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# Trait-dependent diversification in angiosperms: patterns, models and data

Andrew J. Helmstetter<sup>1,\*</sup>, Rosana Zenil-Ferguson<sup>2</sup>, Hervé Sauquet<sup>3,4</sup>, Sarah P. Otto<sup>5</sup>, Marcos Méndez<sup>6</sup>, Mario Vallejo-Marin<sup>7</sup>, Jürg Schönenberger<sup>8</sup>, Concetta Burgarella<sup>9</sup>, Bruce Anderson<sup>10</sup>, Hugo de Boer<sup>11</sup>, Sylvain Glémin<sup>12</sup>, Jos Käfer<sup>13</sup>

<sup>1</sup>*Fondation pour la Recherche sur la Biodiversité - Centre for the Synthesis and Analysis of Biodiversity, 34000 Montpellier, France. email: andrew.j.helmstetter@gmail.com*, <sup>2</sup>*School of Life Sciences, University of Hawaii Manoa, Honolulu, HI, 96822, USA. email: roszenil@hawaii.edu*, <sup>3</sup>*National Herbarium of New South Wales, Royal Botanic Gardens and Domain Trust, Sydney, New South Wales, 2000, Australia*, <sup>4</sup>*Evolution and Ecology Research Centre, School of Biological, Earth and Environmental Sciences, University of New South Wales, Sydney, Australia. email: herve.sauquet@gmail.com*, <sup>5</sup>*Department of Zoology, 6270 University Blvd., University of British Columbia, Vancouver BC, V6T 1Z4, Canada. email: otto@zoology.ubc.ca*, <sup>6</sup>*Area of Biodiversity and Conservation, Universidad Rey Juan Carlos, 28933 Móstoles (Madrid), Spain. email: marcos.mendez@urjc.es*, <sup>7</sup>*Department of Biological and Environmental Sciences, University of Stirling, Stirling, FK9 4LA, United Kingdom. email: mario.vallejo@stir.ac.uk*, <sup>8</sup>*Department of Botany and Biodiversity Research, University of Vienna, Rennweg 14, 1030 Vienna, Austria. email: juerg.schoenenberger@univie.ac.at*, <sup>9</sup>*Department of Organismal Biology, University of Uppsala, Uppsala, 75236, Sweden. email: concetta.burgarella@gmail.com*, <sup>10</sup>*Department of Botany and Zoology, University of Stellenbosch, Private Bag X1, Matieland 7602, South Africa. email: banderso.bruce@gmail.com*, <sup>11</sup>*Natural History Museum, University of Oslo, 0318 Oslo, Norway. email: h.d.boer@nhm.uio.no*, <sup>12</sup>*CNRS, Ecosystèmes Biodiversité Evolution (Université de Rennes), 35000 Rennes, France. email: sylvain.glemin@univ-rennes1.fr*, <sup>13</sup>*Université de Lyon, Université Lyon 1, CNRS, Laboratoire de Biométrie et Biologie Evolutive UMR 5558, F-69622 Villeurbanne, France. jos.kafer@univ-lyon1.fr*

**Correspondence:** Andrew J. Helmstetter, FRB-Cesab Institut Bouisson Bertrand, 5, rue de l'École de médecine - 34000 MONTPELLIER. Tel: +33 4 11 28 20 58. Email: andrew.j.helmstetter@gmail.com

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## 1 **Abstract**

2       Variation in species richness across the tree of life, accompanied by the incredible variety of  
3 ecological and morphological characteristics found in nature, has inspired many studies to link  
4 traits with species diversification. Angiosperms are a highly diverse group that has fundamentally  
5 shaped life on earth since the Cretaceous, and illustrate how species diversification affects ecosystem  
6 functioning. Numerous traits and processes have been linked to differences in species richness within  
7 this group, but we know little about how these interact and their relative importance. Here, we  
8 synthesized data from 152 studies that used state-dependent speciation and extinction (SSE) models  
9 on angiosperm clades. Intrinsic traits related to reproduction and morphology were often linked to  
10 diversification but a set of universal drivers did not emerge as traits did not have consistent effects  
11 across clades. Importantly, dataset properties were correlated to SSE model results - trees that  
12 were larger, older, or less well-sampled tended to yield trait-dependent outcomes. We compared  
13 these properties to recommendations for SSE model use and provide a set of best practices to follow  
14 when designing studies and reporting results. Finally, we argue that SSE model inferences should  
15 be considered in a larger context incorporating species' ecology, demography and genetics.

## 16 Introduction

17 Species diversity is unevenly distributed across the tree of life and while substantial research  
18 has investigated why some clades are more diverse than others, many fundamental questions  
19 remain unanswered. The causes behind this unevenness can be diverse, from catastrophic mass  
20 extinctions that decimate diversity (Raup & Sepkoski, 1982) to key innovations that spur on rapid  
21 speciation (Hodges & Arnold, 1995) to ecological factors such as competition that shapes species  
22 co-existence (Drury et al., 2016; Rabosky, 2013). A greater understanding of the drivers of species  
23 diversification is important because they can provide insights into the assembly of communities and  
24 their phylogenetic structure, the evolution of functional traits that underpin a species' role in its  
25 environment, the formation of species interaction networks, and simply how biodiversity has evolved  
26 through time (Morlon, 2014). Research aiming to link species characteristics to macroevolutionary  
27 dynamics has been boosted over the last decade by the increasing availability of large phylogenetic  
28 trees (Jetz et al., 2012; Rabosky et al., 2018; Smith & Brown, 2018; Upham et al., 2019) and the  
29 continuing development of a range of statistical models to infer patterns in species diversification and  
30 the drivers behind them (Barido-Sottani et al., 2020; Beaulieu & O'Meara, 2016; Maliet et al., 2019;  
31 Rabosky & Huang, 2016). The increasing amount of empirical knowledge provides an opportunity  
32 to synthesise what we know so far about a wide range of ecologically diverse and species-rich clades  
33 to uncover general dynamics about the traits that have driven their diversification.

34 Species diversification can be linked to traits via state-dependent speciation and extinction  
35 (SSE) models. This popular family of models are based on birth-death processes where the  
36 diversification rates (birth is speciation, and death is extinction) are dependent on character states,  
37 and where transition rates between states define how state changes occur. The simplest SSE model  
38 is the binary-state speciation and extinction (BiSSE) model (Maddison et al., 2007) that takes as  
39 input a phylogenetic tree and state values (0 or 1) for each species in the tree. This allows users to

40 uncover whether lineages with one state diversify faster than those with the other. SSE models can  
41 also be used to test whether the transition rates between states in one direction (0 to 1) are faster  
42 than the other (1 to 0). The original model has been extended in various ways (Fig. 1) to address  
43 different types of macroevolutionary questions. For example, ClaSSE (Goldberg & Igić, 2012) and  
44 BiSSE-ness (Magnuson-Ford & Otto, 2012) are extensions of BiSSE that include cladogenetic events  
45 (speciation simultaneously associated with change in state), and GeoSSE (Goldberg et al., 2011)  
46 explicitly models how diversification differs among geographic regions. Other developments include  
47 models with more than two character states (MuSSE; FitzJohn, 2012), quantitative traits (QuaSSE;  
48 FitzJohn, 2010) and semi-parametric models (FiSSE; Rabosky and Goldberg, 2017). Perhaps the  
49 most important innovation after the initial wave of SSE models was the introduction of hidden  
50 states into SSE models (Beaulieu & O’Meara, 2016; Caetano et al., 2018; Herrera-Alsina et al.,  
51 2019) as a way to account for background heterogeneity that can lead to false positives (Rabosky  
52 & Goldberg, 2015). The incorporation of hidden states into SSE models allowed diversification  
53 rates to be influenced by the focal traits as well as an unobserved trait(s) and provided a new set  
54 of more complex null hypotheses (the character independent (CID) models). This allowed users to  
55 test how relevant the focal trait is to species diversification (Beaulieu & O’Meara, 2016; Caetano  
56 et al., 2018) in the context of other factors. Here we focus on synthesizing results from SSE models  
57 used to investigate trait-dependent diversification in flowering plants, or angiosperms. There have  
58 been more than 150 such studies, providing an opportunity for an updated perspective on the role  
59 different traits have played in angiosperm diversification (Vamosi et al., 2018).

60 Angiosperms form a clade of more than 350,000 extant species, despite their relatively young  
61 age of a 140 to 270 million years (Crepet & Niklas, 2009; Foster et al., 2017; Li et al., 2019; Magallón  
62 et al., 2015; Sauquet et al., 2021; Silvestro et al., 2021). Almost all of terrestrial life is linked, directly  
63 or indirectly to angiosperms (Benton et al., 2021) and their success makes them an ideal study group

64 for uncovering the intrinsic traits and extrinsic factors driving their diversification. Previous work  
65 has suggested that the origins of angiosperm diversity can neither be tied to major global events  
66 nor the evolution of a single key innovation. Instead various combinations of traits, environment  
67 and ecology acting to stimulate diversification in different groups (Davies et al., 2004; Magallón &  
68 Castillo, 2009; Sauquet & Magallón, 2018), creating a landscape of macroevolutionary dynamics  
69 that vary substantially across different angiosperm clades (Magallón et al., 2019). One hypothesis  
70 proposes that the traits driving the differences in diversification are a range of vegetative and  
71 reproductive characteristics, some of which are unique to angiosperms (Stebbins, 1974). In sexual  
72 systems, for example, dioecy originated in 890-5000 independent instances (Renner, 2014) but these  
73 appear to have led to quite different macroevolutionary dynamics (Käfer et al., 2014; Sabath et al.,  
74 2016; Wang et al., 2021). In the majority of studied traits, we do not know how pervasive such  
75 differences are, nor have broad-scale empirical studies of trait-dependent diversification provided a  
76 general consensus on which traits are most important for angiosperm diversification.

77 In this study we bring together the latest empirical knowledge on angiosperm diversification  
78 to compare the effects of traits in different evolutionary contexts and identify those that have  
79 repeatedly stimulated diversification. We also investigate the relationship between the properties  
80 of datasets (e.g. tree size and global sampling fraction) and the results of published studies,  
81 highlighting how biases in our use of SSE models can affect our conclusions when searching for  
82 general trends. Finally, we identify gaps in our current knowledge and provide a set of best practices  
83 for diversification result-reporting to enhance our ability to fill these gaps in the future.

## 84 **Materials & Methods**

### 85 **Data collection**

86 We collected all published studies that cited SSE methods papers (Beaulieu & O'Meara, 2016;  
87 Caetano et al., 2018; FitzJohn, 2010, 2012; Freyman & Höhna, 2018; Goldberg & Igić, 2012;  
88 Goldberg et al., 2011; Herrera-Alsina et al., 2019; Maddison et al., 2007; Magnuson-Ford & Otto,  
89 2012; Nakov et al., 2018; Rabosky & Goldberg, 2017; Verboom et al., 2020) using Google Scholar,  
90 last accessed 18th May 2021. To facilitate data collection from papers using SSE models, we  
91 developed a new R package called 'papiermache' (<https://github.com/ajhelmstetter/papiermache>).  
92 This package has two main purposes (1) to classify papers into different categories based on the  
93 frequency of term use in the text and (2) to pull out sections of the main text that contain a keyword  
94 or a pair of keywords while highlighting relevant information. We identified the SSE studies on  
95 angiosperms by using the keywords 'angiosperm', 'flowering' and 'plant' subsequently validating the  
96 subset of papers by hand and removing any studies on groups other than angiosperms. We then  
97 collected up to 30 different dataset properties from each paper relating to the trait investigated, the  
98 group studied, the phylogenetic tree and the outcome of the SSE model used (see appendix S1 for  
99 a detailed explanation of each property). In cases where there was uncertainty in how to interpret  
100 or collect data from a study we contacted the authors for their assistance and clarification, where  
101 possible.

### 102 **Trait classification**

103 While some sets of character states were the same among studies (e.g. annual vs perennial;  
104 diploid vs polyploid), many of them did not overlap. We classified traits into different categories to  
105 facilitate comparisons among different trait types. At the broadest classification these were intrinsic  
106 (traits belonging to the species), extrinsic (environmental or geographic traits), interaction (traits

107 related to other species), and combination (multiple traits belonging to different categories that were  
108 grouped, e.g. species that have both small fruits and are found on islands). To allow for analyses  
109 at different grouping levels we developed a trait ontology (Table S1) starting at the broadest level  
110 as just described and becoming more specific, up to level six.

## 111 **Data analysis**

112 To examine the effect of particular traits on diversification we used the trait categories defined  
113 above and calculated the proportion of models in which trait-dependent diversification was inferred.  
114 In many cases multiple models are run per study, typically to investigate the effect of a single  
115 trait across different clades or the effects of different traits on diversification in a single clade.  
116 We considered each model separately here with an outcome of 1 (trait-dependent diversification  
117 detected) or 0 (no effect of trait detected) recovered per model. We examined patterns at different  
118 levels of trait categorization, as well as using only those models with hidden states. Whether  
119 or not trait-dependent diversification was detected was typically based on significance in model  
120 comparisons and/or posterior distributions of rates among states. However, if significance wasn't  
121 inferred or reported, we followed the study narrative and statements made in the text. If model  
122 comparisons were conducted and reported, only the best-fitting model was considered, unless other  
123 models were explicitly referred to in the study. To facilitate comparison, we mainly consider  
124 whether or not a trait has an effect on diversification, irrespective of the direction of the effect (i.e.  
125 increase or decrease of diversification), as the direction is only defined at the state level. When  
126 both the effect and the absence of an effect of a trait on diversification has been inferred in different  
127 studies, we consider these studies 'inconsistent'. Note that inconsistency doesn't necessarily imply  
128 a contradiction, as the differences in the results of SSE models might be caused by differences in  
129 statistical power, type I errors, or biological differences between clades, as we will discuss below.

130 In models where information was available, net diversification rates (lineages per million years)  
131 were extracted for each character state. At a broad scale, relative differences in net diversification  
132 rates were calculated as  $(r_{max} - r_{min})/r_{max}$  and were used to represent the magnitude of the effect  
133 of a given trait on diversification, while taking into account general variation in diversification  
134 rates among clades. Comparisons were then made across trait level 1 and 2 categories. For ease of  
135 interpretation, these analyses were restricted to those models where all net diversification rates were  
136 positive. At a narrower scale, we identified eight traits for which there was enough replication to be  
137 able to assess whether one character state was consistently inferred to have higher net diversification  
138 rates than the other(s). We ensured these traits had been tested at least five times, in at least two  
139 different studies and two different clades.

140 We examined the relationship between SSE model inferences and continuous dataset properties;  
141 number of tips, root age, number of genetic markers, sampling fraction (here referring to global  
142 sampling fraction unless stated otherwise) and tip bias (here calculated as the number of tips  
143 with the most common state divided by the number of tips with rarest state). For each of these we  
144 constructed two density plots representing the distributions of values in cases where trait-dependent  
145 diversification was, and was not, inferred and compared the overlap between densities. We also  
146 fitted generalized additive models (GAM, Hastie and Tibshirani, 2017) to the continuous dataset  
147 properties with the SSE model result as a binary response variable (trait-dependent diversification  
148 vs no effect). The GAM approach allows linear or non-linear smooth functions to be used for  
149 predictor variables, giving greater flexibility in the estimation of relationships between predictors  
150 and the dependent variable. When analysing continuous data, all variables were log-transformed  
151 (or arcsine in the case of sampling fraction) to conform better to a normal distribution. Initially,  
152 we constructed a GAM using all five variables and assigned the mean of the known values to  
153 any missing values. We also assessed each variable individually to determine the shape of each



154 relationship when examined in isolation. In all cases we used smoothing functions (cubic regression  
155 splines) and the dimension of the basis used to represent the smooth term was set to  $k = 5$  for each  
156 variable.

## 157 **Predicting results based on dataset properties**

158 After collecting information from all studies we found that the dataset properties were sometimes  
159 associated with the outcome of the SSE model, that is, whether trait-dependent diversification was  
160 inferred or not. We therefore attempted to predict SSE model results (inference of trait-dependent  
161 diversification vs no effect) from dataset properties alone, and identify those properties with  
162 the largest predictive power. We used all available dataset properties except for highly-specific  
163 categorical variables (e.g. trait levels 5-6, clade, family) and those that varied among different  
164 states (putative root state, sampling per state, samples per state). We used a machine learning  
165 approach, extreme gradient boosting, with the R package ‘xgboost’ (Chen & Guestrin, 2016), a  
166 supervised learning approach based on gradient boosting machines. This family of methods uses a  
167 labelled dataset (the outcome is known) and an ensemble of weak prediction models (e.g. decision  
168 trees) whereby new models are added on to existing models per iteration to minimize error. The  
169 xgboost algorithm improves upon other boosting methods with its increased speed and enhanced  
170 regularization to minimize overfitting (Chen & Guestrin, 2016). Prior to running our models,  
171 categorical variables with more than two categories were converted into binary, dummy variables  
172 using one-hot encoding (i.e. each unique category is converted into its own binary variable) to  
173 facilitate model building. We trained models on a random selection of 80% of our dataset and  
174 tested them on the other 20%. After a parameter optimisation step we repeated this process 500  
175 times to produce a range of accuracy values, the percentage of cases where the real outcome matched  
176 the classification, to account for stochasticity in the test and training datasets. For each iteration

177 we also recovered the relative importance of each variable, which allowed us to determine which  
178 dataset properties had the most influence on the model. Given the inter-dependency of variables  
179 across the different decision trees, it is difficult to uncover whether a given property generally leads  
180 to trait-dependent diversification or not with xgboost. We avoid interpreting the results in this  
181 way, focusing on how accurate prediction can be and the variables that are most important to the  
182 model's predictive ability.

## 183 **Results**

### 184 **Traits studied and their effects on diversification**

185 We collated information on trait-based diversification from 152 studies using a total of 629 SSE  
186 models to study angiosperm diversification. We found that 124 studies were conducted on a single  
187 clade, the rest examined diversification patterns across multiple clades. Variation in breadth of  
188 different traits investigated was also observed within studies. In total, 92 studies examined just a  
189 single trait (i.e. one level 6 category, see Table S1), while 38 studies looked at diversification patterns  
190 in sets of traits that belonged to more than one trait category at the highest level (e.g. extrinsic and  
191 intrinsic traits). In terms of taxonomic level, SSE models were most often run on focal genera, or  
192 families (Fig. S1) and study clades were relatively evenly-distributed across the angiosperm tree of  
193 life (Fig. S2). Studies have focused on 36 out of 64 angiosperm orders, and 83 out of 416 families.  
194 As expected, diversification interest is generally proportional to the amount of species diversity  
195 in different parts of the angiosperm tree of life. There was a clear, positive correlation between  
196 the number of species in a clade (order, family) and the number of state-dependent diversification  
197 studies applied to the clade (Fig. S3, S4).

198 At the highest level of classification, intrinsic traits (i.e. those belonging to the plant species

199 itself) were tested more often (295 models or 47% of models run) than extrinsic traits (i.e. those  
200 related to the species' habitat and geography, 255 models or 41%). Researchers tended to study  
201 intrinsic traits relating to reproduction (e.g. flower morphology, fruit morphology, breeding system),  
202 traits related to species' biogeography (e.g. biome, geographic region) and vegetative traits (e.g.  
203 life form, leaf morphology), investigating less often physiological characters (e.g. photosynthesis)  
204 or those related to interaction (e.g. symbiosis or dispersal) (Fig. 2). We compared the proportion  
205 of trait-dependent diversification outcomes in SSE models at different category levels. In general,  
206 intrinsic traits were found to be associated with diversification slightly more often than extrinsic  
207 traits (57.3% vs 52.5%).

208 If a trait has been studied more than once we can compare the effect of this trait on diversification  
209 in different evolutionary contexts to see if similar trends are found. Our collation of data showed that  
210 results inferred with SSE models were inconsistent at both broad and narrow scales (grey vs coloured  
211 portions of bars in Fig. 2). For example, traits such as lifespan (Azani et al., 2019; Drummond  
212 et al., 2012; Salariato et al., 2016; Soltis et al., 2013) and ploidy level (Folk & Freudenstein, 2014;  
213 Han et al., 2020; Landis et al., 2018; Zenil-Ferguson et al., 2019) yielded different results depending  
214 on the angiosperm group studied. Polyploidy has been linked to increased diversification in *Allium*  
215 (Han et al., 2020), while it had no effect on the diversification of Brassicaceae (Román-Palacios et al.,  
216 2019). Among those trait level 2 categories that have been tested using >25 models, vegetative  
217 traits yielded trait-dependent diversification more often than any other trait type, while pollination  
218 yielded the lowest proportion (Fig. 2a).

219 Though replication among character states was typically low we found eight traits that were  
220 tested often enough to assess whether there was a consistent effect of one state on diversification  
221 and the magnitude of the effect (Fig. S5). In three of these traits (lifespan, sexual system  
222 and woodiness) trait-dependent diversification was rarely found while in the remaining traits

223 (epiphytism, biome, ploidy, photosynthesis and self-compatibility) results more often indicated  
224 trait-dependent diversification. However, we did find conflict in which states increased in diversification  
225 among different models in all traits except epiphyte form and self-incompatibility. Examining the  
226 absolute net diversification rates among states of seven traits (sexual system could not be assessed as  
227 most rates were not time-calibrated) we found that patterns across clades reflected those detailed  
228 above (Fig. S6). Net diversification rates in traits rarely associated with diversification (e.g.  
229 woodiness or lifespan) were generally similar among the different states (Fig. S6). To understand  
230 the effect of major trait categories on diversification we plotted the distribution of relative differences  
231 in net diversification rates for models belonging to each trait category (Fig. S7). Generally we  
232 found that there was a wide range of relative differences in each trait category but no statistically  
233 significant differences among categories.

## 234 **The evolution of SSE model use and methodological innovation**

235 As SSE models themselves have diversified, the relative frequency of model-use has evolved.  
236 We collated data on the types of SSE model used in each study, and plotted their use by year  
237 of publication (Fig. 3). BiSSE has remained popular even as newer more complex models have  
238 emerged. Models with multiple states, predominantly MuSSE, have also been commonly used  
239 showing that researchers are interested in the effects of more complex traits or trait groups with  
240 more than two states. There has also been a consistent focus on using SSE approaches related  
241 to geography in models like GeoSSE and GeoHiSSE. When examining the number of studies that  
242 use SSE models each year we find a rapid increase since the first use of BiSSE on angiosperms in  
243 2009 until a conspicuous slowdown and slight drop in 2015 (Fig. 3). This appears to coincide with  
244 the publication of a number of influential papers that criticised the propensity of SSE methods for  
245 false positives (Maddison & FitzJohn, 2015; Rabosky & Goldberg, 2015) and pointed out power

246 limitations (Davis et al., 2013). After this, SSE model use continued with a greater variety of  
247 models owing to the development of models with hidden states (Beaulieu & O'Meara, 2016), which  
248 have since spread to all aspects of SSE model use (Fig. 1), becoming the dominant set of models  
249 by 2019 (Fig. 3). We tested whether the use of hidden state models (30 studies) lead to more  
250 consistent results than those reported for all studies (see above). We found that the proportion of  
251 trait-dependent outcomes increased for pollination, remained about the same for reproduction and  
252 decreased substantially for biogeography, vegetative and habitat (Fig. S8).

### 253 **The importance of dataset properties**

254 The input data for macroevolutionary studies have grown in size and quality, in parallel with  
255 the innovations in the SSE models. For example, we found evidence that over time, trees used with  
256 SSE models have gradually grown larger (Fig. S9). We examined the relationship between tree size  
257 and whether or not trait dependent diversification was inferred, regardless of the trait investigated.  
258 We found that, in general, trait-dependent diversification was detected less often when trees had  
259 smaller numbers of tips (Fig. 4a, S10a). The number of tips in a tree is important for robustness  
260 of SSE model results and guidelines for adequate power were put forward by Davis et al. (2013)  
261 who suggested that results from models using trees with fewer than 300 tips should be treated with  
262 caution. But has this recommendation shaped SSE model use? We examined sizes of trees used  
263 before and after this guideline was published, across all SSE models. The proportion of models  
264 run on trees with fewer than 300 tips was initially very high (94% of 139 total models) in studies  
265 published up until 2013. It then decreased to 57% (277 of 482) models in studies published from  
266 2014 onwards. Despite this reduction, more than 60 models were run on trees with fewer than 50  
267 tips after Davis et al. was published in 2013.

268 Tree size and root age are closely linked because trees with larger numbers of tips are generally

269 older (Fig. S11). Indeed, we found that trait-dependent diversification was detected more often  
270 when trees with an older root age were used (Fig. 4b, S10b). Regardless of their size or age, trees  
271 that more accurately represent the true phylogeny of a group will allow us to more reliably estimate  
272 its diversification history. We used information on the total number of molecular markers (nuclear  
273 + plastid + mitochondrial) as a proxy for tree quality. We found a difference in the distributions  
274 indicating that models with trait-dependent outcomes usually had better quality trees than those  
275 that did not (Fig. 4c, S10c).

276 Another issue that has been repeatedly brought up in simulation studies is the potential effect  
277 of inflated tip bias (Davis et al., 2013; Maddison et al., 2007). Tip bias increases when there is a  
278 higher frequency of one state than the others across the tips of the tree. Upon examining the data  
279 used with SSE models we found substantial overlap between densities (Fig. 4e) except for extreme  
280 values of tip bias where SSE models tended to find no effect of the trait studied (Fig. S10e). Tip  
281 ratio bias recommendations were also made by Davis et al. (2013), who cast doubt on inferences  
282 made when the rarest state occurs in less than 10% of the taxa. Prior to 2014, 83% of SSE models  
283 (55 of 66) had suitable tip ratios and this figure remained similar (87%, 313 of 360) for the studies  
284 that came after.

285 Global sampling fraction is the proportion of known species that are present in the tree. If  
286 the sampling fraction is low it can drastically affect diversification rate estimation (Chang et al.,  
287 2020; FitzJohn et al., 2009; Sun et al., 2020). The sampling fraction was explicitly modeled in SSE  
288 methods by Fitzjohn et al. (2009), who recommended that the sampling fraction should be at least  
289 25% to adequately capture diversification dynamics. In our data set, sampling fraction ranges from  
290 <0.1% to complete (100%) sampling. All 10 models published in 2009 and earlier had sampling  
291 fractions greater or equal to 25% compared to 60% of 606 models after its publication. This trend  
292 (Fig. S12) probably reflects easing of assumptions on complete species sampling, but also indicates

293 that high levels of incomplete sampling are common in recent literature.

294 Furthermore, we found a striking pattern, showing that those models that used trees in which  
295 sampling fraction was low generally yielded trait-dependent diversification, particularly when sampling  
296 was less than 40% (Fig. 4d, Fig. S10d). Conversely, high sampling fraction was more often  
297 associated with a lack of trait-dependent diversification. Given that the inference of trait-dependent  
298 diversification varies with tree size (Fig. 4a), we wondered whether there may also be a relationship  
299 between sampling fraction and tree size. However, upon examination we found only a weak, negative  
300 trend where trees with more tips had slightly lower sampling fractions (Fig. S13). We then looked at  
301 the relationship between sampling fraction and the number of species in the study clade of interest  
302 and found a steeper negative relationship (Fig. S14) meaning that the larger the clade of interest is,  
303 the less well-sampled it tends to be. Datasets of small clades with low sampling fraction generally  
304 dont exist (as they should not be studied) and large clades with high sampling are currently very  
305 rare, causing points in the bottom left and top right of figure S14 to be missing. These negative  
306 trends remain similar regardless of whether trait-dependent diversification is inferred or not.

### 307 **How predictable is the inference of trait-dependent diversification?**

308 Empirical results in angiosperms clearly exhibit strong relationships between various dataset  
309 properties and whether trait-dependent diversification is inferred by the SSE model. To assess the  
310 importance of the continuous dataset properties together we fit a GAM including the number of  
311 tips, root age, the number of markers, the percentage of sampling and the tip bias (Fig. S15). We  
312 found that all variables except age of tree were significant when predicting SSE model outcome  
313 ( $r^2 = 0.239$ , see Table S2 for full details).

314 If we had comprehensive information about the input data, including the dataset properties  
315 investigated above but also information about taxonomy and traits, could we predict whether

316 trait-dependent diversification would be inferred? Using a machine learning approach, extreme  
317 gradient boosting (Chen & Guestrin, 2016), we were able to correctly predict, with approximately  
318 72% accuracy (60-80%, Fig. S16), whether SSE models would infer trait-dependent diversification.  
319 The most important factors were the information-dense, continuous variables (Fig. 5), further  
320 reinforcing earlier observations about their potential influence on SSE model outcomes (Fig. 4,  
321 S10, Table S2). Generally, categorical variables related to the trait studied (e.g. fruit morphology),  
322 SSE model used (e.g. HiSSE) and order investigated (e.g. Poales) played a smaller but still  
323 important role in the model's predictive ability (Fig. 5).

## 324 Discussion

### 325 No consistent drivers of angiosperm diversification

326 Previous work has proposed that diversity in different angiosperm groups may have been shaped  
327 by various combinations of ecology, traits and environment (Davies et al., 2004; de Queiroz, 2002;  
328 Donoghue, 2005; Donoghue & Sanderson, 2015; Hernández-Hernández & Wiens, 2020; Magallón &  
329 Castillo, 2009). Indeed, our compilation of the results of 152 studies on trait-dependent diversification  
330 in angiosperm clades supports this proposal; that is, the factors driving angiosperm diversification  
331 are more complex than a set of universal drivers. When we compared studies investigating the  
332 same trait types we found that conclusions generally differed with some indicating that the trait  
333 does have an effect on diversification and others concluding there is no effect. We note that the  
334 inconsistency observed might reflect real trends in the data, or be due to dataset properties (lack  
335 of power, model mis-specification). In the following, we will first discuss the biological conclusions  
336 of our study, before considering dataset and model properties.

337 Our analyses and results centered around how traits (e.g. pollination-related traits) rather



338 than the character states of these traits (e.g. bee vs bird pollination) affect diversification. After  
339 grouping traits into several levels of categories (Table S1), we found that some types of traits  
340 were more often found to affect angiosperm diversification than others. It may come as no  
341 surprise that floral traits, are among the most investigated and influential (Fig. 2b). Indeed,  
342 the flower contains the organs needed for sexual reproduction, making it central to the biology,  
343 ecology and evolution of angiosperms, and flower characteristics certainly have a large role in  
344 determining differences in diversification (Vamosi et al., 2018). In particular, reproductive systems  
345 are highly variable in angiosperms (Barrett, 2013) and are again thought to be closely linked to  
346 their success (Barrett et al., 1996). Results from SSE models lend some support to this idea - for  
347 example, trait-dependent diversification was commonly inferred when mating system traits were  
348 investigated (Fig. S5). Even so, we found that in most cases, breeding system (the higher level trait  
349 classification including all aspects of mating and sexual systems) often did not yield trait-dependent  
350 diversification, due to variability in the effects of sexual systems. Vegetative traits (those related to  
351 the growth and non-floral morphology of the plant) and other intrinsic traits including those related  
352 to photosynthesis and the genome have received less attention than floral traits (Fig. 2). However,  
353 they were more consistently associated with trait-dependent diversification than reproductive traits.

354 Unfortunately we could say little about which state was advantageous for a given trait because  
355 a lack of overlap among states across the 152 studies. Nevertheless we were able to examine how  
356 particular states affected diversification in eight traits. Five of these demonstrated how different  
357 states of the same trait (e.g. woody and herbaceous species) can increase diversification in different  
358 groups (Fig. S5) meaning that only three showed consistent patterns where one state was associated  
359 with elevated diversification rates (epiphytism, non-C3 photosynthesis and self-incompatibility).  
360 However it is difficult to say whether these have truly consistent effects on diversification as they  
361 have only been investigated a handful of times in a relatively small proportion of angiosperm species

362 (e.g. self-incompatibility has been tested in Solanaceae and Onagraceae only).

363 Despite some general patterns in those traits that are more often influencing angiosperm  
364 diversification, the overarching trend is that the effect of a trait on diversification is clade-dependent.  
365 Therefore, the main question remains open: what drives differences in diversification among angiosperms?  
366 The fact that a definitive answer has yet to be found suggests that it's the complex interplay  
367 between trait evolution, biotic interactions and geography that matters. Indeed, geography (range  
368 size, biome) has been identified many times as an important factor (Hernández-Hernández & Wiens,  
369 2020; Vamosi et al., 2018), but it is unclear whether this is a cause or a consequence of differences  
370 in diversification. Others have suggested that it is not the presence or absence of a trait that  
371 determines the evolutionary success of a clade, but rather the capacity to change (Onstein, 2019;  
372 Ricklefs & Renner, 1994). This could partly explain the inconsistency of the inferences, but again,  
373 trait diversity could be both a cause and a consequence of species richness. Furthermore, the choice  
374 of clades and traits, as well as the quality of the input data, also influence whether or not differences  
375 in diversification are detected, and therefore our conclusions.

## 376 **The importance of evolutionary scale and context**

377 Users of models of trait-based diversification face an important challenge - choosing the context  
378 in which to conduct analyses. In the simplest scenario, where a trait only evolved once in the  
379 study clade, its effect on diversification cannot be tested (Maddison & FitzJohn, 2015) and thus  
380 this type of context should be avoided. At the intermediate scale a trait may have evolved multiple  
381 times in closely-related clades but their evolutionary context (i.e. species' genomes, morphology,  
382 ecology, or external environments) is much more similar than distantly-related ones. So, associations  
383 between states and rates cannot be interpreted as a general pattern in this limited phylogenetic  
384 scope. Broadening the scope of the analysis, by way of either a larger tree, or multiple trees in a

385 meta-analytic framework (Sabath et al., 2016) can help to reveal these general patterns but leads  
386 to different challenges.

387 At larger phylogenetic scales, trees with many taxa are more likely to contain a range of  
388 branching patterns where lineage accumulation is faster in some parts of the tree than in others. In  
389 older clades there has been more time for macroevolutionary processes to have an impact on the trees  
390 we infer and the traits we observe today. As we observed, larger, older trees more commonly yield  
391 trait-dependent diversification (Fig. 4). However, their heterogeneity (due to e.g. molecular clock  
392 rate variation; Shafir et al., 2020) would also make them more susceptible to false-positive errors  
393 that could over-inflate the number of times trait-dependent diversification is detected (Rabosky &  
394 Goldberg, 2015). Indeed, one of the major criticisms of early SSE models was the propensity to  
395 infer false positives due to model inadequacy: the models were based on the assumption that only  
396 the trait of interest would influence diversification, so any kind of heterogeneity would lead to the  
397 rejection of the null hypothesis (Maddison & FitzJohn, 2015; Rabosky & Goldberg, 2015). This  
398 could explain the inconsistency of the effects of traits across clades - it may be that false positives  
399 caused by lineage-specific factors correlated with the shared focal trait are driving the disparate  
400 patterns. Models with hidden states go some way towards alleviating this issue as they can account  
401 for lineage-specific factors. When only considering results from models with hidden states we found  
402 that the proportion of trait-dependent diversification changed substantially for some traits, though  
403 inconsistency was still common (Figs. 2, S8). As more studies with hidden states are conducted,  
404 we will find out whether these trends are general. While hidden states models certainly are an  
405 improvement, they assume that these states are categorical and have constant transition rates,  
406 which very likely doesn't capture all sources of heterogeneity. They cannot handle all cases of  
407 possibly misleading inferences, e.g. when the effect of a trait that evolved multiple times is driven  
408 by one clade where it strongly influences diversification while leaving it unchanged in other clades

409 (Beaulieu & O’Meara, 2016; Maddison & FitzJohn, 2015). Furthermore, there has yet to be a study  
410 that thoroughly assesses the model adequacy of HiSSE, as has been done for BiSSE (Rabosky &  
411 Goldberg, 2015).

## 412 **Best practices for SSE model use and result reporting**

413        Though a number of recommendations have been made for accurate inference with SSE models,  
414 most empirical studies do not meet them. When using the strict thresholds suggested in the  
415 literature (25% taxon sampling, 300 tips and minor tip state frequency of 10%; Davis et al., 2013;  
416 FitzJohn et al., 2009) we find that just 20 of 152 studies contain models that meet all criteria. The  
417 apparent relationship between sampling fraction and inference of trait-dependent diversification  
418 (Fig 4) should invite us to be cautious about studies using low sampling fractions, as it has been  
419 shown that better sampled trees yield more accurate estimates of diversification rates (Chang  
420 et al., 2020; FitzJohn et al., 2009). However, publication bias may also be playing a role. If no  
421 trait-dependent diversification is detected in a poorly sampled clade this may be attributed to a  
422 lack of power that ultimately prevents publication, thereby inflating the number of studies with  
423 low sampling that detect trait-dependent diversification. To clarify these observations, simulation  
424 studies should be undertaken to investigate the influence of sampling fraction together with model  
425 inadequacy on SSE model inference.

426        In most studies, some of the information we consider crucial for the interpretation of the results  
427 was lacking, or it was difficult to access. Collecting data for many properties (e.g. samples per  
428 state) required us to count from figures or extract statistics from archived raw data, which were not  
429 always freely available. For example, we were unable to extract and use the number of independent  
430 origins of each character state. Robust estimates of associations between traits and diversification  
431 rates necessitate multiple independent origins (but not too many (Rabosky & Goldberg, 2015))

432 and corresponding rate changes (FitzJohn et al., 2009), so an idea of this value per study, inferred  
433 using ancestral state reconstructions, would be useful for interpretation of the robustness of results.  
434 This could be done by combining stochastic mapping of traits with an SSE model (Freyman &  
435 Höhna, 2019), though this is generally not available for SSE approaches. Likewise, diversification  
436 and transition rates were often not reported in an easily-accessible and standardized manner, or in  
437 some cases, not at all. These should be reported, and if possible, with confidence metrics around  
438 rate estimates e.g. Bayesian credible intervals.

439 Louca & Pennell (2020a) recently pointed out how diversification rate estimation can be susceptible  
440 to issues of unidentifiability. Though SSE models are not directly implicated (Helmstetter et al.,  
441 2021), one potential way to help ‘future proof’ analyses from unidentifiability caused by overfitting  
442 would be to avoid reporting and assessing speciation and extinction rates separately, focusing  
443 instead on compound parameters such as net diversification rate ( $\lambda - \mu$ ), turnover rate ( $\lambda + \mu$ )  
444 and extinction fraction ( $\mu/\lambda$ ) that are typically used in more recent SSE models (e.g. HiSSE). To  
445 encourage standardized result reporting we propose an initial set of characteristics that should be  
446 made available in all future studies using SSE models (Supplementary Data 1).

447 Given that evolutionary context appears to be important for understanding trait-dependent  
448 diversification, how to best choose a trait and clade to study? Trait choice can be helped by  
449 preliminary knowledge of the phylogenetic tree and ancestral state reconstruction, which could be  
450 used to ensure that the derived state(s) arose multiple times and that the ratio among different  
451 states is not extreme (<10:1). In terms of choosing a clade, it is first important to adhere, as best  
452 as possible, to the recommendations for using SSE models e.g. avoid clades much smaller than 300  
453 taxa and focus on those that are well sampled (>25%). If recommendations cannot be followed,  
454 because of natural limitations in clade size, for example, these should be stated clearly as caveats.

455 Working at a much larger scale, e.g. angiosperm-level analyses, is certainly appealing but creates

456 a range of issues related to confounding factors that current models will find difficult to disentangle.  
457 To better learn about the factors that influence angiosperm diversity we therefore suggest studies  
458 focus on multiple intermediate-sized clades i.e. large genera, families or tractable orders. However, if  
459 these clades are well-sampled they would approach the limit of our current computational feasibility  
460 (but see Louca and Pennell, 2020b). Working with many smaller clades may therefore be more  
461 feasible in the near future and also yield important insights via the comparison of diversification  
462 patterns among many different groups (e.g. Sabath et al., 2016), which we think is an acceptable  
463 tradeoff for reduced power in standalone analyses. Examining the effect of the same trait in multiple  
464 clades would allow researchers to account for the unique and shared aspects of their biology (e.g.  
465 through the use of hidden states or trait combinations), and then to combine results (Rabosky &  
466 Goldberg, 2015) to uncover general patterns.

## 467 **Knowledge gaps and future avenues**

468 Our review allowed us to identify groups that are understudied and therefore good focal points  
469 for future research to gain a more well-rounded picture of angiosperm macroevolutionary dynamics.  
470 One of the most obvious is Asteraceae, species-rich yet subject to relatively few trait-based diversification  
471 studies (Fig. S4), or Alismatales, an order that has more than 4,500 species (Fig. S3) but just a  
472 single study on their trait-based diversification (Canal et al., 2019). In addition, some families with  
473 more than 1,000 species, such as Phyllanthaceae or Orobanchaceae have yet to be studied in this  
474 way.

475 High-quality phylogenetic trees are not the only ingredient for SSE studies; trait data also need  
476 to be available. We highlight traits related to lifespan, dispersal and symbiosis as ripe avenues for  
477 future work that have potential to unearth important patterns in trait-dependent diversification.  
478 However, apart from a few traits such as geographical range or climatic preferences, gathering

479 high-quality data for large numbers of species is a time-consuming activity. We encourage the  
480 integration of trait data generated from SSE studies (and others) into large, global trait databases  
481 such as eFLOWER (Sauquet et al., 2017), TRY (Kattge et al., 2020) or more focused databases  
482 (e.g. AusTraits (Falster et al., 2021)). These will act as important resources as researchers consider  
483 several traits in tandem when testing for context-dependent effects of traits, or when disentangling  
484 the traits hiding in the hidden-state approaches. Most importantly, studies should be conducted  
485 on traits where clear hypotheses can be generated about their effect on diversification in the chosen  
486 study clade.

487 SSE methods are statistical tools that are aimed to uncover correlations, and cannot themselves  
488 discover causal relationships. By definition, macroevolutionary models try to capture the result of  
489 many aggregated small-scale processes in a few high-level parameters. Speciation is an instantaneous  
490 split of one branch into two in most macroevolutionary models, although in reality there might be  
491 a wide range of different dynamics depending on environmental heterogeneity, biotic interactions,  
492 and intrinsic traits (e.g. breeding systems, genomic incompatibilities) (Coyne & Orr, 2004). Thus,  
493 if a trait is predicted to affect speciation and extinction, high-quality inferences of diversification  
494 rates, for which our synthesis provides some guidelines, should be able to detect a signal. However,  
495 this signal is only a piece of the puzzle, as it is through various ecological and genetic processes that  
496 can also be put to the test. For example, Park et al. (2018) compared sister species with contrasted  
497 mating systems (selfing vs. outcrossing) and showed that niche breadth tended to decline over time  
498 in selfing lineages, in agreement with the dead-end scenario proposed for this trait and detected  
499 in macroevolutionary analyses (Goldberg & Igić, 2012; Höhna et al., 2019). Additionally, we can  
500 identify traits that have an effect on ecological and genetic mechanisms that control speciation  
501 and extinction, such as traits affecting coexistence and niche partitioning (Adler et al., 2013) (e.g.  
502 specific leaf area or seed mass), genetic differentiation between populations or species (Gamba

503 & Muchhala, 2020) (e.g. pollination mode, mating system, growth form) or those associated with  
504 commonness and rarity (Murray et al., 2002) (e.g. seed production). Such traits come with *a priori*  
505 hypotheses and could be ideal candidates for macroevolutionary studies exploring their effect on  
506 diversification.

## 507 **Conclusions**

508       When bringing together the last 12 years of study on trait-dependent diversification in angiosperms,  
509 it is the inconsistent effects of traits that stand out, rather than the importance of a particular set  
510 of universal drivers. This highlights the important role the evolutionary context of a clade plays  
511 in determining how a particular trait affects diversification. Furthermore, the nature of the data  
512 itself, relating to factors such as how well-sampled or large a clade is, was shown to have substantial  
513 influence on SSE model results. The guidelines we set out in this review will help to improve how  
514 we use trait-dependent models and our template for reporting results will facilitate future synthesis  
515 as SSE models continue to be used and developed. We have only touched the surface of what we can  
516 learn about trait-dependent diversification in angiosperms. Will results from novel studies change  
517 the trends we observe here? Given the production of new datasets that meet recommendations  
518 for robust inference, future methodological developments enabling studies at wider scopes and the  
519 potential for new discoveries in understudied traits and clades, we think it is certainly possible.  
520 Though our study focused on angiosperms the conclusions we draw about consistency, context  
521 dependence and SSE model use will apply to studies of trait-dependent diversification across the  
522 entire tree of life.



## 523 **Acknowledgements**

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## 526 **Supplementary Material**

527 Code and data associated with this manuscript is available from <http://github.com/ajhelmstet>  
528 [ter/sseReview](http://github.com/ajhelmstetter/papieRmache). [Papiermache](http://github.com/ajhelmstetter/papieRmache) can be found at <http://github.com/ajhelmstetter/papieRmache>.

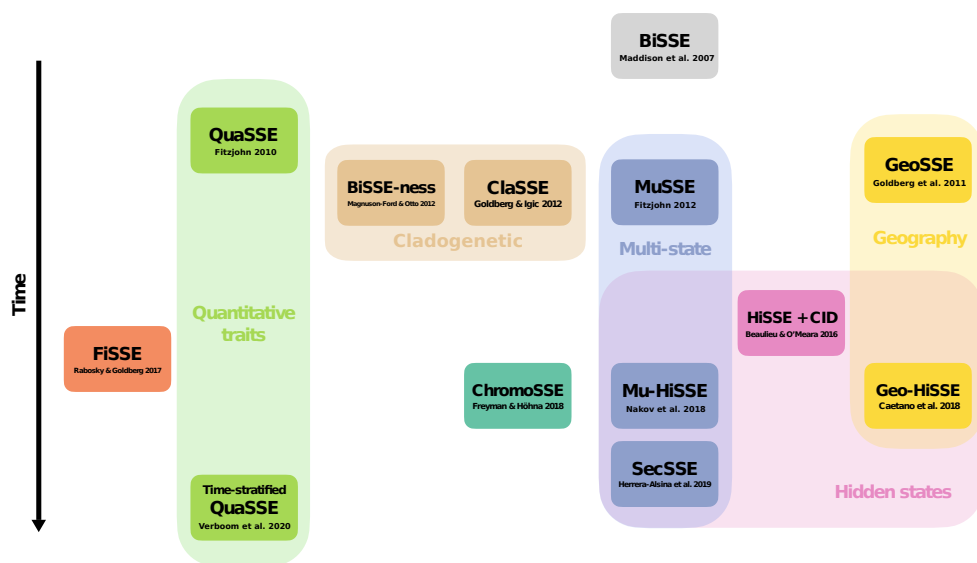


Figure 1: The development of state-dependent speciation and extinction (SSE) models. The original binary-state speciation and extinction model (BiSSE) model (Maddison et al., 2007) is shown at the top of the diagram with all other models depicted below, in the order of their publication. Acronyms are defined as follows; Binary-State Speciation and Extinction–node enhanced state shift (BiSSE-ness; Magnuson-Ford and Otto, 2012), Cladogenetic and Anagenetic Models of Chromosome Number Evolution (ChromoSSE; Freyman and Höhna, 2018), Character-Independent Diversification (CID Beaulieu and O’Meara, 2016), Cladogenetic State change Speciation and Extinction (ClaSSE; Goldberg and Igić, 2012), Fast, intuitive State-dependent Speciation-Extinction (FiSSE; Rabosky and Goldberg, 2017, Geographic State Speciation and Extinction (GeoSSE; Goldberg et al., 2011), Hidden Geographic State Speciation and Extinction (GeoHiSSE; Caetano et al., 2018), Hidden State Speciation and Extinction (HiSSE; Beaulieu and O’Meara, 2016), Multi-State Speciation and Extinction (MuSSE; FitzJohn, 2012), Multicharacter Hidden State Speciation and Extinction (Mu-HiSSE; Nakov et al., 2018), Quantitative State Speciation and Extinction (QuaSSE; FitzJohn, 2010; Verboom et al., 2020), Several examined and concealed states-dependent speciation and extinction (SecSSE Herrera-Alsina et al., 2019). Each box shows the name of the model and the associated citation. Models that share similar attributes (e.g. those with hidden states) are colour coded and grouped with boxes. This is not an exhaustive list of SSE models and does not include, for example, models used in epidemiology that allow tips to be sampled at various points in time (Scire et al., 2020).

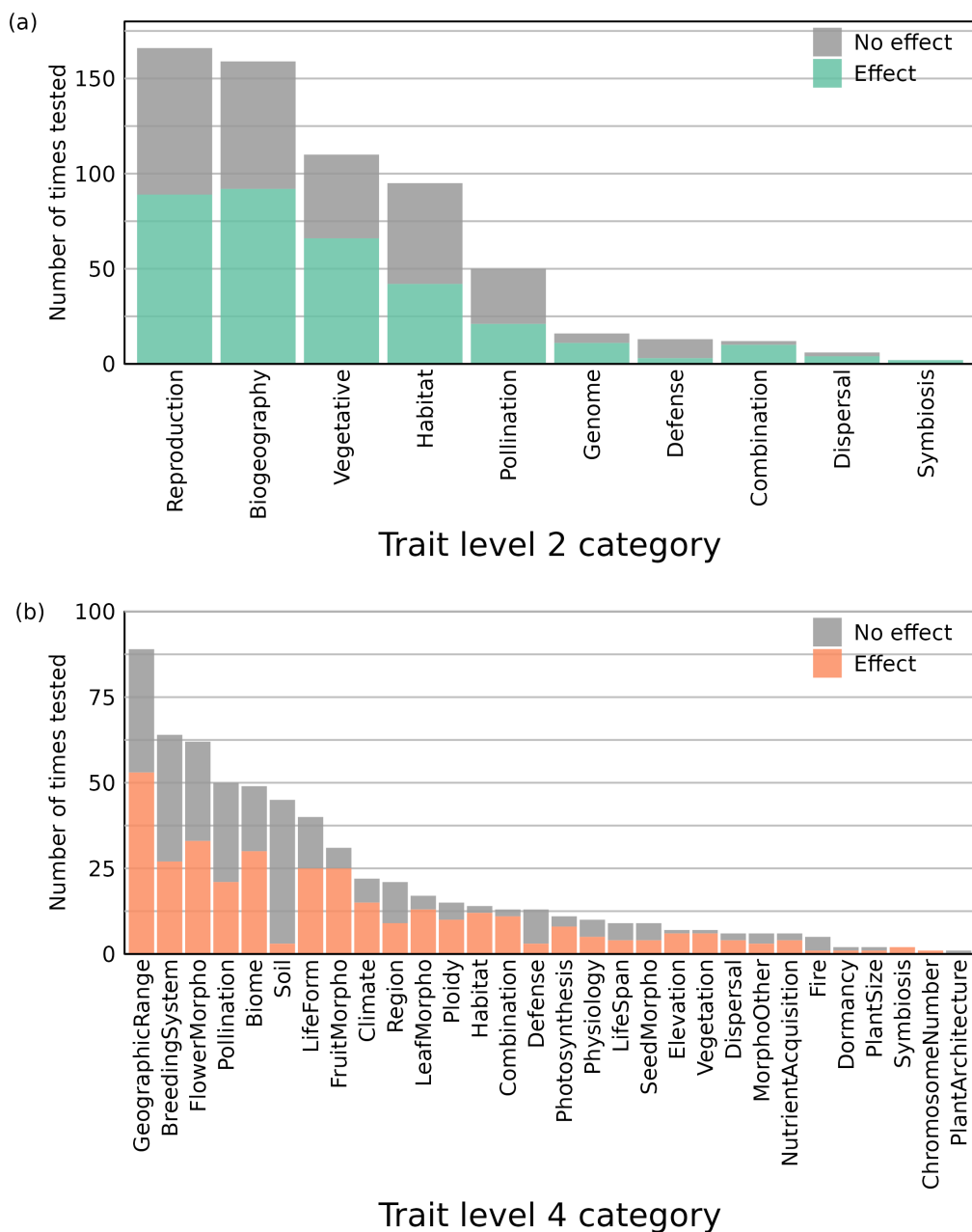


Figure 2: Stacked barplots showing how often particularly trait types were tested with state-dependent speciation and extinction (SSE) models. Bars are coloured to depict how often trait-dependent diversification was detected per trait type. If multiple SSE models were used in a single study they were considered separately i.e. each model contributed one result to the totals for each trait category. Two plots are shown, (a) one with relatively broad trait categories (level 2) and (b) one with narrower categories (level 4). An ontology depicting how different trait classification levels are connected can be found in Table S1.

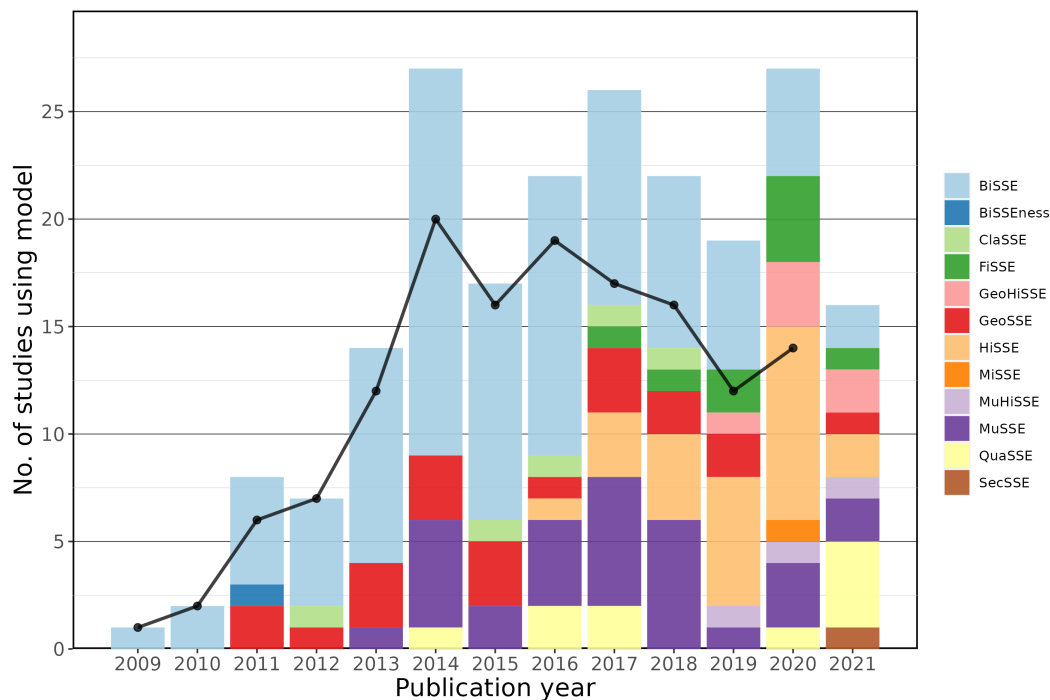


Figure 3: A stacked barplot showing the change in state-dependent speciation and extinction (SSE) models used on angiosperm clades over time. Each bar indicates the number of unique SSE model types per study totaled over the publication year. Bars are coloured according to the proportion of each SSE model type published in that year (see legend on the right of the plot). If the same SSE model was used multiple times in a single study it is only counted once (e.g. if BiSSE was used four times in a study published in 2012 this contributes an increase of one to the BiSSE portion of the 2012 bar). The black line shows the total number of studies using SSE models on angiosperms per year. Note that studies published after May 2021 were not included, so this year is incomplete.

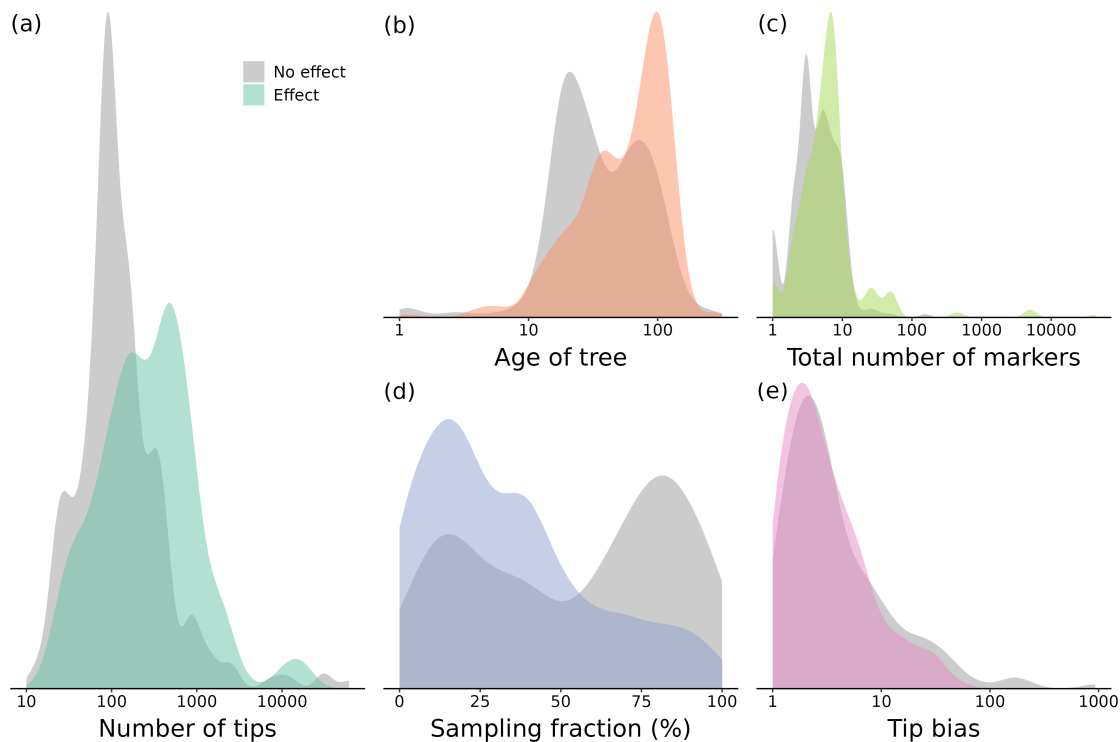


Figure 4: A set of densities depicting the distribution of values for five dataset properties in SSE models that infer trait dependent diversification (coloured densities) and those that do not (grey densities). The dataset properties shown are (a) number of tips in the phylogenetic tree used with the SSE model (data taken from  $n = 621$  models), (b) the age of the tree used with the SSE model ( $n = 523$ ), (c) the total number of genetic markers (nuclear + plastid + mitochondrial) used to infer the phylogenetic tree used with the SSE model ( $n = 615$ ), (d) the global sampling fraction ( $n = 616$ ) and (e) the tip bias, here calculated as the largest tip frequency divided by the smallest ( $n = 429$ ).

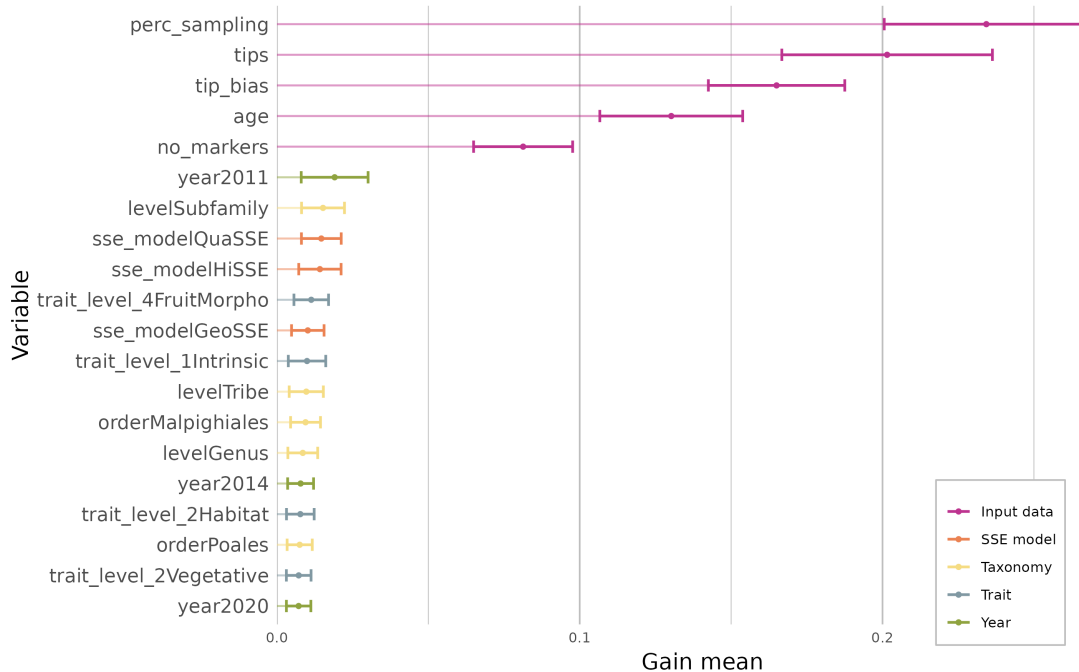


Figure 5: A horizontal barplot showing the relative influence of the 20 most important features included in the xgboost model used to predict the outcomes of SSE models, whether or not trait-dependent diversification is inferred, using input data properties and other characteristics of each study. Points are the mean gain values calculated from the 500 iterations that were run. Error bars represent one standard deviation around the mean. Bars are coloured based on the type of variable they represent. Variable are named using the column headers in the dataset (see appendix S1). For example 'levelPoales' indicates that the variable was the category 'Poales' from the 'level' column.

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