding, and anagenetic speciation (Foote 1996, Silvestro *et al.* 2018). These modes define the relationship between the ancestral species and its descendants, thus contributing to determining species longevities (Wagner *et al.* 1995, Rosenblum *et al.* 2012) (Fig. 2). Most phylogenetic trees are depicted in the rectangular shape where the two descending lineages split symmetrically from an ancestral lineage, thus suggesting a bifurcating speciation mode where two new species replace the ancestral lineage (Baum *et al.* 2005, Caetano & Quental 2022). However, the often-unstated assumption of all birth-death processes commonly used to model phylogenetic branching times, is that speciation occurs as a budding process, with a speciation event leading to a single new species and the survival of the parent species. Anagenetic speciation, in contrast, does not lead to a branching event and is therefore not visible on a phylogenetic tree.

All speciation modes may reflect plausible biological processes, and evidence for each mode has been found in the fossil record [refs]. Bifurcating speciation can be linked with vicariance or allopatric speciation (Willmann & Meier 2000), and the Hennigian species concept considers all speciation events as bifurcating (Henning 1999). Under the assumption of bifurcating speciation and with no extinction events, phylogenetic ages equal the true age of extant species. However, with extinction events, extinct sister species would cause the branch lengths of the surviving sister to appear longer than they are (Figure 2), resulting in an overestimation of species age. Budding speciation can be interpreted as the result of peripatric speciation (Anacker & Strauss 2014, Caetano & Quental 2022) and is related to the evolutionary species concept, which considers any species as descendant of an ancestral lineage and that possesses its own evolutionary identity regarding other lineages (Simpson 1951). A phylogenetic tree typically lacks information about the which of the two descendent branches is the new species after a speciation event [but see ref]. In the case of budding speciation, the phylogenetic age for the ancestral species would be an underestimation of its true age because a phylogeny alone does not reveal which is the ancestral lineage of two sister species. Also, due to incomplete fossil or extant species sampling, phylogenetic age can overestimate true age, given that recent species, if the ancestral species is missing, could seem older than they genuinely are. Anagenetic speciation is not associated with a branching event but can be used to describe different species (or morphospecies (Emerson & Patiño 2018)) delimited by substantial phenotypic change occurring along a lineage (Roopnarine *et al.* 1999). For anagenetic speciation, the phylogenetic age always overestimates the true age, given that the ancestral and new species branches are fused in the phylogeny.

Here we use simulations to quantify the predictability of species age from phylogenetic trees of extant taxa, under different diversification scenarios. Since the potential effects of incomplete taxon sampling are mitigated by the ever-growing taxonomic coverage of phylogenetic research and advances in augmenting trees with the missing species (e.g., Chang et al. 2020; Thomas et al. 2013), here we focus on the effects of extinction and speciation modes on our ability to infer the age of extant species. Specifically, we performed simulations where we know the true age of species to: (1) quantify the error in estimated species ages under various scenarios of different speciation modes and diversification (speciation – extinction) rates; (2) examine whether this error affects our ability to make qualitative decisions on the order of species ages; and, (3) explore whether the signal of simulated age-correlated extinction risk labels is preserved in the phylogenetic age of species. Finally, we propose a way to efficiently quantify the uncertainty in species age under the assumption of a budding speciation mode. We hope this paper will stimulate discussions about the evolutionary information in phylogenetic trees and the reliability of using them to infer phylogenetic ages.

**Methods**

*Simulating species ages*

We generated complete phylogenies of extant and extinct species under a stochastic birth-death process using the package TreeSim 2.4 (Stadler 2010) for the R 4.3.0 statistical programing environment (R Core Team 2023). For all trees, we simulated 100 extant species, while the number of extinct species was stochastically controlled by a fixed extinction rate (as specified below). We mapped species on the complete phylogenies using the R package FossilSim 2.3.1 (Barido-Sottani *et al.* 2019) under different speciation modes, thus assigning species labels across all branches of the tree. We used the labels assigned to terminal extant taxa and used them to determine the true species ages. We then dropped all extinct species from the tree and obtained the length of terminal branches, to quantify the phylogenetic age of extant species. Finally, we rescaled all phylogenetic trees to a root age of one and compared the true and estimated relative ages among different simulation scenarios.

*Error in equating phylogenetic and species age*

To explore whether there is a consistent over or underestimation of species ages and to quantify error in approximating species ages with phylogenetic ages, we simulated a range of datasets with different speciation modes and diversification rates. First, we simulated sets of 100 phylogenetic trees with birth rates set to 0.1, 0.5, and 1, combined with 100 death rates ranging from 0 to 0.99 in equal increments. We defined turnover as birth/death which is sometimes called extinction fraction (Beaulieu & O’Meara 2016). Second, on each of these phylogenies, we then mapped species according to different scenarios of speciation: (1) budding speciation, (2) bifurcating speciation, (3) a combination of budding speciation and anagenetic speciation with the rate of anagenesis set to half of the birth rate, and (4) bifurcating speciation combined with anagenetic speciation.

Across all trees, we obtained in total 120,000 extant species, 30,000 for each speciation scenario. For each speciation mode and turnover rate, we calculated the mean absolute percentage error (MAPE) as a measure of the deviation between the phylogenetic ages from the true age.

MAPE =

Next, for each speciation mode, we plotted the MAPE against the simulated turnover.

*Impact of age error in comparing species ages*

To explore whether the error introduced by approximating species age with phylogenetic age impacts our ability to make qualitative judgements such as which of two extant species is the younger one, we simulated 1,000 phylogenetic trees with values of extinction rates of 0.9, 0.5, and 0, combined with a fixed speciation rate of 1 (3000 trees). Second, on each of these phylogenies, we mapped species according to budding and bifurcating speciation. Thus, we simulated 300,000 extant species for each speciation mode. Next, we calculated the proportion of cases where the younger of two species, according to its phylogenetic age, is, in fact, the older one given the true age of the two species. We performed this comparison from the perspective of an empirical researcher that can only obtain the phylogenetic ages. We made two types of comparisons for each phylogeny: (1) between the youngest and oldest species in the phylogeny, and (2) between two randomly selected species.

Under a budding process a species has equal probabilities to persist into the left and right descendants. Thus, in the absence of extinction, the probability of that a living species originated at the most recent branching event separating it from its sister species is 0.5. Its probability of having originated at the previous branching event is therefore (1 – 0.5) × 0.5. The distribution of probabilities of origination at each node separating a tip from the root thus follows a geometric distribution with parameter p = 0.5. Therefore, the probability for an ancestral node *k* to be the origin of a species is given by the geometric distribution:

(1 – p)(*k* – 1)p,

providing the node count recursively from the tip

*Imprint of extinction risk on phylogenetic ages*

To evaluate whether the assumed relationship between species age and present extinction risk (e.g., Johnson et al. 2002; Tanentzap et al. 2020; Verde Arregoitia et al. 2013) is preserved in the phylogenetic ages, we simulated 1,000 phylogenetic trees with extinction rates of 0.25, 0.15, and 0.05, and a fixed speciation rate of 0.3. Then, using the phylogenies as inputs, we mapped species onto each tree based on a budding speciation process. Next, we binned the true ages in five categories corresponding to the IUCN conservation categories: Least Concern (LC), Near Threatened (NT), Vulnerable (VU), Endangered (EN), and Critically Endangered (CR; Internation Union for the Conservation of Nature 2016). With this, we generated two scenarios: (1) a positive effect with older species being at higher extinction risk), and (2) a null effect where species age and extinction risk are uncorrelated. We then quantified how many trees, for the phylogenetic and geometric ages, were estimated correctly regarding the relationship between the mean true age and all (total) and at least three (partial) conservation status categories.

**Results**

*Error in equating phylogenetic and species age*

Under the assumption of bifurcating speciation and in the absence of extinction, phylogenetic age matched the true age (Figure 3). At low turnover (< 0.25), 96% of the phylogenetic age estimations are congruent with the true age. At high turnover (> 0.75), this was also the case for most species (73%). However, age overestimation increased with turnover, and in some cases the phylogenetic age suggests that the species is as old as the root age. For budding speciation, there were both under and overestimations (Figure 3). At low turnover, most ages were underestimated (96%). With higher turnover, phylogenetic ages overestimated true age more often (17%), and in few cases phylogenetically older species were indeed too young. In datasets simulated under a mixture of anagenetic and bifurcating speciation, phylogenetic ages were matched or exceeded the true ages (Figure SM1). In a low turnover scenario, species ages were overestimated in 32% of cases, increasing to XX% in datasets with high extinction. Datasets with mixed anagenetic and budding speciation, showed high levels of error (XYZ%) with limited impact of extinction.

We found that the main factor affecting the relative error in species ages under both budding and bifurcating speciation was the extinction fraction, while speciation rates did not have a substantial impact (Fig. 4). For strictly bifurcating speciation, there was no error in the absence of extinction but the MAPE increased to up to 150% with extinction fractions exceeding 0.75 (Fig. 4a). In contrast, under budding speciation, the MAPE was around 25% in the absence of extinction, increasing to ca. 30-120% with extinction fractions exceeding 0.75 (Fig. 4b). In datasets that included anagenetic speciation, the MAPE reached as high as 500% in some simulations (Figure SM2).

*Impact of age error on comparing species ages*

For the combination of strictly bifurcating speciation and all extinction scenarios, selecting the phylogenetically youngest and oldest species never resulted in a case where the presumed older species has been in fact the younger of the two species according to their simulated age (Figure 5). Thus, for this speciation mode, there is no risk of a qualitative error when comparing species at the extremes of the age range of a time-calibrated phylogeny, assuming complete extant species sampling. In contrast, for budding speciation, the age rank of the oldest and youngest species was erroneously determined in 2.2% of the simulations in the absence of extinction, increasing to 7.5% and 12.2% for intermediate and high extinction, respectively.

Under bifurcating speciation, the age ranking of two randomly selected was incorrect in 6% and 8%, respectively, for intermediate and high extinction, respectively (Figure 6). Under budding speciation, the error exceeded 25%, irrespective of the extinction level (Figure 6).

*Imprint of extinction risk on phylogenetic ages*

The mean phylogenetic age incorrectly recovered the ranking of five simulated extinction risk categories (*sensu* IUCN Red List) in 25% with low extinction. The error rate increased to 31 and 44% with intermediate and high relative extinction, respectively (Fig. 7).

When acknowledging partial correct estimation (3 or more conservation status estimated corrected), the mean phylogenetic age showed the same pattern with 97% in a low, 94% in an intermediate, and 91% in a high extinction scenario. Moreover, the mean probable age slightly improved with 99% in a low, 97% in an intermediate, and 87% in a high extinction scenario.

*Quantifying uncertainty in species age under budding speciation*

The modal age from the geometric function has almost the same accuracy as the phylogenetic age for estimating true age in a budding speciation scenario (Figure SM5). The mean estimated age from the truncated geometric function is inaccurate regarding any true age but unbiased in all extinction scenarios (Figure SM6).

The coverage of our estimator is comparatively high, with true ages included in the 95% confidence interval in 94% the simulations with low relative extinction. This, however, decreased to 90% and 76% for intermediate and high extinction scenarios (Figure 8). However, the width of the confidence intervals is large, ranging often from the root of the phylogeny to the present, highlighting the low precision of this estimator.

**Discussion**

Our study shows that extinction rates and speciation modes greatly influence the mismatch between true and phylogenetic age. Moreover, the error patterns are different regarding the combination of both processes. As we expected, a phylogeny whose taxonomy was derived from a bifurcating speciation process presents no or low mismatch between true and phylogenetic age due to the bifurcating node structure of phylogenies and the way phylogenetic age is measured (Meier & Willmann 2000). Our study has also shown that under budding speciation phylogenetic age shows a high error even with no extinction rates (Figure 4). Likewise, anagenetic speciation, combined with budding or bifurcating speciation, resulted in high errors. The anagenetic error is not affected by extinction rates, suggesting that if a clade experiences a degree of anagenesis, it should be discouraged to estimate ages from phylogenies. The geometric function did not improve the accuracy regarding the true age estimation (Figure SM5). Its large confidence intervals and the high coverage, suggest that there is little signal of the species age in a phylogeny under budding speciation. Since the coverage is also relatively high with low extinction, the main source of uncertainty is indeed the budding speciation mode. Thus, our study points out that budding and anagenetic speciation modes are the principal source of inaccuracy regarding estimating species ages from time-calibrated phylogenies branch lengths.

For bifurcating speciation, the mean error between true and phylogenetic age was low, even in scenarios of high extinction. This is because taking the most recent ancestral node as phylogenetic age results in sister species to be identical in age, the same as implied by bifurcating speciation. Due to only introducing bias by extinction, there was a low risk of confusing the oldest with the youngest species. Therefore, under a bifurcating speciation scenario, the phylogenetic age indeed captures the signal of the true species age. For budding speciation, there is a high mismatch between ages, even in no-extinction scenarios; however, the overall error does not increase considerably with increasing extinction rates. Half of the phylogenetic age estimations in no-extinction scenarios always underestimate the true age, while when extinction rates increase, overestimation appears and rises until balancing with underestimation at high extinction scenarios. This pattern happens due to the phylogenetic estimation assumption of considering sister species as identical in age, which, in no extinction scenario, only correctly estimates the youngest species of any bifurcation. Moreover, when extinction rates increase, the youngest species of a clade evolving through bifurcation speciation can be wrongly taken as phylogenetically old (i.e., having a long terminal branch) if all ancestral species to that branch are extinct. Due to these misinterpretation patterns, the qualitative error is high and increases considerably with extinction rates in the example of the oldest vs. youngest species (Figure 5). Thus, for clades diversifying predominantly through budding speciation, the phylogenetic age is not equal to the true age for half of the species, and some of these mismatches would be time substantial regarding the true age.

Given the large inaccuracy of phylogenetic age, especially for phylogenies diverging under budding speciation, the question is whether this affects the inferences made from the relationship between species longevities and eco-evolutionary variables, such as extinction risk, range size, or clade’s diversity (Gaston and Blackburn 1997; Johnson et al. 2002; Tanentzap et al. 2015). If phylogenetic ages capture the true age signal, it could be argued that phylogenetic age is a valuable measure of species longevity. Some authors acknowledge the problems associated with measuring species age from phylogenies, and have proposed approaches to account for them by combining phylogenetic, biogeographic, and ecological information (Swenson 2019). For example, Tanentzap et al. (2020) used the stem age, given that it requires only one species to be estimated within each clade to reflect its evolutionary history (Scholl & Wiens 2016), to explore the relationship between taxon age, range size and extinction risk in plants. Additionally, Sonne et al. (2022) determined young and old Andean hummingbirds by generating 1000 trees and listing the species that fell into the first and fourth branch length quartile, respectively, and then used a sensitivity analysis to evaluate the consequences of different species composition in their results (Fjeldså *et al.* 2012). Nevertheless, neither strategy acknowledges the real problems of age uncertainty: the unknown extinction rates, which for most groups is probably high (Pimm *et al.* 2014), and speciation modes of phylogenies. Our evaluation of the imprint of extinction risk on phylogenetic ages makes this point clear because it showed that, even with the strong signal we assigned on purpose to the true ages, the number of incorrect inferences is considerably high among extinction scenarios (Figure 7).

Our results point out the errors associated with budding and bifurcating speciation; however, how do we know which is the predominant speciation mode of a clade to contemplate a likely percentage error in the phylogenetic age? Anacker and Strauss (2014) proposed, for example, that budding speciation leaves some signatures in sister species: they should have overlapped or adjacent ranges, their range sizes should be asymmetrical, and specific ecological traits should differ between them. These signatures are associated with sympatric and peripatric speciation (Barraclough *et al.* 1998). In this sense, bifurcating speciation can be associated with allopatric speciation and the signatures it leaves in the range of sister species: ranges should not be overlapping or adjacent, range sizes should not necessarily be asymmetrical, and ecological traits should not necessarily differ between them (Barraclough & Vogler 2000, Fitzpatrick & Turelli 2006). Thus, assessing a clade’s spatial dynamics before performing species age analyses could give us insights into the speciation modes and an approximate error of phylogenetic ages. In the case of the errors associated with different extinction scenarios, combining phylogenetic information with fossil data is recommended, although the fossil record is scarce in some groups (Rabosky 2010, Silvestro *et al.* 2014, Brée *et al.* 2022, López-Martínez *et al.* 2023).

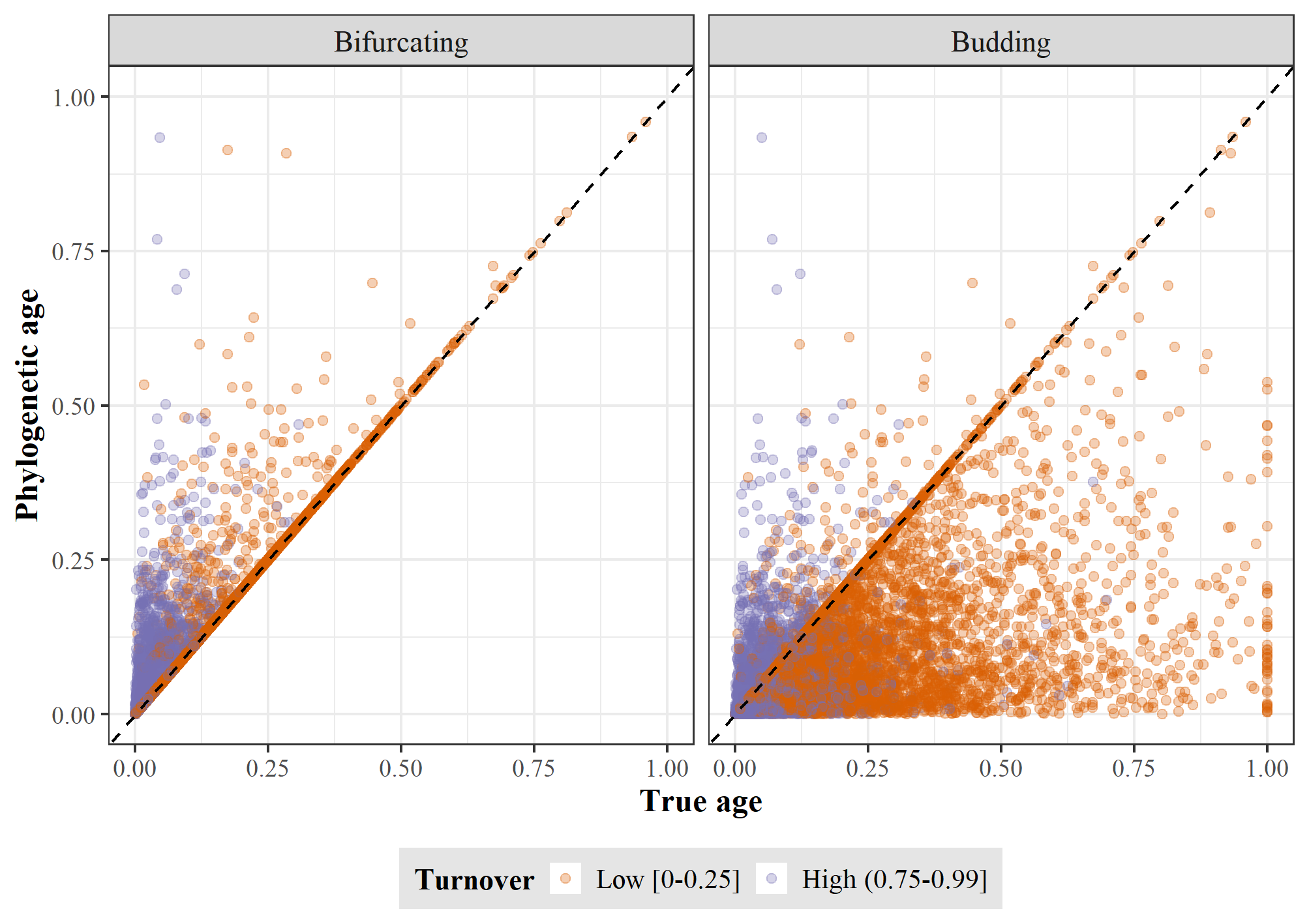
Using simulations, we showed the problems in estimating species age from phylogenetic trees and quantified the estimation errors under different scenarios. The challenges of using phylogenetic age as a proxy for species longevity are not merely methodological. Time-calibrated phylogenetic trees of extant species do not contain information on speciation modes and extinction rates. Thus, the phylogenetic age provides some information about true age, but it is a weak proxy to measure evolutionary history. Assessing the speciation modes with the methods suggested here, such as spatial range signatures, and estimate extinction rates by combining paleontological and neontological data, might help to estimate the ages percentage error. Approaches combining phylogenies, biogeography, diversification rates, and traits might provide a more comprehensive understanding on the relationship of species longevity and eco-evolutionary processes.



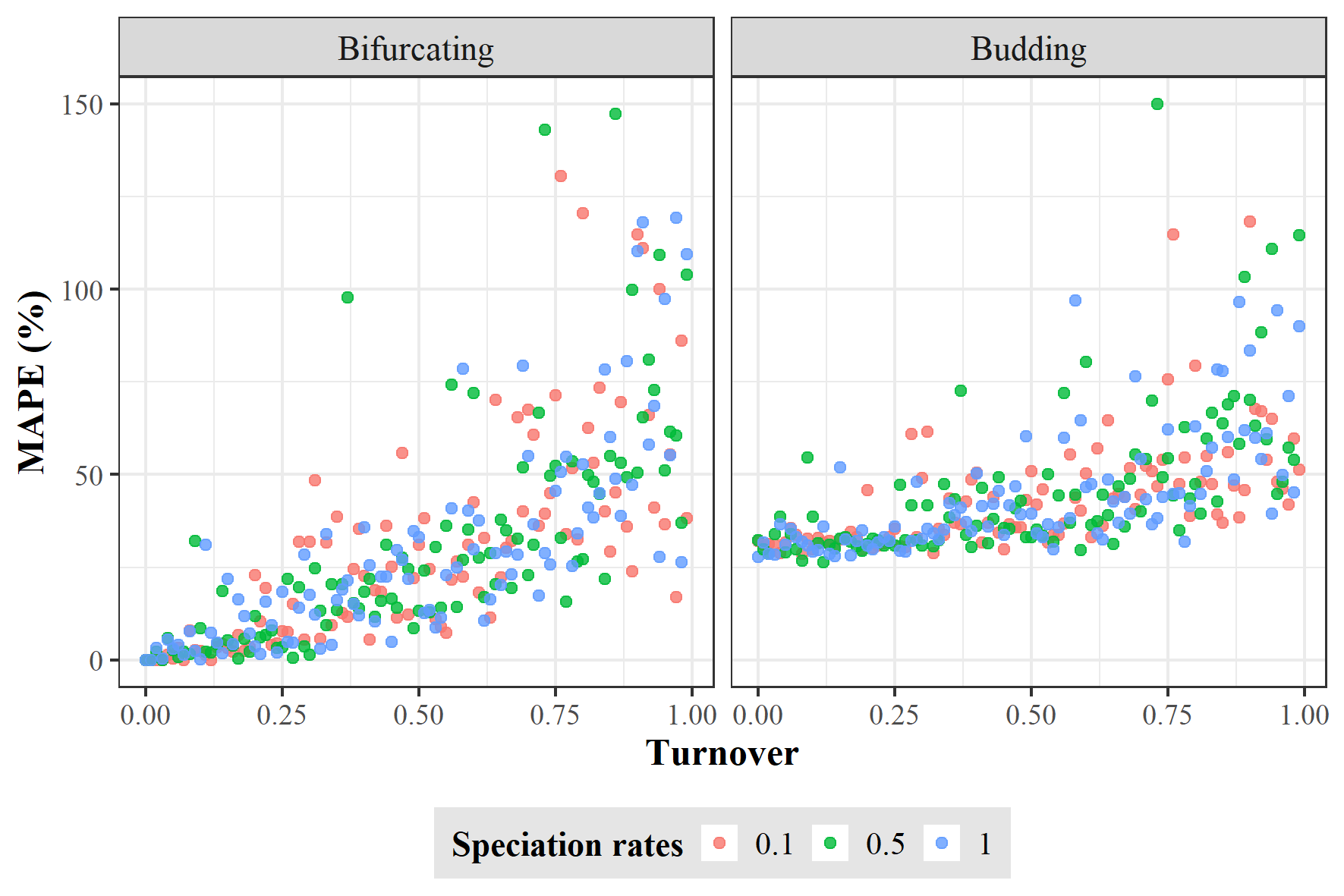
**Figure 1.** Discrepancy between species ages. Estimations based on the length of the terminal branch in a time-calibrated phylogeny (red) and the first appearance in the fossil record (green). Shark data (*Trianenodon obesus* and *Carcharhinus obscurus*) obtained from Brée et al. (2022). Mammals’ phylogenetic data (except *Homo sapiens*) obtained from Upham et al. (2019). Mammals’ phylogenetic data (except *Homo sapiens*) obtained from. *Homo sapiens* fossil and phylogenetic data obtained from Callaway (2017) and Rivas-Gonzáles et al. (2023), respectively.



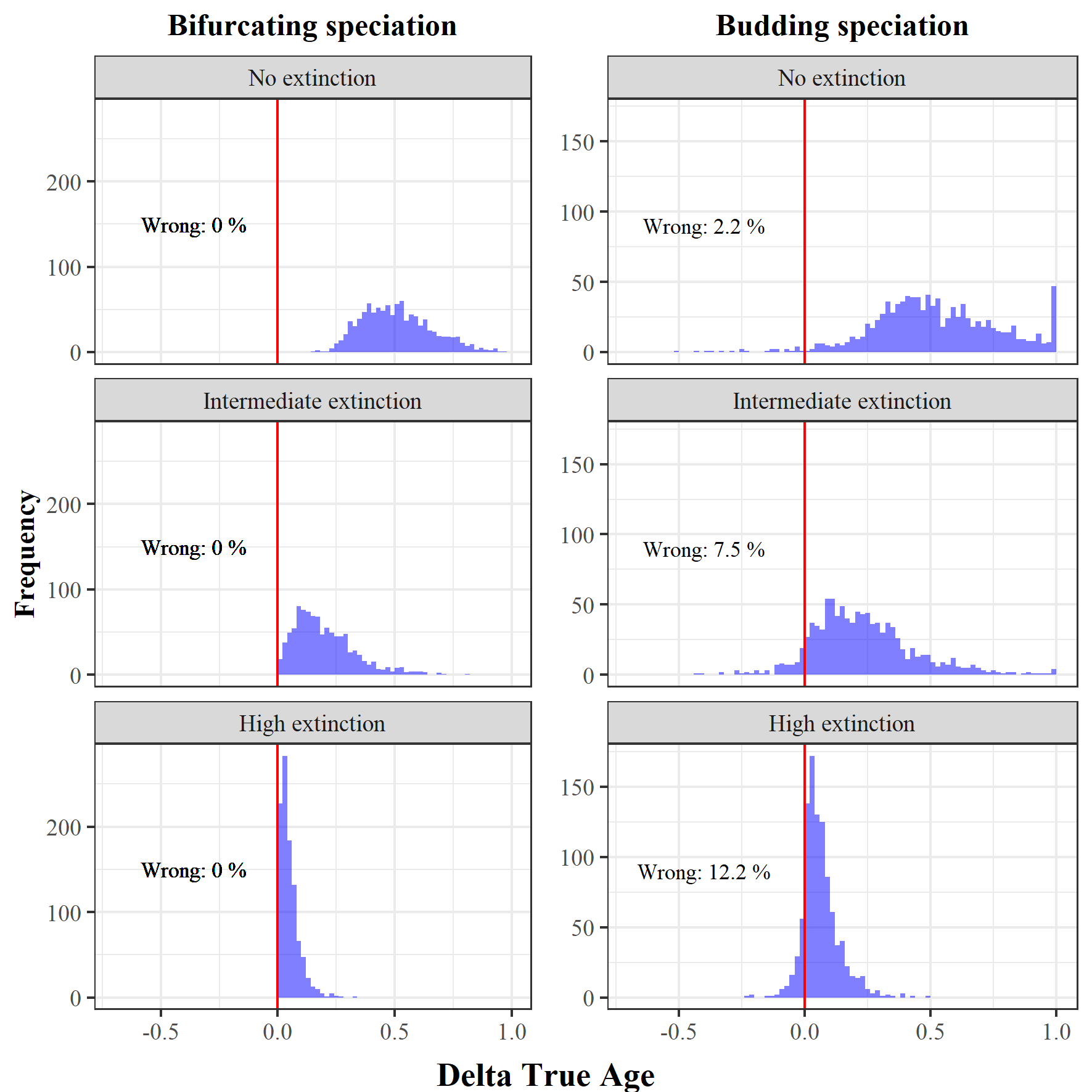
**Figure 2.** Impact of speciation mode and extinction on species age. For the same hypothetical time-calibrated phylogeny of extant species, the continuation of the same color indicates the same species, solid and dashed lines represent extant and extinct species, respectively, under different speciation modes and extinction scenarios. The number displays the resulting age of the respective species in million years (myr).

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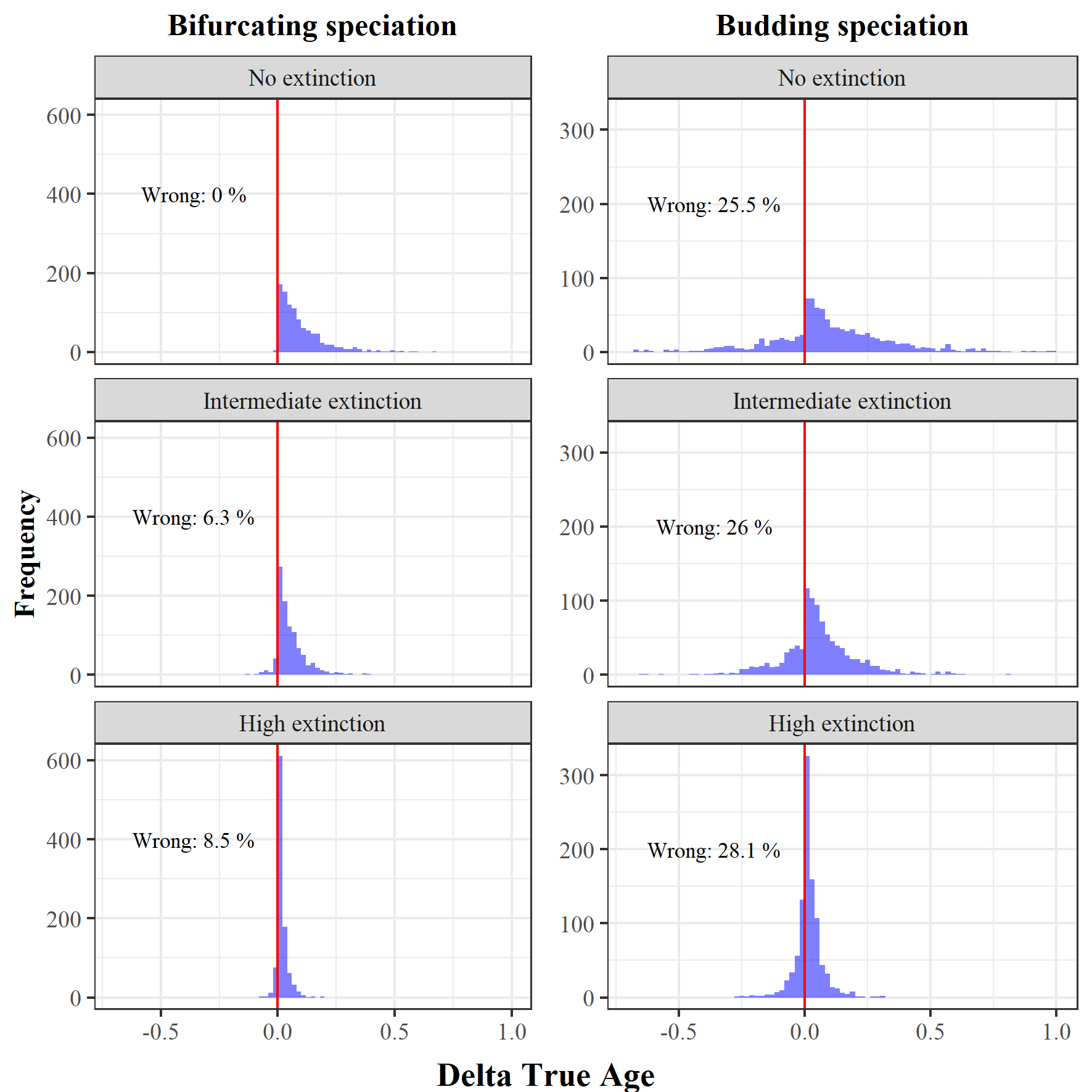
**Figure 3.** True age versus phylogenetic age at low and high turnover for bifurcating (left) and budding (right) speciation. Each point represents a species and both ages, True and Phylogenetic, are scaled to the root age of the correspondent phylogenetic tree.

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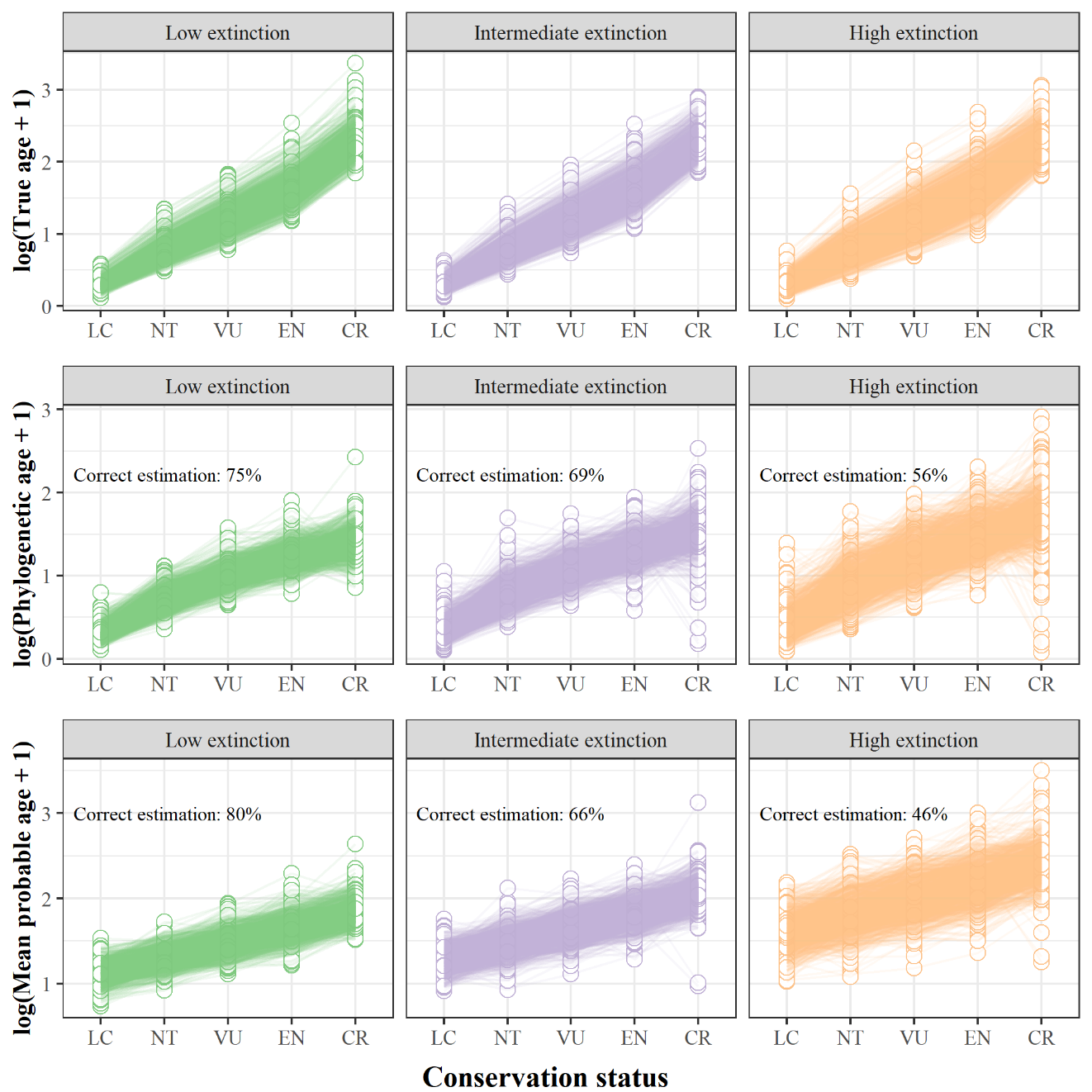
**Figure 4.** Error in equating phylogenetic age with speciation age. The error was quantified as mean absolute percentage error (MAPE) between the true and phylogenetic ages of 100 species simulated under bifurcating (left) and budding speciation (right). Each dot represents one replicate of the 300 simulations for each speciation mode using different rates of speciation and turnover.



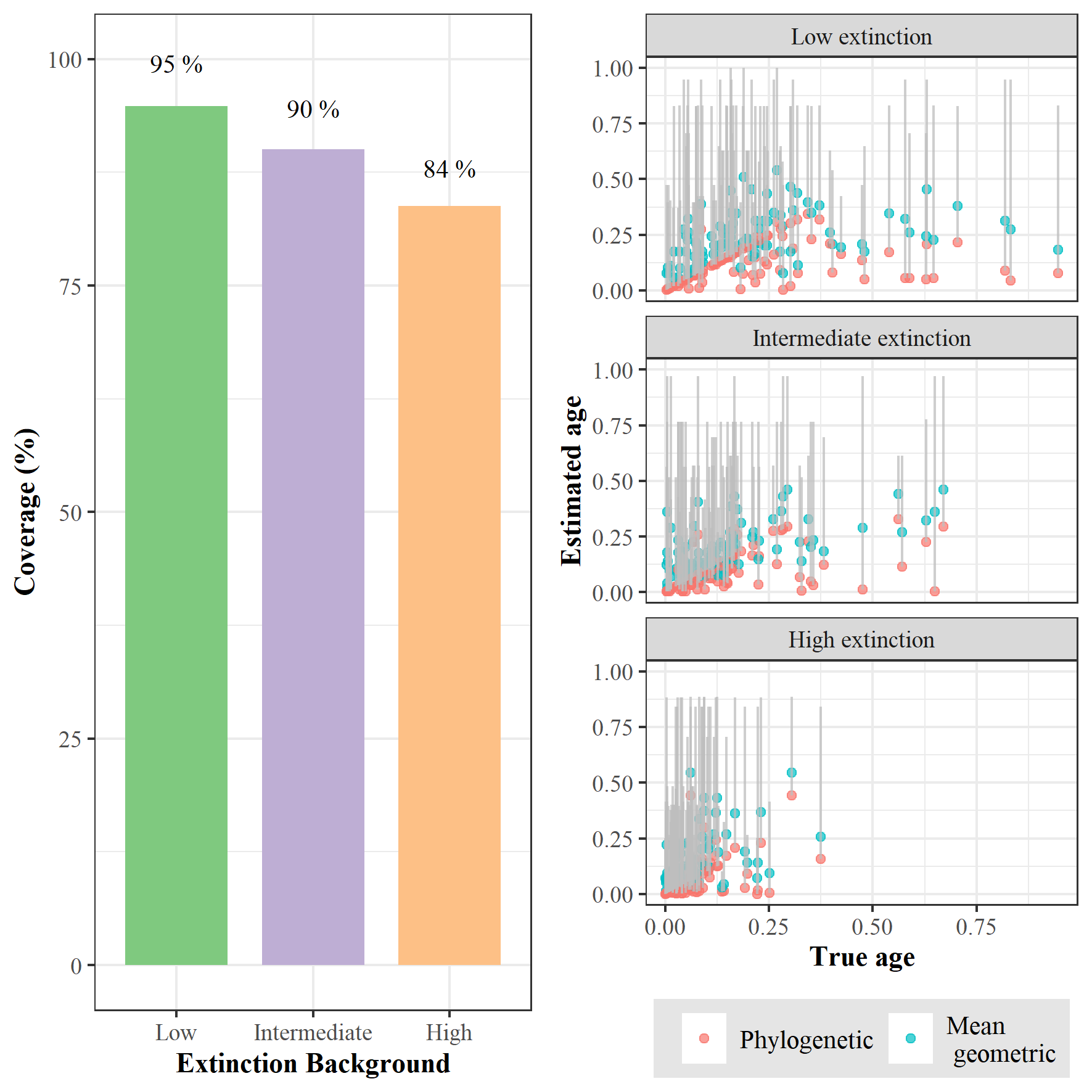
**Figure 5.** Risk to confuse the oldest with the youngest species. For each of the 1000 simulations under bifurcating (left) and budding (right) speciation, combined with three different extinction levels, we selected the oldest and youngest species according to the phylogenetic ages, and calculated the difference in their true ages (Delta True Age). A Delta True age smaller than 0 indicates that the phylogenetic oldest species was in fact younger than the phylogenetically youngest species, and therefore, the comparison of phylogenetic ages is qualitatively wrong.



**Figure 6.** Risk to confuse older with younger random species. For each of the 1000 simulations under bifurcating (left) and budding (right) speciation, combined with three different extinction levels, we selected two random species and defined which was the older and younger according to the phylogenetic ages, and calculated the difference in their true ages (Delta True Age). A Delta True age smaller than 0 indicates that the phylogenetic older species was in fact younger than the phylogenetic younger species, and therefore, the comparison of phylogenetic ages is qualitatively wrong.



**Figure 7.** Positive Extinction signal comparison between True age, Phylogenetic age, and the Mean probable age generated by the geometric function, for three extinction scenarios (Low, Intermediate, and High) regarding the phylogeny simulation (1000 trees). Extinction signal is represented by the conservation status categories (LC = Least Concern; NT = Near Threatened; VU = Vulnerable; EN = Endangered; CR = Critically Endangered). The correct estimation for the Phylogenetic and Mean probable age is based on the percentage of trees that were estimated completely right (positive effect) regarding the relationship between the True age and the Conservation status categories.



**Figure 8.** Coverage of the geometric function for three extinction levels. On the left, the total coverage of geometric function’s confidence intervals regarding the true age of 100000 species for each extinction level. On the right, the specific coverage of geometric function’s confidence intervals (grey lines) regarding the 100 species of one random phylogeny; red and sky-blue dots represent the phylogenetic and mean geometric age, respectively, for each species true age.

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