1  **Title:** Hidden-state-only speciation and extinction models provide accurate tip estimates of

2  diversification rates

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8  **Running headline:** Hidden-rate-only models of diversification

9

10  **Abstract**

11  1. State-dependent speciation and extinction (SSE) models provide a framework for testing

12  potential correlations between the evolution of an observed trait and speciation and extinction

13  rates. Recent expansions of these models allow for the inclusion of "hidden states" that, among

14  other things, allow for rate heterogeneity often observed among lineages sharing a particular

15  character state. However, in reality, multiple circumstances and interacting traits related to a

16  focal character play a role in changing diversification dynamics of a lineage over time, restricting

17  the use of available SSE models that require trait information to be assigned at the tips.

18  2. Here we introduce MiSSE, an SSE approach that infers diversification rate differences from

19  hidden states only. It can be used similarly to other trait-free methods to estimate varying

20  speciation, extinction, but also different functions of these parameters such as net-

21  diversification, turnover rates, and extinction fraction. Given the size of the model space, we

22  also describe an algorithm designed for efficiently searching through a reasonably large set of

23  models without having to be exhaustive.

24  3. We compare the accuracy of rates inferred at the tips of the tree by MiSSE against popular

25  character-free methods and demonstrate that the error associated with tip estimates is generally

26  low. Due to certain characteristics of the SSE models, this method avoids some of the recent

27  concerns with parameter identifiability in diversification analyses and can be used alongside

28  regular phylogenetic comparative methods in trait-related diversification hypotheses.

29  4. Finally, we apply MiSSE, with a renewed focus on classic comparative methods, to

30  understand processes happening near the present, rather than deep in the past, to examine

31  how variation in plant height has impacted turnover rates in eucalypts, a species-rich lineage of

32  flowering plants.

33

34    **Key words**: diversification, *Eucalyptus*, hidden-states, Myrtaceae, plant height, turnover, state-

35    dependent speciation and extinction.

## 1.    INTRODUCTION

37        Molecular phylogenies, when scaled in relation to time, are powerful sources of data to

38    understand the diversification dynamics of organisms and have become crucial in multiple areas

39    of ecology and evolution (Wiens & Donoghue, 2004). As the trees themselves become bigger,

40    more robust, and increasingly complete in proportion to species sampled (e.g. Beaulieu &

41    O'Meara, 2018; Smith & Brown, 2018), the statistical tools used to infer macroevolutionary

42    patterns from them also become more biologically realistic (e.g. Beaulieu & O'Meara, 2016).

43    Modelling the dynamics of lineage origination and extinction through time have allowed us to

44    understand, for example, how shifts in pollination and dispersal strategies are connected to

45    changes in diversification rates of angiosperms (e.g. Lagomarsino et al., 2016; Vasconcelos et

46    al., 2019; Reginato et al., 2020) or the role of environmental instability in the diversification of

47    several vertebrate groups (e.g. Harvey et al., 2020; Morales-Barbero et al., 2021).

48        Recently, however, a renewed wave of criticisms regarding these methods calls into

49    question whether diversification rates from time-calibrated trees of extant-only organisms should

50    even be estimated at all (Louca & Pennell, 2020). While it is true that phylogenies are often

51    used to address problems beyond their capabilities (Losos, 2011; Cooper et al., 2016; Uyeda et

52    al., 2018), there is still a considerable amount of information that extant-only phylogenies can

53    provide about the diversification process. For instance, O'Meara and Beaulieu (in prep.)

54    demonstrate that state-dependent speciation and extinction (SSE) models can identify different

55    likelihoods for the generating parameters of trees with different topologies but identical lineage

56    through time plots. However, the uncertainty around parameter estimates increases as one

57    moves from tip to root in the tree, due to the decreasing amount of information in ancestral rate

58    reconstructions. A solution, then, could be to continue using SSE models to model

59    diversification dynamics, but focus only on rates estimated near the present or at the tips of the

60    tree, rather than deep in time. Such an approach can have additional advantages for its

61    flexibility in testing for correlations between multistate discrete and continuous traits (Harvey &

62    Rabosky, 2018; Title & Rabosky, 2019).

63        Here we formally describe MiSSE, a new extension of the SSE framework that uses

64    hidden-states only and provides accurate estimates of various metrics of diversification rates at

65    the tips of a tree. We compare its accuracy against other popular approaches for estimating tip

66    diversification rates, and further demonstrate the capabilities of MiSSE with an empirical

67     example that examines the correlation between turnover rates and plant height in eucalypts

68     (Eucalypteae, Myrtaceae), a diverse lineage of flowering plants. Finally, we argue why focusing

69     on tip estimates can be advantageous in testing complex hypotheses of diversification and

70     discuss some caveats of MiSSE and possible ways forward for modeling diversification.

71     2. MATERIALS AND METHODS

72     **2.1. The MiSSE model**

73     State-dependent speciation and extinction models expand the birth-death process to

74     account for speciation ($\lambda$), extinction ($\mu$), and trait evolution ($q$, the transition rates between

75     character states), estimating parameters that maximize the likelihood of observing both the

76     character states at the tips of the tree and the tree itself (Maddison et al., 2007). SSE models

77     were initially developed to overcome three main perceived shortcomings in the field: (1) the

78     need for greater flexibility in tests of key-innovation hypotheses, which, at the time, typically

79     involved sister-clade comparisons that could only measure differences in net-diversification and

80     assumed constant rates within the clades under comparison (Barraclough et al., 1998); (2) the

81     need to incorporate differences in speciation and/or extinction rates associated with a particular

82     character state in analyses of trait and geographical range evolution (Goldberg et al., 2010;

83     Goldberg & Igic, 2012; Ree & Sanmartin, 2018); and (3) the potentially confounding effects of

84     different transition rates and diversification rates when looking at diversification or character

85     evolution, respectively (Maddison, 2006).

86     All discrete SSE models exist within the following generalized ordinary differential

87     equations (corresponding to eq. 1a-b in FitzJohn, 2012):

88

$$\frac{dE_i}{dt} = \mu_i - (\lambda_i + \mu_i + \sum_{i \neq j} q_{ij})\, E_i(t) + \lambda_i E_i(t)^2 + \sum_{j \neq i} q_{ij} E_j(t)$$

89                  (1a)

$$\frac{dD_{N,i}}{dt} = -(\lambda_i + \mu_i + \sum_{i \neq j} q_{ij})\, D_{N,i}(t) + 2\, \lambda_i\, D_{N,i}(t)\, E_i(t) + \sum_{j \neq i} q_{ij}\, D_{N,j}(t)$$

90                  (1b)

91

92     The probability $E_i(t)$ is the probability that a lineage starting at time $t$ in state $i$ leaves no

93     descendants at the present day ($t = 0$), and $D_{N,i}(t)$ is the probability of a lineage in state $i$ at time

94     $t$ before the present ($t > 0$) evolved the exact branching structure as observed.

95        With these ordinary differential equations, any number of states can be included in an

96    SSE model. For example, in character-based models, such as BiSSE (Maddison et al., 2007), $i$

97    and $j$ represent two observed states of a focal character (e.g. observed states 0 and 1). A

98    potential issue in this case is that when comparing a simple model where there is no variation in

99    rates among states against a model of trait-dependent diversification there is almost always

100    strong support for a trait-dependent diversification process in empirical settings (Maddison &

101    Fitzjohn, 2014; Rabosky & Goldberg, 2015). The HiSSE model (Hidden-State Speciation and

102    Extinction model; Beaulieu & O'Meara, 2016) partially corrects this issue by harnessing the

103    properties of hidden-Markov models to allow rate heterogeneity to depend not only on the focal

104    trait, but also to be correlated with other factors that were not explicitly scored as character

105    observations at the tips (see also Caetano et al., 2018; Nakov et al., 2019; Boyko & Beaulieu,

106    2021). Thus, with HiSSE, $i$ and $j$ represent the different observed and hidden states

107    combinations specified in the model (e.g. observed states 0 and 1, hidden states $A$ and $B$).

108        Although hidden state SSE models made hypothesis testing in diversification studies

109    more realistic, existing SSE models are still generally used to understand the correlation of a

110    particular observed trait or geographical range distribution and the diversification dynamics of a

111    group. However, in reality, it is not a single factor but, rather, a combination of circumstances

112    that are responsible for the heterogeneous diversification rates among clades in a phylogenetic

113    tree (Donoghue & Sanderson, 2015; Nürk et al., 2020). To understand heterogeneous

114    processes that arise from the effect of multiple traits on the dynamics of speciation, extinction,

115    and trait evolution is one of the main utilities of hidden Markov models in phylogenetic

116    comparative methods (Caetano et al., 2018).

117        It is natural, then, to completely drop the observed trait from the analysis and focus only

118    on the impact of the "unobserved" traits, or the hidden states, in the diversification dynamics of a

119    clade. This is what our MiSSE model, an extension of the HiSSE framework, is intended to do.

120    MiSSE is a direct extension of HiSSE with the main difference between the two models being

121    that with HiSSE, we have an observed character with states 0 or 1, as in BiSSE (Fig.1a), *and*

122    hidden states $A$ and $B$ (Fig. 1b). Essentially, MiSSE operates in the same way, but simply

123    ignores the observed states altogether and performs the calculations of the hidden rate classes

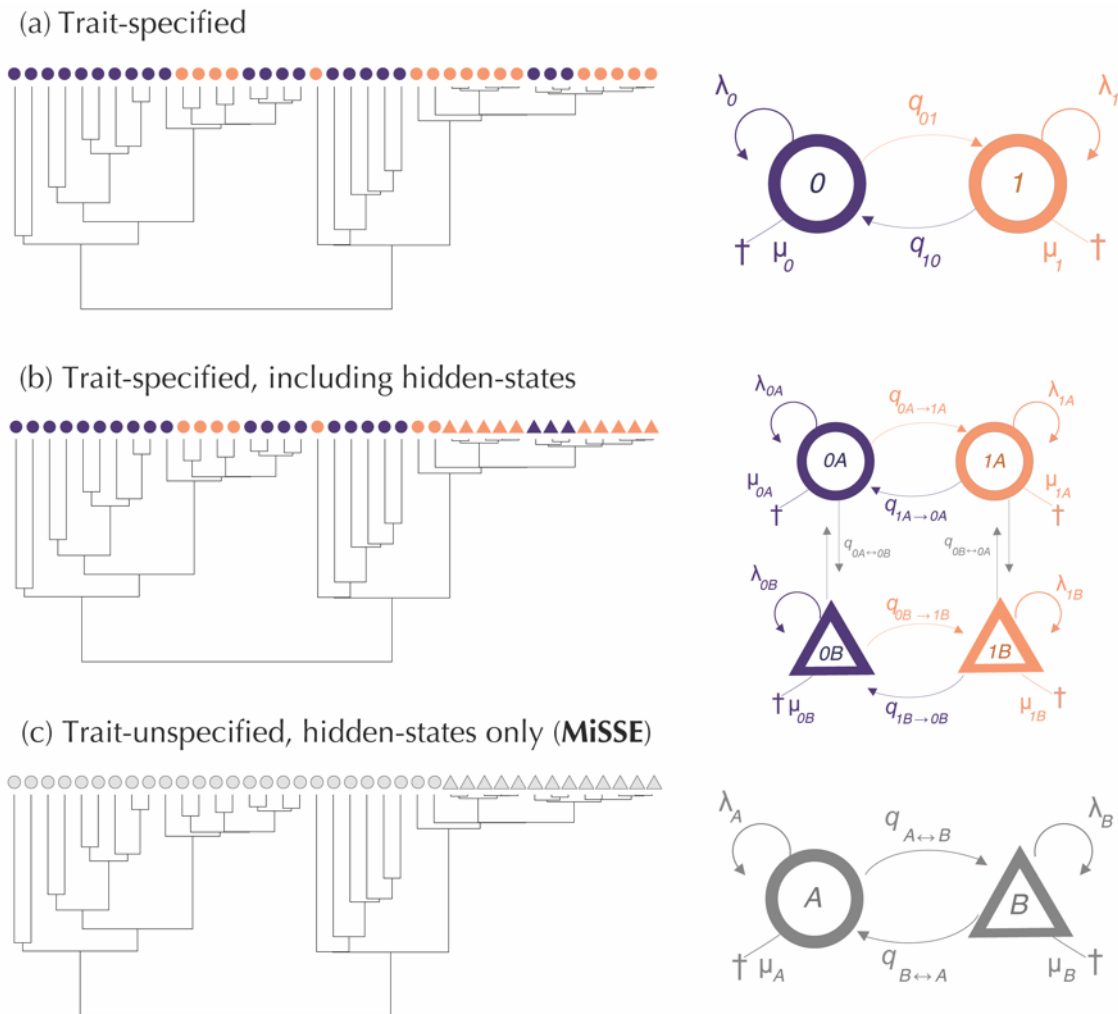124    directly (Fig.1c).

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**Figure 1:** Diagrammatic representations of state-dependent speciation and extinction models that: (a) use only observed trait data in parameter estimation (e.g. BiSSE, MuSSE and GeoSSE), (b) use both observed trait data and hidden-states in parameter estimation (e.g. HiSSE, MuHiSSE, GeoHiSSE), and (c) use only hidden states in parameter estimation (e.g. MiSSE).

The assignment of particular hidden state to each tip is based on probabilities of the data, which, in the case of MiSSE, is just the structure of the tree. This process is like the maximum likelihood calculations in other hidden state methods. These calculations are described thoroughly in Caetano et al. (2018), so here we provide only a brief overview. The first step is to search for rate estimates that maximize the probability of observing the tree at the root by marginalizing over all possible histories at internal nodes and along branches. This search consists of a bounded stochastic simulated annealing, run for 5000 iterations, followed

142    by a bounded subplex routine that runs until the maximum likelihood is found. The use of

143    simulated annealing helps ease MiSSE away from finding local optima.

144    Suppose that, in an iteration, rate class $A$ has $\lambda = 0.1$ and $\mu = 0.05$, and rate class $B$ has

145    $\lambda = 0.2$ and $\mu = 0.1$. The node subtending the branch subtending a tip could have started in $A$

146    giving rise to an $A$ or $B$, or it could have started in $B$ giving rise to an $A$ or a $B$. Each of these

147    scenarios has a probability associated with them. The sister edge has the same set of scenarios

148    and its own set of probabilities. These probabilities are combined at the nodes (which includes

149    the speciation rate to account for the speciation event at a node) and carried down the tree in

150    the same way as in other SSE models. Once at the root, marginal probabilities for whether the

151    root is in $A$ or $B$ based on a set of rates can be calculated, as well as the overall log-likelihood

152    that these rates produced the observed tree.

153    At this point, all other branches, nodes, and tips are assumed to be in all possible

154    states. The second step, then, is to take the MLE of the rates and determine which of the states

155    at a given node and given tip is more likely than any of the other possible states. For that,

156    MiSSE simply chooses a node (or tip), fixes it to be in rate class $A$, traverse the tree, and

157    calculates the overall likelihood. Then it does the same for that same node, but this time it fixes

158    it to be in rate class $B$. At the end, MiSSE calculates the marginal probabilities by dividing the

159    probability that a node was in each state divided by the sum of the probabilities across all

160    states. In that way, every tip and node have a probability of being in both states $A$ and $B$, but

161    often one state will be more probable than the other. For example, in a clade where speciation

162    occurred more rapidly, the higher $\lambda$ associated with $B$ will be a better fit to the shape of that part

163    of the tree, and so the marginal probabilities will reflect higher support for $B$. In another clade,

164    where speciation is slower, lower $\lambda$ will be the better fit, so the marginal probabilities will reflect

165    the higher support for hidden state $A$ in that part of the tree. And in other clades they may be

166    uncertain, given frequent transitions in and out each hidden state.

167    Note that $A$ and $B$ are arbitrary labels that can and will shift positions at the tips in

168    different runs. What really matters is the parameter combination that underlies each label in

169    each run, which should not change their MLE between runs. Note too that MiSSE is still a model

170    of tree and character states like other SSE models, and so the topology matters to assign tips to

171    the correct (hidden) states. Because it uses data from the topology as well as branch lengths,

172    MiSSE likelihood can distinguish between trees that have the same lineage through time plot,

173    but different topologies (O'Meara & Beaulieu, in prep.).

174    **2.2. Implementation**

175       MiSSE is available within the R package *hisse* (Beaulieu & O'Meara, 2016). Some

176    details of MiSSE's implementation differ from other SSE models also implemented in *hisse*.

177    While these differences are summarized here, readers are encouraged to follow the example

178    code available at https://github.com/bomeara/missecomparison when using MiSSE for their

179    empirical analyses. The main difference between MiSSE and other SSE models in *hisse* is how

180    MiSSE models are fit. The user can set and fit MiSSE models individually with a standalone

181    function (hisse::MiSSE) (Table 1). However, it is difficult to know how many different hidden

182    states the models will fit for a given empirical tree. As of now, MiSSE can fit models with up to

183    26 hidden states each representing a given "rate class", which defines a combination of turnover

184    rates ($\tau = \lambda + \mu$) and extinction fraction ($\varepsilon = \mu / \lambda$). In total there are 676 ($26^2$) possible model

185    combinations, each with a different combination of rate class number that range from a

186    minimum of two diversification parameters (one hidden state) and a maximum of 52 (26 hidden

187    states).

188       Performing an exhaustive search by fitting all possible models is not only

189    computationally expensive, but also time-consuming. Furthermore, in general, the complexity of

190    the models with the lowest AICc scale with the size of the tree, meaning that more complex

191    models will tend to be more important in larger trees. In the same way, complex models with

192    many rate classes are likely to be a poor fit for most small trees. To alleviate having to decide

193    which set of models to fit, we developed an heuristic algorithm (hisse::MiSSEGreedy) to search

194    through a reasonably large set of models that terminates after the set of models evaluated no

195    longer provide meaningful support in terms of AICc. The default search starts with a random

196    selection of models. This first set is biased towards simpler models, as initial experimentation

197    showed that these models usually have the lowest AICc for most trees. The subsequent model

198    "chunks" are then models that are neighbors to the ones recovered with the best AICc values in

199    the previous rounds. The path of the MiSSEGreedy search can be visualized with the function

200    hisse::PlotMisseSpace. MiSSEGreedy will continue to fit new "chunk" of models until the lowest

201    ΔAICc of the new "chunk" is higher than that specified by the user (Fig. 2). The user is therefore

202    advised to set the arguments "stop.deltaAICc" and "chunk.size" in a sensible way according to

203    the size of the tree. Based on preliminary tests, we recommend a ΔAIC of 10 for trees with up to

204    1000 tips, which is the current default setting.

205       Once MiSSEGreedy terminates, one can select the best fitted model or average across

206    a set of models in relation to their Akaike weight to estimate the diversification parameters at the

207    tips using a marginal reconstruction algorithm with hisse::MarginReconMiSSE. In addition to

208    marginal probabilities of states at nodes, MiSSE will also return marginal probabilities for the

209 tips. The states can be used as indexes for the estimates of speciation, extinction, and the

210 orthogonal transformations of these rates, namely, net-diversification ($r = \lambda - \mu$), turnover ($\tau = \lambda +$

211 $\mu$) and extinction fraction ($\varepsilon = \mu / \lambda$) returned by the model fit. A tip rate estimate for a given

212 model, then, becomes the weighted average of the diversification rates with the marginal

213 probabilities used as weights.

214

215 **Table 1:** New functions implemented in R package *hisse* to fit, reconstruct and visualize

216 implementation of MiSSE models on phylogenetic trees.

| Function name | Brief description |
|---|---|
| *PlotMisseSpace* | Imports from package igraph to plot a network showing which models have lower AICc weight in relation to their neighbors. |
| *MiSSEGreedy* | Uses greedy algorithm to fit a series of MiSSE models with different complexities in chunks. It will stop when delta AIC does not have significant improvement in the new chunk of models. |
| *MiSSE* | Standalone MiSSE function. |
| *MarginReconMiSSE* | Uses marginal reconstruction algorithm to reconstruct rates along the tree. |
| *plot.misse.states* | "Paints" the averaged rate reconstruction along the branches of the tree. However, inferences of rates through time should not be interpreted literally (see Discussion). |
| *PruneRedundantModels* | Prune models that are effectively identical in terms of likelihood and parameter estimates before model averaging. |
| *TipCorrelation* | Performs linear regression between phylogenetic independent contrasts of tip rates and continuous traits, with the option to prune out cherries (see Discussion). |

217

218       We have also added functionality for eliminating redundant models for all models

219 implemented within *hisse*. When calculating model weights, it is best not to include multiple

220 copies of the same model (Burnham & Anderson, 2002). However, such cases can arise

221 inadvertently: for example, a birth death model and a Yule model are essentially the same

222 (other than in number of free parameters) if the best estimate for extinction rate is zero. In the

223 case of MiSSE, where there can be many models compared, including multiple different models

224    that are in fact identical (in terms of likelihood and parameter estimates) increases the Akaike

225    weights for these models artificially. We thus prune these redundant models with the function

226    hisse::PruneRedundantModels.

227
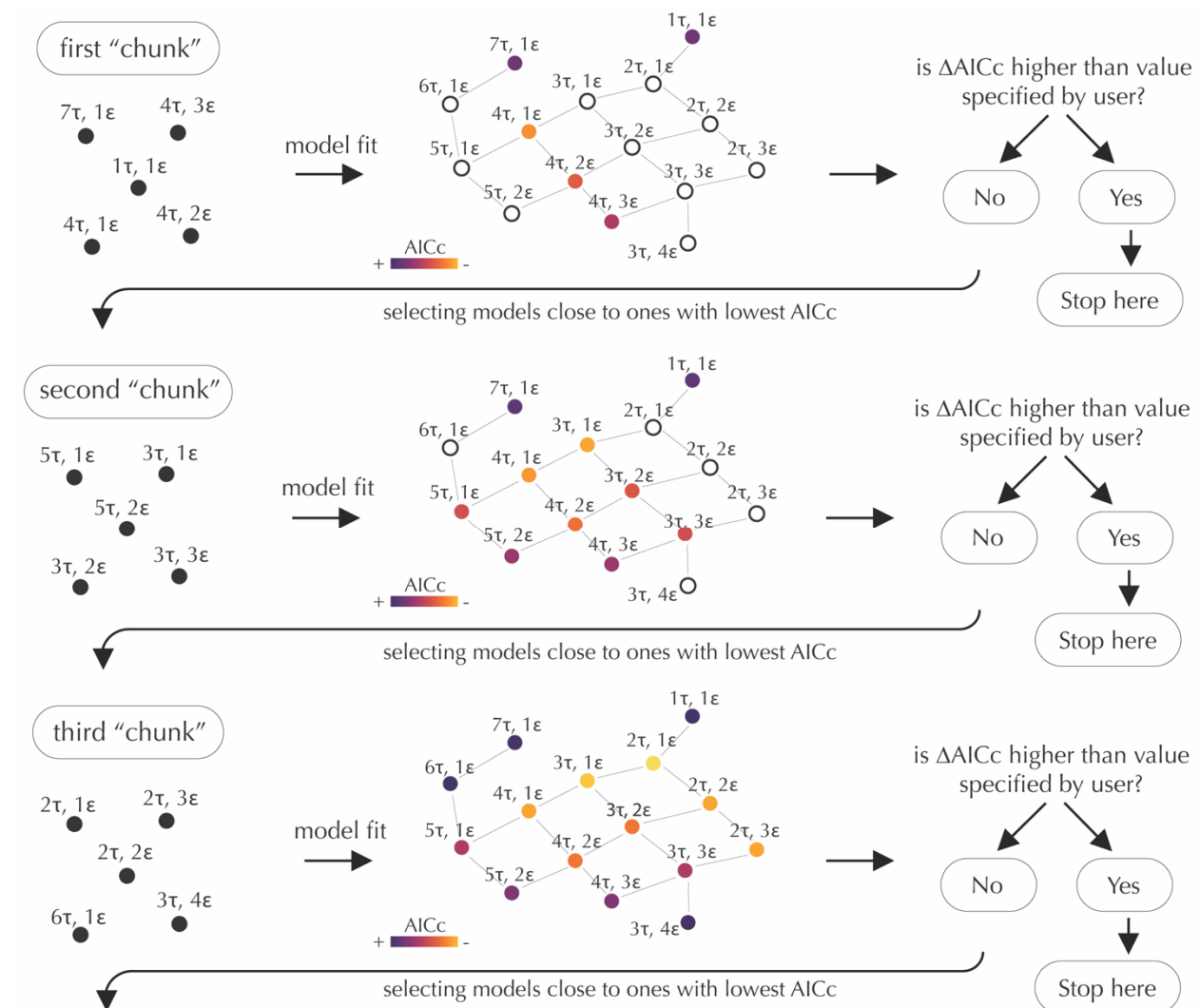


228    [more iterations]

229    **Figure 2:** Rationale behind MiSSEGreedy. The search start with a random set of simple models

230    (first "chunk"). After AICc are calculated for this set, the search continues by fitting the models

231    closest to the ones with lowest AICc in previous "chunks". The search continues until the ΔAICc

232    of the new chunk is higher than the threshold specified by the user. Here the search is

233    represented by a "chunk" size of five, where five models are fitted at each time. The mock

234    example in the figure is inspired by the analysis of *Lupinus* (Fabaceae) available as sample

235    code at https://github.com/bomeara/missecomparison.

236    **2.3. Comparing MiSSE's accuracy against other popular trait-independent methods**

237    To test MiSSE's accuracy, we compared tip-estimates of diversification rates in a set of

238    simulated trees extracted from Title and Rabosky (2019). Briefly, these authors compared the

239    accuracy of four popular tip-rate metrics: DR statistics (Redding & Mooers, 2006), BAMM

240    (Rabosky, 2014), node density (ND; Freckleton et al., 2008) and the inverse of terminal branch

241    length (TB; Steel & Mooers, 2010). They used a set of 5200 trees simulated using nine different

242    models to test the accuracy of the metrics under different scenarios. For speed, we selected a

243    random sample of 10% of their original set of simulations, i.e. 521 trees. We then excluded trees

244    simulated under the "multi-regime, constant-rate birth–death" of Meyer and Wiens (2018)

245    because those were represented by only two trees in our set. The final 519 trees analyzed here

246    have different sizes, though most of them are < 500 tips (Table 2).

247    Besides the range of simulation conditions used for the trees, an advantage of using

248    Title and Rabosky (2019) is that priors and other settings for BAMM were chosen by the authors

249    of BAMM, and thus are likely good approximations to what a skilled user would do. When

250    comparing Bayesian models, either with each other or with non-Bayesian models, priors and

251    MCMC runs may matter greatly in the accuracy of results: one could set priors that exclude the

252    truth and find terrible performance, or set priors at the true values and find excellent

253    performance even in the absence of data. Title and Rabosky (2019) used priors set by

254    BAMMTools (Rabosky et al., 2014) and thus this is a fair test with no special foreknowledge of

255    the true parameters given to BAMM.

256    We extended the original Title and Rabosky (2019) tip rate comparisons to include

257    MiSSE, where we used the following: (1) tip-rates estimated from the model with overall lowest

258    AICc (i.e. the "best" model); and (2) the tip-rates estimated by averaging all models according to

259    their Akaike weight. We followed the same statistical metric as Title and Rabosky (2019),

260    namely, we compared mean absolute error, given by the formula $\sum_{i=1}^{N_i} |\text{rate}_i - \text{rate}_{TRUE_i}| / N$,

261    and the RMSE is given by $\sqrt{\sum_{i=1}^{N_i} (\text{rate}_i - \text{rate}_{TRUE_i})^2 / N}$, where *i* is a single tip and N is the total

262    number of tips in all trees of a given type of simulation. In all cases, the lower the error values

263    the more accurate is the metric. Note that TB, ND and DR are non-parametric (i.e. not based on

264    an    underlying    model)    and    only    estimate    λ.    We    then    used    the    function

265    posthoc.kruskal.conover.test from the R package PMCMR (Pohlert, 2014) to perform a pairwise

266    test for multiple comparisons of mean rank sums and calculate whether errors are significantly

267    different between metrics, assuming a significance value of p < 0.05. All code required to

268    reproduce this comparison can be found at: https://github.com/bomeara/missecomparison.

269

270 **Table 2:** Simulated trees used in comparisons between tip rate metrics. * The original dataset

271 from Title and Rabosky (2019) contains 1200 diversity-dependent trees, but 117 instead of 120

272 (10%) of those trees were included here due to our method of radomly sampling trees.

| Simulation model | Number of trees | Tree-size | Source |
|---|---|---|---|
| Single-regime, constant-rate birth–death | 10 | 100 | Mitchell and Rabosky (2017) |
| Single- and multi-regime, constant-rate birth–death | 10 | 100 | Moore et al. (2016) |
| Single- and multi-regime, constant-rate birth–death | 40 | 10 - 3157 | Rabosky et al. (2017) |
| Single- and multi-regime, constant-rate birth–death | 19 | 9 - 3458 | Mitchell et al. (2019) |
| Single-regime, constant-rate birth–death, lambda uniform | 100 | 100 | Title and Rabosky (2019) |
| Single-regime, constant-rate birth–death, net diversification uniform | 100 | 100 | Title and Rabosky (2019) |
| Pure birth root regime, 1–4 discrete shifts to diversity-dependent regimes | 117* | 54 - 794 | Rabosky (2014); Mitchell and Rabosky (2017) |
| Speciation rate evolves via diffusion process | 120 | 25 - 662 | Rabosky (2010); Beaulieu and O'Meara (2015); Rabosky (2016); Title and Rabosky (2019) |

273 **2.4. Empirical example: plant height and turnover in Eucalypts**

274     We demonstrate the capabilities of MiSSE with an empirical example. Body size is

275 considered an important trait in studies of animal evolution (Cooper & Purvis, 2010) and it has

276 been interpreted as a potential correlate of diversification rates in vertebrates (Cope's rule;

277 FitzJohn, 2010). A similar argument can be made for plants (Boucher et al., 2017). Life span

278 and generation time are often positively correlated with plant height (Westoby, 1998), which

279 would reduce the number speciation and extinction events on a per time basis (Petit & Hampe,

280    2006); i.e. slower turnover rates. Although these correlations are expected in theory, surprisingly

281    few studies have compared them in practice using model-based approaches (e.g. Boucher et

282    al., 2020). The MiSSE framework allows us to easily test this correlation by using regular

283    comparative phylogenetic methods and tip-rates as a response variable.

284    We examined turnover rates in relation to tree height in eucalypts, one of the most

285    distinctive components of the Australian landscape (Wilson et al., 2005). Eucalypts are

286    members of the tribe Eucalypteae in the flowering plant family Myrtaceae, a group that includes

287    some of the tallest trees in all angiosperms (e.g. *Eucalyptus regnans* can reach up to 120 m

288    height) (Wilson et al., 2005; Nevill et al., 2010). Eucalypts are also unusual for being considered

289    a relatively speciose (c. 800 species) lineage of trees. It is thought that the tree habit tends to

290    decrease speciation rates, which is offered as reason that clades comprised of predominantly

291    tree growth forms are frequently found to be less diverse than their herbaceous or shrubby

292    relatives (Petit & Hampe, 2006). However, many eucalypts species are also large shrubs to

293    treelets between 1.5 and 5m height (EUCLID, 2015), which led to the hypothesis that the

294    radiation is driven primarily by the smaller representatives of the clade (Petit & Hampe, 2006).

295    Here we test this idea by contrasting tip turnover rates with plant height in this diverse clade of

296    angiosperms.

297    We used the "ML1" time calibrated phylogenetic tree from Thornhill et al. (2019), which

298    covers 716 out of the c. 800 species of eucalypts. We then collected data on plant height for

299    673 species available at EUCLID Eucalypts of Australia Edition 4 (2015) (EUCLID, 2015). All

300    measurements represent plant maximum height and are given in meters. Again, we use the

301    default implementation of MiSSE, that is, stop.deltaAICc=10 and chunk.size=10, to estimate tip

302    turnover rates in Eucalypteae. We also pruned redundant models with the function

303    hisse::PruneRedundantModels. Next, we estimated tip turnover rates averaging all models

304    according to their AICc weights with the function hisse::GetModelAveRates. To explore the

305    differences between tip reconstructions in MiSSE and BAMM, we also ran BAMM for this tree

306    using the same configuration settings as Thornhill et al. (2019).

307    To test correlations between plant height and tip turnover rates, we used the function

308    hisse::TipCorrelation, which performs a regression-through-the-origin of positivized phylogenetic

309    independent contrasts (PICs, Felsenstein, 1985) between tip rates and a continuous trait. This

310    function also gives the option of pruning out PICs from cherries, i.e. two tips that are sister to

311    each other and share the same branch length to the direct ancestral node, before regressions.

312    We reasoned that because cherries theoretically inherit the exact same rate class probabilities

313    in MiSSE they may: (1) present identical tip rates, forcing the slope of the regression to be close

314  to 0 since all PICs for cherries will be 0; and therefore (2) constitute pseudoreplicates in the

315  analyses. Note that the function will prune PICs and not individual tips that constitute a cherry.

316  Pruning single tips might not be adequate because it would affect all other PIC calculations in

317  the tree; it also can make the results sensitive to which tip is pruned and gives less information

318  for computing contrasts deeper in the tree. Rates and maximum plant height were log scaled

319  before analyses so that they conformed with Brownian motion evolution (Felsenstein, 1985;

320  Garland et al., 1992). All the code necessary to replicate these analyses are available at:

321  https://github.com/bomeara/missecomparison.

322  3. RESULTS

323  **3.1. Simulation studies**

324  Comparisons between tip rate metrics using simulated data show that, in general,

325  MiSSE has a similar accuracy as BAMM (Fig. 3). We present the results for mean absolute

326  error, though RMSE results are practically the same (SM1; Supplementary Material). Both

327  MiSSE and BAMM are more accurate than the non-parametric methods TB, ND and DR for

328  speciation rates, the only parameter estimated by the latter three metrics. There was no

329  significant difference in error measurements between the best MiSSE model and the AICc-

330  weighted average of MiSSE models in any simulated scenario, and therefore these two results

331  will be henceforward treated as a single MiSSE category.
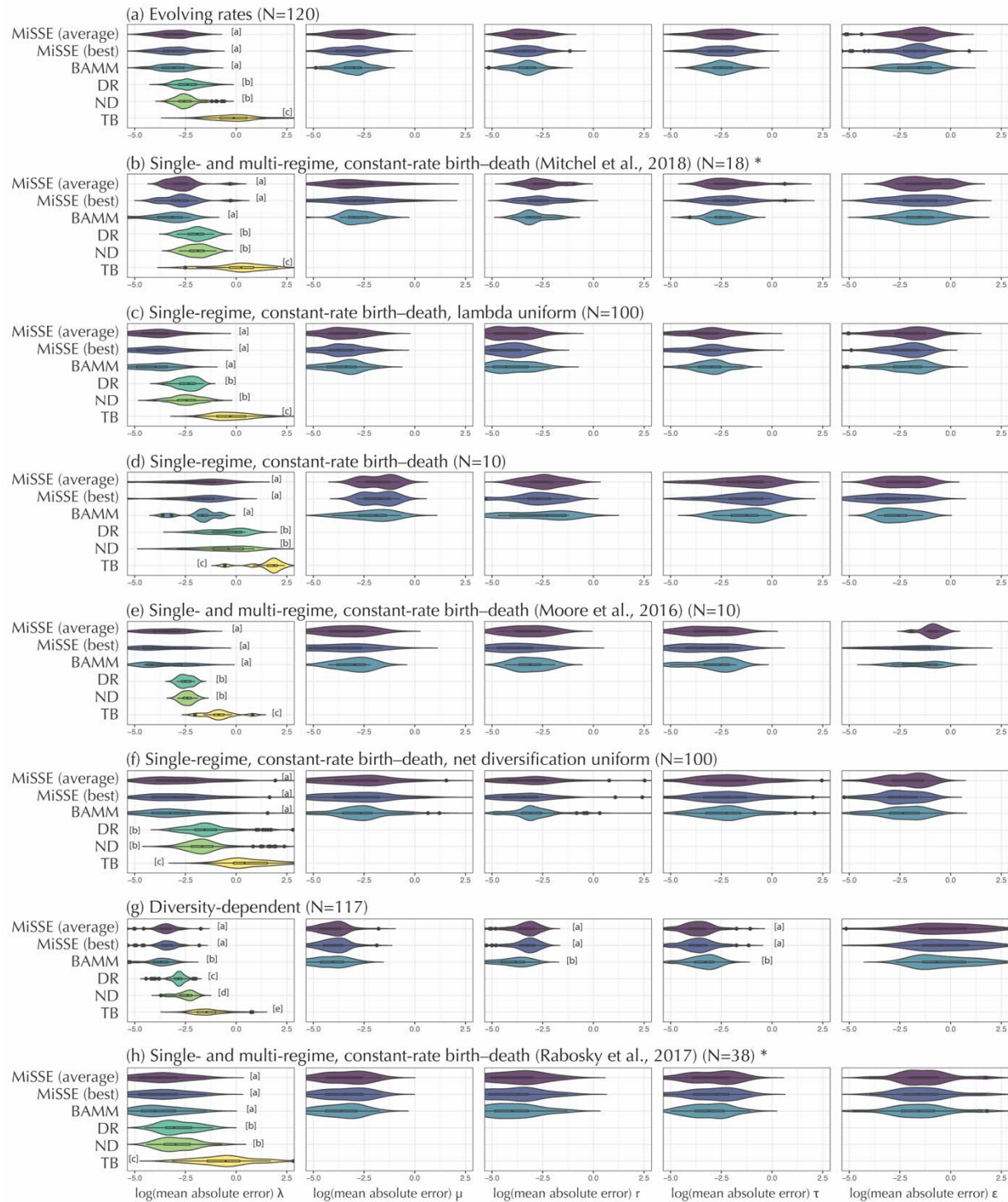
**Figure 3:** Violin plots showing the distribution of mean absolute error between true and estimated tip rates using six different metrics. Each data point corresponds to the mean absolute error between all tips in one tree. λ = speciation, μ = extinction, = turnover, and r = net-diversification, = extinction fraction. Different letters between brackets indicate when metrics are significantly different from each; same letter indicates mean absolute errors that are

338 not significantly different. [NB: at the time of submission, rates reconstructions had not finished

339 in three out of the 519 trees. We expect that the inclusion/exclusion of these trees will not affect

340 the general results of the comparisons].

341

342   TB is significantly less accurate than other methods in all simulation scenarios, and in

343 seven out of the eight simulation scenarios there was no significant difference between error

344 measurements in the pairs ND and DR (lower accuracy) and BAMM and MiSSE (higher

345 accuracy). The only type of tree where all metrics perform significantly differently from one

346 another is in trees simulated under a diversity dependent scenario (Fig.3g). In that case, DR

347 performs significantly better than ND ($p < 0.01$) for speciation rates, though still significantly

348 worse than BAMM and MiSSE ($p < 0.01$) for the same parameter. BAMM performs significantly

349 better than MiSSE for speciation and net-diversification rates ($p < 0.01$), whereas MiSSE

350 performs significantly better than BAMM for turnover rates ($p < 0.05$). However, the magnitude

351 of differences between BAMM and MiSSE were slight, typically differing by less than 10%. All

352 pairwise comparisons can be found at the Supplementary Material (SM2).

### 3.2. Tip-correlation between plant height and turnover

354   Despite the idea that smaller plants have driven the radiation in eucalypts, maximum

355 plant height appears uncorrelated with turnover across the tips of the tree. This correlation is

356 generally weak no matter the metric used to estimate tip rates (MiSSE $R^2 < 0.001$, Fig.4d;

357 BAMM $R^2 < 0.001$, SM3). The general lack of correlation is mainly because: (1) higher turnover

358 rates are not always restricted to clades of small shrubs and treelets, as it can be seeing by

359 comparing the distribution of tip-rates and plant height (Fig.4a-c); and (2) plant height (Fig.4c)

360 appears to be a much more labile trait than turnover rates, regardless of the methods used to

361 infer tip-rates (Fig.4a,b). We note, however, that MiSSE (Fig.4b) recovers more heterogeneity in

362 tip rates than BAMM (Fig.4a), including some accelerations in turnover that are not

363 reconstructed by the latter (clades marked with asterisk, Fig.4a). We note that pruning cherries

364 from the tree minimally changes the slope of the regression line in this example and it does not

365 change our main conclusion that turnover and plant height are likely uncorrelated in eucalypts,

366 given that contrasts of maximum plant height explain less than 0.1% of the contrasts of

367 turnover. In any event, the inclusion of cherries can force the slope of the PIC regression

368 towards 0 in other tip rate comparisons and therefore they should be pruned before analyses.
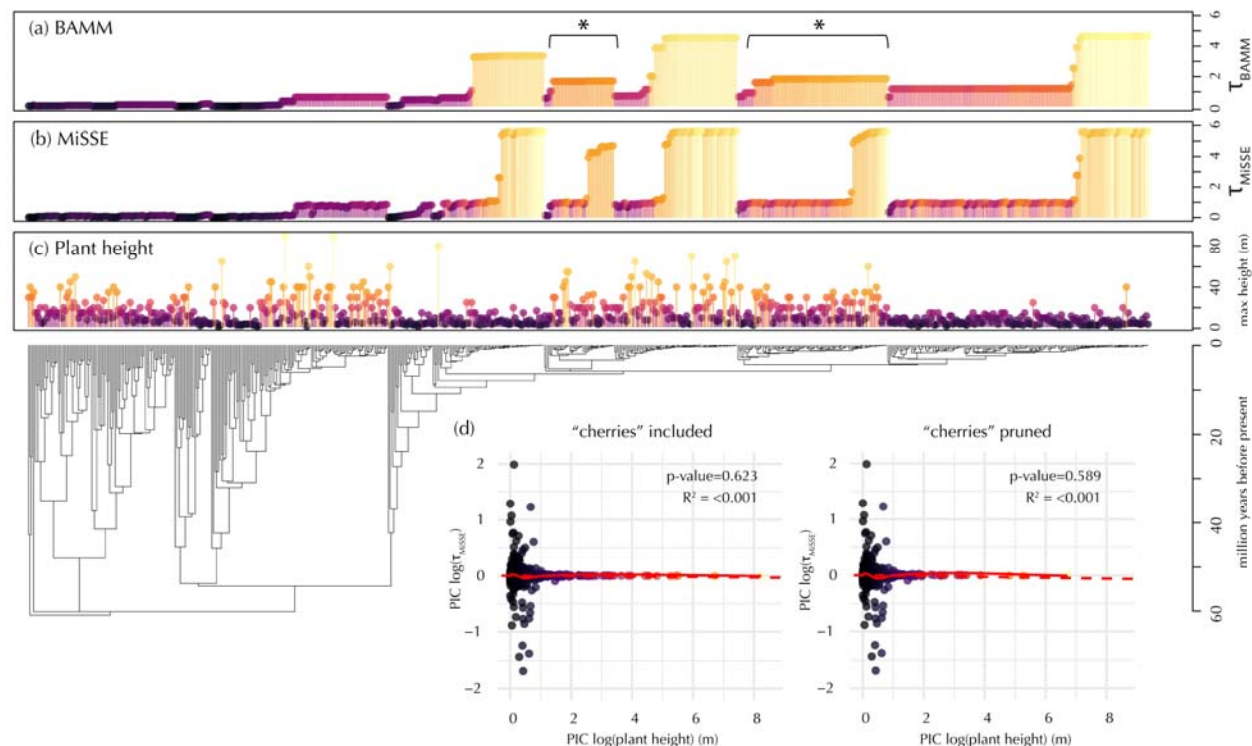
369

**Figure 5:** Comparison between maximum plant height and tip turnover rates estimated by MiSSE and BAMM in Eucalypteae. (a) BAMM turnover rates at the tips; (b) MiSSE turnover rates at the tips; (c) Maximum plant height in meters; (d) Regression through the origin between PICs of MiSSE turnover rates and plant height, with cherries included and pruned. Solid line: smoothed line using the loess method; dashed line: regression line.

## 4. DISCUSSION

### 4.1. MiSSE provides accurate estimates of diversification rates

Here, we describe our "trait-free" MiSSE framework and show how it can be used to estimate accurate diversification rates at the tips of the tree. Our results show that the difference in accuracy in parameters estimated by averaging all MiSSE models or using only the best MiSSE model seem to be minimal and may depend on the tree (Fig. 3). However, as discussed in previous publications (Beaulieu & O'Meara, 2016; Caetano et al., 2018), the user is strongly encouraged to focus mainly on parameter estimation rather than which model fits "best" when using MiSSE, since the former is more informative about the biology of a clade. We note also that, although extinction fraction and turnover are sometimes used as synonyms in the literature (e.g. Alfaro et al. 2009; Title & Rabosky, 2019), as used here turnover rate is a parameter that is explicitly orthogonal to extinction fraction. We emphasize this difference here because many

388    diversification hypotheses may be better described by turnover rates rather than net-
389    diversification or extinction fraction (e.g. Vrba, 1993; Vasconcelos et al., 2021; our empirical
390    example). Also, given that extinction and speciation should tend to correlate through time
391    (Marshall, 2017), net-diversification should tend to approach 0. In those scenarios, turnover can
392    naturally become a better metric for understanding the nuances of ups and downs in
393    diversification dynamics than its isolated components.

394        Key differences between MiSSE and analogous trait-free methods are also highlighted
395    by our analyses of simulated data and our empirical example. Although estimates from MiSSE
396    are as accurate as BAMM, the two methods make very different assumptions. BAMM is based
397    on inferences of rate shifts and has no model underlying rate heritability (Laudanno et al., 2021),
398    so that all tips after a shift inherit a similar rate (e.g. Fig.4). MiSSE may also have some shift-like
399    properties in areas where the probabilities of being in different rate classes change abruptly, but
400    because at every moment in the tree, including at the tips, there is a combined probability of
401    being in all possible rate classes, the evolution of diversification rates becomes smoother.
402    Closely related tips do have similar rates because it is likely that they will be in the same rate
403    class, but they do not inherit the absolute same rate after a shift. The exception is, perhaps the
404    cherries, which will likely inherit the same exact rate. Pseudoreplication from cherries will afflict
405    any model that uses just branch lengths to estimate tip rates. We suspect that, for that reason, it
406    may make sense to prune out cherries from PIC analyses when performing tip-rate correlations
407    using MiSSE, BAMM, DR, or similar tree-only diversification approaches, as we have done in
408    our analysis of eucalypts.

409        Our main objective with the analyses of simulated data, and comparisons among
410    metrics, is not to demonstrate that MiSSE is necessarily a better alternative to other tip rate
411    metrics, nor to compare MiSSE exhaustively against all other available methods for
412    diversification rate estimation at the tips. Our aim is mainly to take one step forward in
413    understanding the limitations of diversification modeling using SSE and hidden-Markov-models.
414    As we continue learning about the behavior of these models, future comparisons may also
415    include other tip-rate metrics that have become available recently in software such as RevBayes
416    (Höhna et al., 2019) and ClaDS (Maliet et al., 2019). Still, we expect that MiSSE will continue to
417    be a good alternative for prior-free, likelihood-only analysis, since all others currently available
418    methods are based on Bayesian frameworks.


419    **4.2. Plant height and turnover rates are uncorrelated in eucalypts**

420     Our empirical analyses demonstrated that the correlation between plant height and
421     turnover rates is weak within Eucalypteae. The use of tree height as a proxy for longevity is
422     common in plants, but it may be that plant height is not the best proxy for longevity in eucalypts.
423     Tall eucalypt trees are often native to productive environments with fertile soils (Pryor, 1976;
424     Thornhill et al., 2019) and it may be that they present fast life cycles for their size, as observed
425     in other parts of the world where soils are also fertile (Russo et al., 2008). In fact, many eucalypt
426     trees are known to be fast-growing plants (e.g. Barnard et al., 2003; Almeida et al., 2004) and
427     fast growth is linked to higher mortality through the growth-survival trade-off (Reich, 2014),
428     which could potentially lead to higher turnover rates even in lineages of tall trees (Baker et al.,
429     2014). If that is the case, perhaps plant height is not the trait that best captures the variation that
430     we sought to explore in our hypothesis. Other proxies, such as leaf mass area and seed size
431     (Westoby, 1998; Wright et al., 2004) may be a better proxy of longevity in these scenarios and
432     should also be tested.

433     Alternatively, if plant height is, in fact, a good proxy for longevity in eucalypts, it may be
434     that longevity is generally uncorrelated with turnover in the clade. A similar trend of uncorrelated
435     body size and speciation rates has been observed in other groups (FitzJohn, 2010; Boucher et
436     al., 2020), but it is difficult to ascertain if the lack of correlation is a particularity of the groups
437     that have been analyzed so far or a general rule. Given the heterogeneity of evolution,
438     identifying what is a rule and what is an exception in macroevolution requires analyses of
439     multiple natural replicates. Similar tests in several clades would be ideal to rule out this
440     possibility. A different approach would be to use QuASSE (FitzJohn, 2010) to construct a model
441     of turnover and height; the disadvantage of this is the need to model the relationship and the
442     (current) impossibility of including additional observed or unobserved factors.

443     One benefit of MiSSE (and similar methods) is that, even though our hypothesis was not
444     supported, we still have new information about the tips: turnover rate (and the other
445     diversification parameters if one wishes). In the same way that looking at two traits, such as
446     height and rainfall, or biome and pollination syndrome, may generate new hypotheses to test,
447     having estimates of turnover rate at tips as in Figure 5 may also lead to new ideas about the
448     factors leading to higher turnover rates in some eucalypts. These can be tested in various ways,
449     including by testing them in other groups.

450     **4.3. Tip rates and best practices in using MiSSE**

451     MiSSE is intended to be used to estimate rates at the tips of the tree, which are also
452     referred to as species-specific diversification rates (Title & Rabosky, 2019; Maliet et al., 2019).

453   Tip rates are, technically, an emergent property of how diversification dynamics are modeled

454   along the branches of the tree (Freckleton et al., 2008; Title & Rabosky, 2019). However, rate

455   estimates are not unique per tip species, so species should not be analyzed in isolation. In other

456   words, a tip with extinction-fraction of 0.9, for instance, does not necessarily indicate that that tip

457   is about to go extinct, but rather that a lot of the species in that same clade are relatively short-

458   lived in comparison to the rest of the tree. Tip rates can then be seen as a "snapshot" of the

459   diversification potential of the species in a clade. In the MiSSE framework, this diversification

460   potential may be interpreted as the combined effect of the many (hidden) states evolving in the

461   tree, which are represented by the different rate classes.

462       From a mathematical standpoint, there is an advantage in using tip rates because it is at

463   the tips where the certainty around the probability of being in a particular rate class is the

464   highest (O'Meara & Beaulieu, in prep). The certainty around these probabilities decreases as

465   one moves towards the root of the tree, and so the ability to point out changes in rate classes

466   also decreases. Of course, the model *does* use information from the whole phylogenetic tree in

467   the calculations of tip-rates, but as one moves towards the present in the tree, the more

468   information is available to reconstruct those rates and thus we are more likely to be certain

469   about the probabilities of being in different rate categories (see O'Meara & Beaulieu, in prep.).

470       The intuitive question that follows is how far back in the past one can go to interpret how

471   the observable diversification potential at the tips came to be and how far into the future can we

472   use it to make predictions about how clades will diversify. The answer is, again, not

473   straightforward and it may depend on the size and age of the phylogenetic tree under analysis.

474   Tip rates will not be able to tell us about mass extinction events deep in the past as these are

475   arguably only measurable from the fossil record (Barnosky et al., 2011), but they may represent

476   a good reflection of diversification dynamics above the species level in times slices close to the

477   present. We therefore recommend great caution with literal interpretations of rate classes deep

478   in time. That is why although MiSSE can "paint" the averaged rate reconstruction along the

479   branches of the tree (i.e. with the function hisse::plot.misse.states), inferences of rates through

480   time should not be interpreted literally. The "painting" should be used just to visualize the rates

481   inferred with MiSSE and should not be used to support narratives of past diversification

482   dynamics for a group. Interpreting past rates is risky given limited information; it could be even

483   riskier with methods like BAMM where there are inheritability problems (Moore et al. 2016).

484   Similarly, modern drivers of diversification dynamics (climate change, invasive species, habitat

485   destruction, and more), which affect especially extinction rates at the present, will not be

486   reflected in the rate estimates returned by MiSSE or similar methods.

487     Another issue is the non-independence of the tip rates. The identical rates for both taxa

488     in a cherry have been discussed above, but even taxa that do not form a cherry may have

489     somewhat correlated rates. It is important to realize that though a phylogenetic model was used

490     in the estimation of tip rates, they themselves are not corrected for phylogeny (which is a reason

491     we used independent contrasts above to compare turnover and plant height). There is also

492     limited information: a resolved tree of 100 taxa has 198 edges: though MiSSE, BAMM, DR, and

493     other methods give 100 tip estimates, there is not enough information to take each one as

494     known with great certainty, nor to draw a strong conclusion based on a rate shared by a few

495     taxa.

496     **4.4. Caveats and persistent issues in modeling diversification dynamics**

497     MiSSE is a powerful tool for estimating tip-diversification rates given its flexibility,

498     accuracy and possibly avoidance of some of the identifiability issues recently highlighted for

499     similar methods (Kubo & Iwasa, 1995; Louca & Pennell, 2020; see O'Meara & Beaulieu, in

500     prep.). However, there are several caveats that users should consider when using MiSSE: (1)

501     Contrary to other similar methods, MiSSE deliberately does not include an implementation for

502     clade-specific sampling fraction. Clade-specific sampling fraction was found to lead to an

503     incorrect likelihood behavior in *any* diversification method despite its appeal (Beaulieu, 2020),

504     so in MiSSE all sampling fractions are global and only one sampling fraction is given for the

505     whole tree. (2) How species are defined is the most relevant when looking at tip rates. For

506     diversification rate models, the data come from the distribution of branching events across the

507     phylogeny. Since most of these events are nearer the present, lumping and splitting taxonomic

508     entities at the species level will have a greater impact on tip-rate estimation. We suspect that

509     MiSSE, like all other trait-free diversification methods, are particularly sensitive to taxonomic

510     subjectivity. (3) Contrary to previous SSE models, transition rates ($q$) among rate classes are

511     always set equal. They are informed in the output, but they have no direct interpretable

512     biological meaning like the transition rates in BiSSE, which represent the frequency of state

513     changes among observed character states, or in GeoSSE, which can be interpreted as the

514     frequency of dispersal out of a biogeographic area. Our current implementation will continue to

515     treat these rates as fixed until it is clearer whether transition rates are practically identifiable in

516     MiSSE. An implementation where transition rates are allowed to vary would be ideal given that

517     shifts between rate classes are likely to occur at different speeds throughout the evolution of a

518     group. (4) There may be still issues related to ascertainment bias and underestimation of

519     extinction rates (Beaulieu & O'Meara, 2018). In that sense, the larger and broader taxonomic

520    sample one uses to test diversification hypotheses, the more biologically realistic extinction
521    rates will tend to be. Ideally, one would be able to correct the extinction estimates in smaller
522    trees, but that is still not possible with the current implementation of MiSSE nor in any other
523    model we are aware of. So, even though extinction rates are estimated accurately relative to the
524    simulated data, they may still be biologically unrealistic in small and young trees. (5) Finally,
525    given that MiSSE does not account for mass-extinction events, it is unclear what impact such
526    events will have on tip-rate estimation in MiSSE, or any "trait-free" approach currently available.

527    **5. CONCLUSIONS**

528    Time-calibrated phylogenetic trees have been important sources of data to understand
529    fundamental aspects of the evolution of organisms. MiSSE provides a novel tool to explore this,
530    and its independence from priors and its ability to explicitly model rate heritability with a finite set
531    of rates makes MiSSE a powerful alternative for diversification analyses with correct likelihoods.
532    There remain many caveats and cautions about its use, but it is an additional tool to understand
533    diversification processes, including a focus on parameter of perhaps great biological relevance
534    such as turnover rate. We suggest that tip-rates estimated by MiSSE will be useful to several
535    questions that were previously addressed by other SSE models. Its versatility is appealing to
536    explore integrative questions linking traits, geographical range distribution, or both in time slices
537    close to the present.

538

542

543    **Author contributions**

544    T.V., B.C.O. and J.M.B. designed the study. J.M.B. led software development, B.C.O. led
545    simulation analyses and T.V. led the empirical example. T.V. wrote the first draft and all authors
546    contributed to the final writing of the manuscript.

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