# Trait-dependent diversification in angiosperms

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# Abstract

How species diversity arose and is distributed across the tree of life is the central question in macroevolution and has also increasingly been recognized as a key to community and functional ecology. Flowering plants, a group of more than 350,000 extant species, have fundamentally shaped life on earth since the Cretaceous and clearly illustrate how species diversification affects ecosystem functioning. The diversity of ecological and morphological characteristics in nature has inspired many studies linking traits to trends in species diversification, particularly as powerful macroevolutionary models and detailed phylogenies have become increasingly available. Using flowering plants as an example, we synthesize data from studies using one of the most popular families of diversification models - the state-dependent speciation and extinction (SSE) models. We find that intrinsic characteristics, such as reproductive and morphological traits, have been identified as major drivers of angiosperm diversification more often than extrinsic factors related to biogeography and habitat. We also show how dataset properties such as the sampling density or clade choice are important determinants of the empirical results observed in the literature and should be carefully taken into account when drawing conclusions. Finally, we provide a list of best practices to follow when designing and reporting results of trait-based diversification and highlight clades and traits that are important avenues for future research.

**Keywords : diversification, traits, macroevolution, BiSSE, HiSSE, angiosperms**

# Introduction

Species diversity is unevenly distributed across the tree of life. While substantial research has investigated why some clades are more diverse than others many fundamental questions remain unanswered. The causes behind this unevenness can be diverse, from catastrophic mass extinctions that decimate diversity [1] to key innovations that spur on rapid speciation [2] to ecological factors such competition that affects species co-existence [3]. Understanding patterns of species diversification is important because they can have far-reaching consequences that affect the assembly of communities and their phylogenetic struture, the evolution of functional traits that underpin a species' role in its environment, the formation of species interaction networks, and simply how biodiversity has evolved through time [4]. Research aiming to link species characteristics to macroevolutionary dynamics has become extremely popular over the last decade due to the increasing availability of large phylogenetic trees [5–8] and the continuing development of a range of statistical models to infer patterns in species diversification [9–12]. The increasing amount of empirical knowledge provides an opportunity to synthesise what we know so far about a wide range of ecologically diverse and species-rich clades to uncover general patterns about the traits that have driven their diversification.

Angiosperms are one of the most successful and diverse clades in the tree of life. There are more than 350,000 extant species of flowering plants, the result of a 140 to 270 million year history [13–17]. Almost all of terrestrial life is linked, directly or indirectly to angiosperms [18] and their success makes them an ideal study group for uncovering the intrinsic and extrinsic traits driving their diversification. Previous work has suggested that the origins of angiosperm diversity can neither be tied to major global events nor the evolution of a single key innovation but instead various combinations of traits, environment and ecology acting to stimulate diversification in different groups [19–21]. Indeed, it appears that macroevolutionary dynamics varied substantially across different angiosperm clades [22]. Historically, it has been proposed that the traits driving these trends are a range of vegetative and reproductive characteristics that are unique to flowering plants [23]. In sexual systems, for example, dioecy originated in 900-5000 independent instances [24] but not all of these led to the same macroevolutionary dynamics [25]. In some groups, dioecy stimulated diversification [26, 27] while in others dioecy had limited effect [28–30], which may depend on dioecy's interaction with other associated traits [31]. In the majority of studied traits, we do not know how pervasive such inconsistency is, nor have

broad-scale empirical studies of trait-dependent diversification provided a general consensus on which traits are most important for angiosperm diversification.

The most common way of linking discrete traits to species diversification is by using state-dependent speciation and extinction (SSE) models. This popular family of models are birth-death processes where diversification rates (birth and death rates) are dependent on character states, and where transition rates between states define how state changes occur. The simplest of all SSE models is the binary-state speciation and extinction (BiSSE) model [32] that takes as input a phylogenetic tree and state values (0 or 1) for each species in the tree. Models that allow for diversification rates (speciation, extinction and net diversification rate) to vary among lineages with different character states can be compared to simple models that do not allow for such variation. This allows users to uncover whether lineages with one state diversify faster than those with the other. SSE models can also be used to test whether the transition rates between states in one direction $(0->1)$ are faster than the other $(0<-1)$. The original model has been extended in various different ways (Fig. 1) to address different types of macroevolutionary questions. For example, ClaSSE [33] and BiSSE-ness [34] are extensions of BiSSE that include cladogenetic events (speciation simultaneously associated with change in state) and GeoSSE [35] explicitly models how diversification differs among geographic regions. Other innovations include models with more than two character states (MuSSE [36]), quantitative traits (QuaSSE [37]) and non-parametric models (FiSSE [38]). Perhaps the innovation with the greatest impact has been the introduction of hidden states into SSE models [9, 39, 40]. Hidden states originally appeared as a solution to various factors increasing the rate of false positives inferred in SSE models including phylogenetic pseudo-replication [41], and diversification patterns driven by traits other than the focal one [42]. This innovation allows diversification rates to be influenced by a hidden state, outside of those being measured. The hidden state models assume a set of more complex null hypotheses (the character independent (CID) models) in which 'noise' that is not linked to the trait of interest affects diversification across lineages. This allows users to test how relevant the trait being studied is to species diversification [9, 39] in the context of other factors.

In this study we bring together current knowledge on flowering plant diversification by synthesizing results from SSE models used in 153 studies. We identify those traits that have repeatedly stimulated diversification, as well as those where the effect is context-dependent.

We investigate the relationship between the properties of datasets (e.g. tree size and sampling fraction) and the results of published studies, highlighting how implicit biases in our use of SSE models can affect our conclusions when searching for general trends. Finally, we identify gaps in our current knowledge and provide a set of best practices for diversification result-reporting to enhance our ability to fill these gaps in the future.
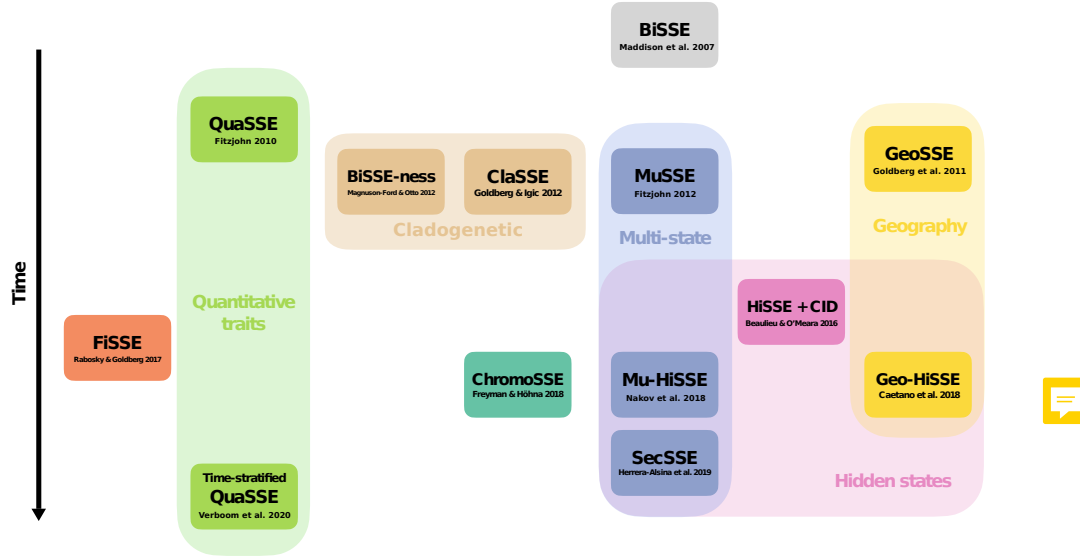
Figure 1: A diagram depicting the wide range of state-dependent speciation and extinction (SSE) models. The original binary-state speciation and extinction model (BiSSE) model [32] is shown at the top of the diagram with all other models depicted below, in the order of their publication. Acronyms are defined as follows; Binary-State Speciation and Extinction–node enhanced state shift (BiSSE-ness), Character-Independent Diversification (CID), Cladogenetic State change Speciation and Extinction (ClaSSE), Fast, intuitive State-dependent Speciation-Extinction (FiSSE), Geographic State Speciation and Extinction (GeoSSE), Hidden State Speciation and Extinction (HiSSE), Multi-State Speciation and Extinction (MuSSE), Quantitative State Speciation and Extinction (QuaSSE), several examined and concealed states-dependent speciation and extinction (SecSSE). 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 by a box. 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 [43].

6

# Materials & Methods

## Data collection

We collected all published studies that cited SSE methods papers [9, 32–40, 44–46] using Google Scholar, last accessed 18th May 2021. To facilitate data collection from papers using SSE models, we developed a new R package, 'papieRmache' (https://github.com/ajhelmstetter/papieRmache). This package has two main purposes (1) to classify papers into different categories based on the frequency of term use in the text and (2) to pull out sections of the main text that contain a keyword or a pair of keywords while highlighting relevant information. We identified the SSE studies on flowering plants by using the keywords 'angiosperm', 'flowering' and 'plant' subsequently validating the subset of papers by hand and removing any studies on groups other than angiosperms. We then collected 27 different dataset properties from each paper relating to the trait investigated, the group studied, the phylogenetic tree and the outcome of the SSE model used (Appendix S1). In cases where there was uncertainty in how to interpret or collect data from a study we contacted the authors for their assistance and clarification, where possible.

## Trait classification

While some sets of character states were the same among studies (e.g. annual vs perennial; diploid vs polyploid), many of them did not overlap. We classified traits into different categories to facilitate comparisons among different trait types. At the broadest classification these were, intrinsic (traits belonging to the species), extrinsic (environmental or geographic traits), interaction (traits related to other species), and combination (multiple traits belonging to different categories that were grouped for multi-state analyses (e.g. species that have both small fruits and are found on islands [47]). To allow for analyses at different grouping levels we developed a trait ontology (Table S1) starting at level one as detailed above and becoming more specific, up to level six. GeoSSE and GeoHiSSE models are specifically designed to assess diversification differences among geographic regions and here we only consider states representing the geographic regions, omitting the special state 'widespread' states used for taxa are present in both regions.

## Data analysis

To examine the effect of particular traits on diversification we used the trait categories defined above and calculated the proportion of models in which trait-dependent diversification was inferred (as opposed to no effect inferred). This was repeated at different levels of trait categorization, as well as using only those models with hidden states. Whether or not trait-dependent diversification was detected was typically based on significance in model comparisons and/or posterior distributions of rates among states. However, if significance ~~wasn't~~ inferred or reported, we followed the study narrative and statements made in the text. If model comparisons were conducted and reported, only the best-fitting model was considered, unless other models were explicitly referred to in the study.

We also examined the relationship between SSE model inferences and dataset properties i.e. the various aspects of the data used as input in the SSE model, such as tree size or sampling fraction. We constructed two density plots for each property of the dataset representing the distributions of values in cases where trait-dependent diversification was, and was not, inferred and compared the overlap between densities. We also fitted generalized additive models (GAM) to the continuous dataset properties (number of tips, root age, number of genetic markers, sampling fraction and tip bias - a transformation of samples per state) with the SSE model result as a binary response variable (trait-dependent diversification vs no effect). When analysing continuous data, variables were log-transformed (or arcsine in the case of percentages) to conform better to normality assumptions. To make use of all available data for each variable we first assessed them individually to examine the shape of each relationship. We then constructed a GAM containing all five variables to which variables had significant explanatory power. In all cases we used smoothing functions (cubic regression splines) with $k = 5$ dimensions for each variable. We first conducted the full GAM analysis with only those models containing no missing values (n=213) and then reran the analysis, this time assigning the mean of the known values to any missing values (n=620). We found results of these two approaches to be very similar so present only the latter here. We identified eight traits in which there was enough replication to be able to assess whether one character state had consistently higher diversification rates than the other(s). We selected this subset of traits by identifying those that had been tested at least five times, in at least two different studies and two different clades.

## Predicting results based on dataset properties

After collecting information from all studies we found that the dataset properties were sometimes associated with the outcome of the SSE model, that is, whether trait-dependent diversification was inferred or not. We therefore attempted to predict SSE model results (inference of trait-dependent diversification vs no effect) from dataset properties alone, and to identify those properties with the largest predictive power. We used all available dataset properties except for highly-specific categorical variables (e.g. trait levels 5-6, clade, family). We used a machine learning approach, extreme gradient boosting, with the R package 'xgboost' [48], a powerful supervised learning approach based on gradient boosting machines. This family of methods uses a labelled dataset (the outcome is known) and an ensemble of weak prediction models (e.g. decision trees) whereby new models are added on to existing models per iteration to minimize error. xgboost improves upon other boosting methods with its increased speed and enhanced regularization to minimize overfitting. Prior to running our models, categorical variables with more than two categories were converted into binary, dummy variables using one-hot encoding to facilitate model building. We trained models on a random selection of 80% of our dataset and tested them on the other 20%. After a parameter optimisation step we repeated this process 500 times to produce a range of accuracy values, the percentage of cases where the real outcome matched the classification, to account for stochasticity in the test and training datasets. For each iteration we also recovered the relative importance of each variable, which allowed us to determine which dataset properties had the most influence on the model. Further details on our predictive modelling approach can be found in the associated annotated R code ( https://github.com/ajhelmstetter/sseReview ).

# Results

**Traits studied and their effects on diversification**

In total, we collated information on trait-based diversification from 153 studies using SSE methods on flowering plants. Overall, we found a clear, positive correlation between the number of species in a clade (family, order) and the number of studies focusing on this clade (Fig. S1, S2). This indicates that research effort is generally proportional to the amount of species diversity in the different orders. There were some families that seemed to be preferentially studied, including the economically important Solanaceae, Poaceae and Arecaceae but also the Plantaginaceae and Proteaceae, which seem to interest researchers mainly because of their species richness (Fig. S2). In terms of taxonomic level, SSE models are most often run on focal genera, or families (Fig. S3). In a phylogenetic context, we found that the use of SSE models is relatively evenly-distributed across the angiosperm tree of life (Fig. S4). We compared the proportion of trait-dependent diversification outcomes in SSE models at different category levels (see ontology Table S1). This revealed that researchers more often studied traits relating to reproduction (e.g. flower morphology, fruit morphology, breeding system), biogeography (biome, geographic region) and vegetative traits (e.g. life form, leaf morphology) and less often physiological characters (e.g. photosynthesis, symbiosis) or those related to pollination or dispersal. Among those trait categories that have been tested using >25 models, vegetative traits yielded trait-dependent diversification at a higher proportion than any other trait type (Fig. 2a). Traits in this category have been studied in 19 different orders suggesting that this is a general pattern across flowering plants. Species' habitat and biogeographic region were also among the most popular categories but resulted in trait dependent diversification less often. Some trait categories such as dispersal or symbiosis were tested in just a small number of studies but often led to trait-dependent diversification (Fig. 2). At the highest level of classification, intrinsic traits (i.e. those belonging to the plant species itself) were tested slightly more often , (46% of models run) than extrinsic traits (i.e. those related to the species' habitat and geography, 42%).
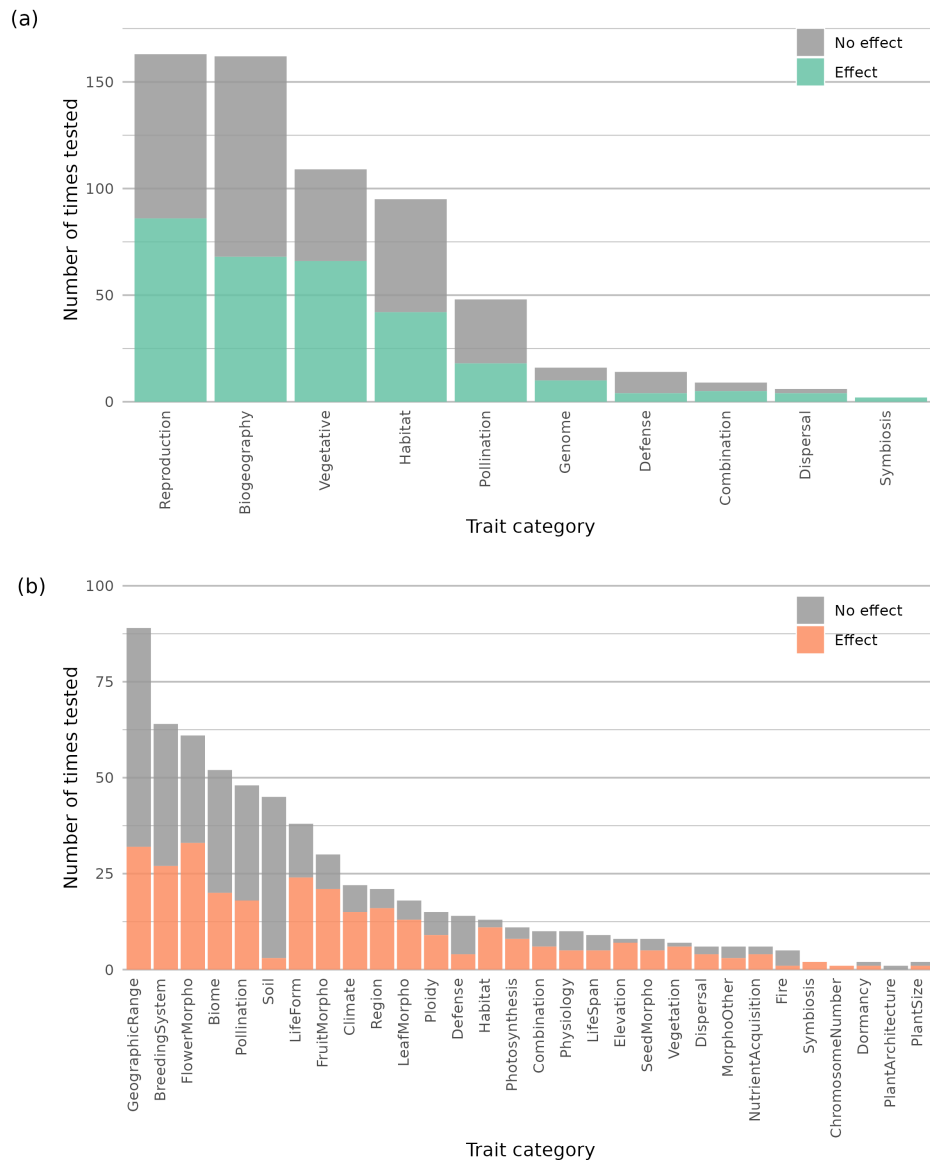
Figure 2: Stacked barplots showing how often particularly trait types were tested with state-dependent speciation and extinction (SSE) models. Bars are coloured to depict how often trait-dependent diversification was detected per trait type. If multiple SSE models were used in a single study they were considered cumulatively. Two plots are shown, (a) one with relatively broad trait categories (level 2) and (b) one with more narrow categories (level 4). An ontology depicting how different trait classification levels are connected can be found in Table S1.

If a trait has arisen more than once we can compare the effect of the same traits on diver-

sification in different evolutionary contexts to see if similar trends are found. Maddison et al. [41] highlighted the requirement for multiple independent associations between a given trait and another factor (e.g. diversification rate) for robust conclusions. Likewise, Rabosky & Goldberg [42] suggested that one option to better-overcome SSE methods propensity for false positives is to apply models to the same trait in multiple independent clades - indeed some of the studies we surveyed have attempted to do so (e.g. [28]) but these were limited in number. Our collation of data allowed us to compare results across different studies and we found that results inferred with SSE models were inconsistent at both broad and narrow scales (grey vs coloured portions of bars in Fig. 2). When the same types of traits were tested for their effect on diversification in different groups some studies found that the traits were associated with trait-dependent diversification while no effect was found others. For example, traits such as lifespan [49–52] and ploidy level [31, 53–55] yielded different results depending on the angiosperm group studied. Taking the latter as an example, polyploidy has been linked to increased diversification in *Allium* [54] while Roman-Palacios et al. [56] found that polyploids and diploids diversified at similar rates in Brassicaceae. This pattern of inconsistency was so widespread that we found it in all level 2 and 4 trait categories that had been tested on more than a few occasions (Fig. 2).

Though replication among character states was typically low we found a number of traits that were tested often enough to begin to assess whether there was a consistent effect of one state on diversification and the magnitude of the effect. We examined patterns in eight different sets of character states (Fig. S5). In four of these traits (lifespan, sexual system, ploidy, tropical biome and woodiness) trait-dependent diversification was rarely found while in the remaining three traits (epiphytism, photosynthesis and self-compatibility) results more often indicated trait-dependent diversification i.e. there were one or two states that drove this pattern. Examining the differences in net diversification rates among states of seven traits (sexual system could not be assessed as rates were no time-calibrated) we find that both epiphytism and self-incompatibility always led to higher net diversification rates while in the case with three states the net diversification rates associated with C4/CAM photosynthesis were generally greater than C3 (Fig. S6). Net diversification rates in traits for which there was a low proportion of trait-dependent diversification were generally similar across states (Fig. S6), indicating that there was no general trend one way or the other.

## The evolution of SSE model use and methodological innovation

As SSE models themselves have diversified, the relative frequency of model-use has changed over time. We collated data on the types of SSE model used in each angiosperm paper, and plotted their use by year of publication (Fig. 3). BiSSE has been consistently popular even as newer more complex models have emerged. This is likely because it was one of few options during the early years of SSE model use, and it remains used in comparison with more complex models such as HiSSE, in which it is nested. HiSSE has become as popular as its predecessor in recent years (Fig. 3) as more papers account for the effect of hidden states to mitigate the effect of false positives. Models with multiple states, predominantly MuSSE, have also been commonly used showing that researchers are interested in the effects of more complex traits or trait groups with many different states. There has also been a consistent focus on using SSE approaches related to geography in models like GeoSSE and GeoHiSSE. When examining the number of studies that use SSE models each year we find a rapid increase since the original BiSSE paper in 2007 until a conspicuous slowdown and slight drop in 2015 (Fig. 3). This appears to coincide with the publication of a number of influential papers that criticised the propensity of SSE methods for false positives [41, 42] and lack of power [57]. After this, SSE model use continued with a greater variety of models owing to the creation of models with hidden states [9]. Hidden states were created in response to the aforementioned criticisms and have since spread to all aspects of SSE model use (Fig. 1), becoming the dominant set of models by 2019 (Fig. 3). Such patterns are a good example of how critical papers can shape the academic landscape and trigger innovation. Recently, SSE model use in angiosperms has stabilized at around 15 studies per year, perhaps declining slightly over time.
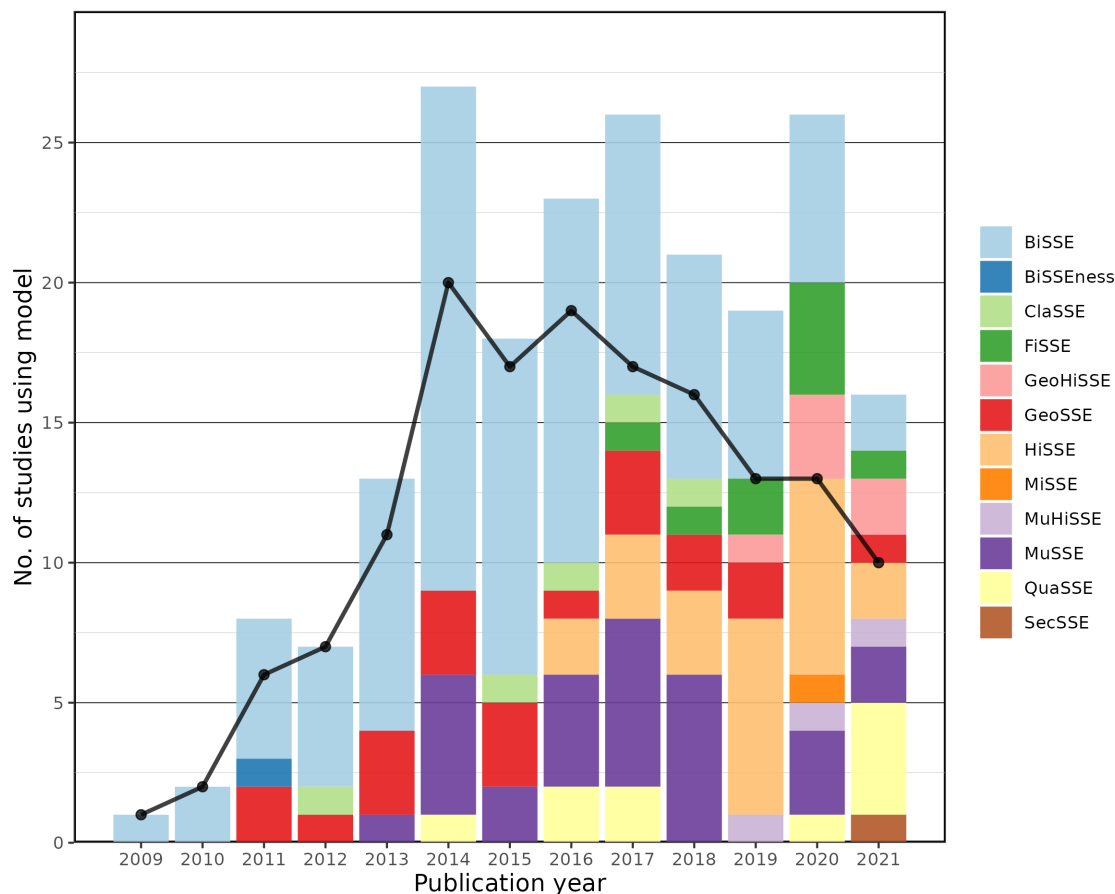
Figure 3: A stacked barplot showing the change in the number of times state-dependent speciation and extinction (SSE) model used on angiosperm clades over time. Each bar indicates a publication year. Bars are coloured according to the proportion of each SSE model type published in that year (see legend on the right of the plot). 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.

## Theoretical recommendations vs empirical practices

The input data for macroevolutionary studies have grown in size and quality, in parallel with the innovations in the SSE models. For example, we found clear evidence that over time, trees used with SSE models have grown larger (Fig. S7). The number of tips in a tree is important for robustness of SSE model results and guidelines for adequate power were put forward by Davis et al. [57] who suggested that results from models using trees with less than 300 tips should be treated with caution. But how have such recommendations shaped SSE model use? We examined sizes of trees used before and after guidelines were published, across all SSE models (though the guidelines were focused on BiSSE). The proportion of studies using SSE models on trees with fewer than 300 tips was initially very high (93%) in studies published up until 2013. It then decreased to 63% in studies published from 2014 onwards. Despite this reduction, more than 50 models were run on trees with fewer than 50 tips after Davis et al. was published. Tip ratio bias recommendations were also made by Davis et al. [57], who cast doubt on inferences made when the rarest state occurs in less than 10% of the taxa. Prior to 2013 [57], 86% of SSE models had suitable tip ratios, and this figure remained similar (85%) for the studies that came after. Note that these figures were calculated only for studies where these data were available (107 studies in total).

Sampling fraction is the proportion of known species that are present in the tree. If the sampling fraction is low it can drastically affect ability to accurately infer changes in diversification rate when using macroevolutionary models [58]. After introducing the possibility to account for incomplete sampling in SSE models, Fitzjohn et al. [59] found that a sampling fraction of 50% was adequate for capturing diversity dynamics. Similarly, Chang et al. [60] showed that there was little difference in terms of likelihood surface between complete trees and trees where only 50% of species were sampled. All studies (n = 9) prior to Fitzjohn et al. had sampling fractions greater or equal to 50% compared to just 42% of studies after its publication. Examining patterns using this cut-off probably reflects the easing of assumptions on complete species sampling, rather than researchers' tendencies to use better or worse sampled trees. For a more interpretable representation of general trends over time we examined sampling fractions in SSE models used before 2016, where 46% had sampling fractions of 50% or higher. From 2016 onwards just 28% of models reported were above this threshold, indicating that high levels of incomplete sampling are common in recent literature (see Fig. S8 for a visual representation

of sampling fraction through time).

## The importance of dataset properties

The recommendations outlined above are largely based on simulations and theory and SSE models are known to behave differently between simulated and empirical trees [42]. So what happens to results of SSE models when dataset properties vary in practice? We used information from empirical studies to assess the relationship between results and various aspects of the input data. We examined the relationship between tree size and whether or not trait dependent diversification was inferred, regardless of the trait investigated. We found that, in general, trait-dependent diversification was detected less often when trees had smaller of tips (Fig. 4a, S9a). Tree size and root age are closely linked because trees with larger numbers of tips are generally older (Fig. S10). Indeed, we found that when trait-dependent diversification was detected, it tended to be when trees with an older root age were used (Fig. 4b, S9b). These patterns are not surprising - trees with many taxa are more likely to contain a range of branching patterns where lineage accumulation is faster in some parts of the tree than in others. In older clades there has been more time for macroevolutionary processes to have an impact on the trees we infer and the traits we observe today. However, this would also make them more susceptible to false-positive errors that could over-inflate the number of times trait-dependent diversification is detected [42].

Regardless of their size or age, trees that more accurately represent the true phylogeny of a group will allow us to more reliably estimate its diversification history. We used information on the total number of molecular markers (nuclear + plastid + mitochondrial) as a proxy for tree quality. We found a difference in the distributions indicating that models with trait-dependent outcomes usually had better quality trees than those that did not (Fig. 4c, S9c).
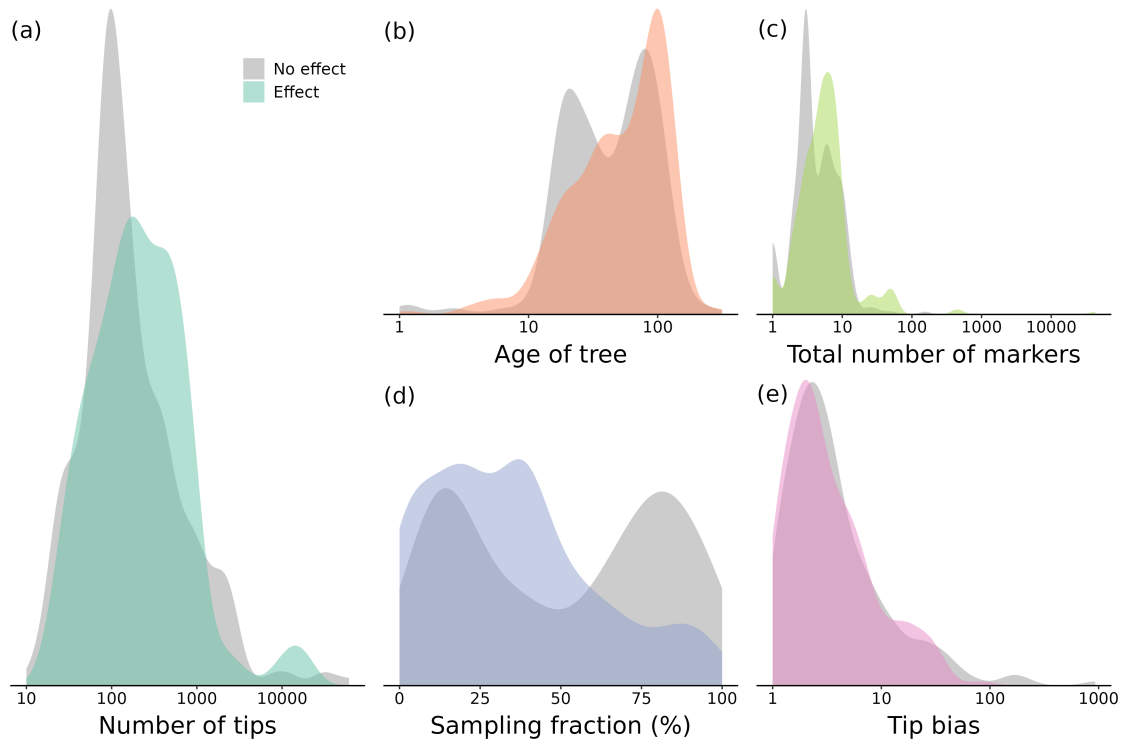
Figure 4: A set of densities depicting the distribution of values for five dataset properties in SSE models that infer trait dependent diversification (coloured densities) and those that do not (grey densities). The dataset properties shown are (a) number of tips in the phylogenetic tree used with the SSE model, (b) the age of the tree used with the SSE model, (c) the total number of genetic markers (nuclear + plastid + mitochondrial) used to infer the phylogenetic tree used with the SSE model, (d) the global sampling fraction and (e) the tip bias, here calculated as the largest tip frequency divided by the smallest.

As previously mentioned, one characteristic that has a major effect on diversification rate inference is sampling fraction [59, 60]. Using a small proportion of known, extant species will typically reduce our ability to reliably detect differences in diversification rate, but modern macroevolutionary models can now account for missing species in a variety of ways [59–61]. In the set of angiosperm studies we use here, sampling fraction ranges from 0.1% to complete (100%) sampling. Even if we are able to account for missing taxa, does this lack of information influence empirical results? We found a striking pattern, showing that those models that used trees in which sampling fraction was low generally yielded trait-dependent diversification (Fig. 4d), particularly when sampling values were less than 40% (Fig. S9). Conversely, high sampling fraction (>70%) was more often associated with a lack of trait-dependent diversification.

Given that the inference of trait-dependent diversification varies with tree size (Fig. 4a), we wondered whether there may also be a relationship between sampling fraction and tree size. However, upon examination we found only a weak, negative trend where trees with more tips actually had slightly lower sampling fractions (Fig. S11), and this trend was steeper in studies where no effect of the trait was found. We then looked at the relationship between sampling fraction and the number of species in the study clade of interest and found a steeper negative relationship (Fig. S12) meaning that the larger the clade of interest is, the less well-sampled it tends to be. Importantly, these two negative trends remain similar regardless of whether trait-dependent diversification is inferred or not, indicating that sampling fraction alone is responsible for this pattern, and not tree or clade size. If we assume that better sampled trees yield more accurate estimates of diversification rates [59, 60] then these results indicate that we should take caution when interpreting results from trees with lower sampling fraction, particularly when trait-dependent diversification is inferred. More simulations should be done to investigate the influence of sampling fraction on SSE models and whether false positives occur more often when sampling fraction is low.

Another issue that has been repeatedly brought up in simulation studies is the potential effect of inflated tip bias [32, 57]. Tip bias occurs when there is a much higher frequency of one state than the others across the tips of the tree. Upon examining the data used with SSE models we found substantial overlap between densities (Fig. 4e). Yet, this does not mean that it is not affecting results, as Davis et al. [57] have suggested, but that any effects cannot be observed using this simple comparison. Indeed, when we fitted a GAM we found that with extreme

values of tip bias, SSE models tended to find no effect of the trait studied (Fig. S9). To assess the importance these variables together we fit a GAM including all five continuous variables and found that percentage sampling, number of markers, and to a lesser extent tip bias, were significant explanatory variables of SSE model outcome (Fig. S13, see Table S2 for full details) while age and number of tips provided little explanatory power despite their distributions (Fig 4).

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

Empirical results in angiosperms clearly exhibit strong relationships between various dataset properties and whether trait-dependent diversification is inferred. If we had comprehensive information about the input data, including the dataset properties investigated above but also information about taxonomy and traits, could we predict whether trait-dependent diversification would be inferred without running an SSE model? To test this we used a machine learning approach, extreme gradient boosting [48]. We were able to correctly predict, with approximately 72% accuracy (65-80%, Fig. S14), whether SSE models would infer trait-dependent diversification. Among the most important factors in the gradient boosting models we constructed were the information-dense, continuous variables such as tip number and the number of markers (Fig. 5). Sampling fraction was by far the most influential variable, followed by number of markers, further reinforcing earlier observations about their potential correlation with results (Fig. 4, S9,S2). Tip bias, while appearing to have similar distributions in SSE models inferring trait-dependent diversification and those that do not (Fig. 4e), was also highly influential in the models reflecting its significance in the full GAM. Its importance could be also because its role in predicting the outcome is dependent on the values of other dataset properties. We looked at the decision trees output by our model and found such relationships. For example, were visualized one iteration of our model (e.g. Fig. S15), and found that tip bias informed choices towards the leaves of the decision tree indicating that its predictive power depended on a prior choices related to other variables. Such patterns were also present for other dataset properties such as the number of genetic markers, which had an important effect after the first decision tree (Fig. S15). Generally, categorical variables played a smaller, but still important, role. Studying the association between geographic range and diversification, using the MuSSE model and working in Poales were all influential in the model's predictive ability (Fig. S15).
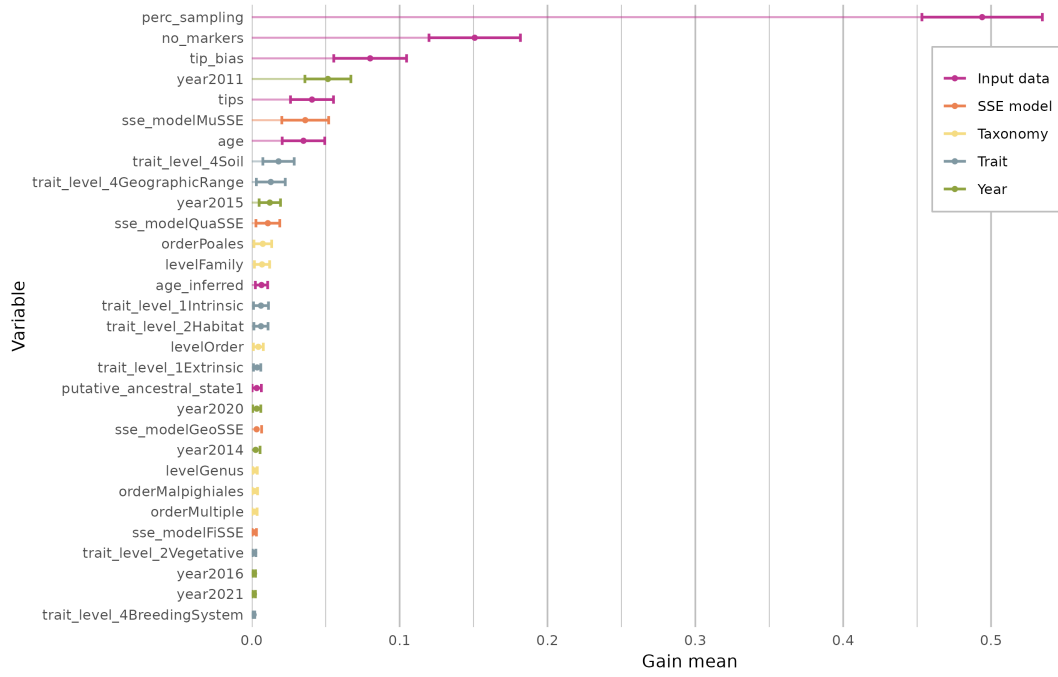
Figure 5: A horizontal barplot showing the relative influence of the 30 most important features included in the xgboost model used to predict the outcomes of SSE models, whether or not trait-dependent diversification is inferred, using input data properties and other characteristics of each study. Points 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.

# Discussion

## Major drivers of angiosperm diversification remain unknown

One of the key questions in angiosperm macroevolution is: what are the drivers of the differences in diversification among clades? [19]. Previous work has proposed that diversity in different angiosperm groups may have been driven by various combinations of ecology, traits and environment [20, 21, 62]. Here, we synthesised evidence from more than 150 studies that looked for trait-dependent diversification using SSE methods. Under the (strong) assumption that current studies represent an unbiased view of diversification, we found that the results support this proposal - the factors driving angiosperm diversification are more complex than a set of universal drivers, which did not emerge from our literature survey. However, trends inferred from this broad compilation of studies should be interpreted with caution (see below).

Our analyses and results centered around whether traits (e.g. pollination) rather than the character states of these traits (e.g. bee vs bird pollination) affect diversification. After grouping traits into several levels of categories ('ontology', Table S1), we found that some types of traits were more consistent in their influence on diversification than others. Given the nature of 'flowering plants' it may come as no surprise that traits related to variation in their defining structure, flowers, are among the most investigated and influential (Fig. 2b). Indeed, the flower contains the organs needed for sexual reproduction, making it central to the biology, ecology and evolution of angiosperms, and flower characteristics certainly have a large role in determining differences in diversification [63]. In particular, reproductive systems are highly variable in flowering plants [64] and are again thought to be closely linked to their success [65]. Results from SSE models lend some support to this idea - for example, when trait-dependent diversification was inferred in mating system, self-incompatibility was always the trait with higher diversification rates (Fig. S6). Even so, we found that more often than not, breeding system (the higher level trait classification including all aspects of mating and sexual systems) did not yield trait-dependent diversification, due to inconsistency in the effect of sexual system (Fig. 2b). Vegetative traits (those related to the growth, physiology and non-floral morphology of the plant) and other intrinsic traits related to photosynthesis, life form and life span have received less attention than floral traits (Fig. 2). However, contrary to expectations, they were more consistently associated with trait-dependent diversification than reproductive traits.

Consistency was also found in extrinsic traits related to biogeography and habitat, but in this case it is their lack of influence on diversification. While traits geographic range was tested on > 60 occasions it was found to influence diversification in just a third of these (Fig. 2b).

Our trait-centric approach allowed us to identify the types of traits that have shaped angiosperm diversification, but we could say little about which state was advantageous. This is largely because a lack of overlap among states across the 153 studies makes comparisons at this level difficult. For example, there were seven studies that examined traits relating to flower shape and of the 18 total states 16 were unique (narrow and wide corollas were examined twice). Nevertheless we were able to examine how particular states affected diversification in eight traits (Fig. S6). Generally, increases in diversification were inferred for all character states, as well as the absence of effect. Three traits showed more consistent patterns where one state was consistently associated with elevated diversification rates: epiphytism, non-C3 photosynthesis and self-incompatibility were associated with increased diversification in the majority of studies investigating them. Therefore it is difficult to say whether these traits and associated states are 'universal drivers' as they have only been investigated a handful of times (eight or fewer) in relatively small proportion of angiosperm species. However, we do note that for self-incompatibility, ~~this consistent~~ increased diversification rates meet predictions [66]. As more studies are published it may be viable to investigate patterns at the character state level, particularly those for which there is a small number of states available (e.g. annual vs perennial, selfing vs outcrossing) yet even these simple states often have nuances that make them more complex than they first appear [65]. For example, the sexual system of some species can vary [67] in response to factors such as climate or pollinator presence [68].

Even though we have outlined some general patterns in those traits that are more often influencing angiosperm diversification, it is evident that the overarching trend is that the same traits can have different effects on diversification, depending on where one is looking in the tree of life. Therefore, the main question remains open: what drives differences in diversification among angiosperms? This question has been posed many times, and the fact that it still motivates a wide variety of studies suggests that ~~it's~~ the complex interplay between trait evolution, biotic interactions and geography that matters. Indeed, geography (range size, biome) has been identified many times as an important factor [62, 63], but one can ask whether this is a cause or a consequence of differences in diversification particularly when more often than not SSE models

testing geography detected no effect (Fig. 2). Species with larger range sizes have more chances to speciate and are less likely to go extinct, but on a higher level, clades with more species are more likely to have large range sizes and to occur in different climates. Others have suggested that it is not the presence or absence of a trait that determines the evolutionary success of a clade, but rather the capacity to change [69, 70]. This may provide an explanation to the inconsistency of the effect of particular states and traits observed here, but again, one wonders here whether trait diversity is a cause or a consequence of species richness. Furthermore, as we will discuss next, the choice of clades and traits, as well as the quality of the input data, also influence whether or not differences in diversification are detected and our conclusions about the traits important for angiosperm diversification.

## Evolutionary scale and context needs careful consideration

The effect of a trait on diversification has long been [71] thought to be linked to geographic, biotic (the presence of other species), environmental and temporal context [72], all of which vary over a lineage's evolutionary history. Users of models of trait-based diversification thus face an important challenge - choosing the context in which to conduct analyses. In the simplest scenario, where a trait only evolved once in the study clade, it is impossible to separate correlation from causation [41]. In this case correlated factors that were not assessed may be driving the observed association between character state and diversification rate and these two factors cannot be pulled apart, and thus this type of context should be avoided when proposing a study.

At the intermediate scale a trait may have evolved multiple times in a closely related group but there is now a problem akin to phylogenetic pseudoreplication of lineage-specific factors [73]. The evolutionary context (i.e. species' genomes, morphology, ecology, or external environments) of closely-related clades is much more similar than distantly-related ones. So, repeated associations between states and rates are not as independent as we might assume. Our ability to pin causality on one trait in particular is weakened when similar sets of associated traits are present in all cases that may be driving inferred patterns of diversification. Increasing the phylogenetic scope of the analysis, by way of either a larger tree, or multiple trees in a meta-analytic framework [42] can help to avoid pseudo-replication. The latter approach does not require that groups are closely related and therefore limits the potential for phylogenetic pseudo-replication. However, our results show that when bringing together evidence from different clades the same

traits often have entirely different effects on diversification (Fig. 2). This is likely because vastly different evolutionary contexts provide the potential for confounding lineage-specific factors to have an influence on the effect of the trait of interest. This may also explain the amount of inconsistency observed with synthesising published results from a wide variety of clades (Fig. 2).

Models with hidden states go some way towards alleviating this issue as they can account for lineage-specific factors. While a handful of undefined states are unlikely to provide concrete answers as to why the same trait may have a greater influence on diversification in one clade than another, they provide a good starting point for uncovering how important lineage-specific factors are. Other potential avenues of research that could help to account for confounding factors include shifting focus from the analysis of a single trait to working with groups of traits [31, 72, 74], informed by previous work or theory. Formulating hypotheses with antagonistic and synergistic factors in mind, rather than just the focal trait, would also act to mitigate such issues but this is difficult without extensive prior knowledge about the biology of the chosen study group or previous studies of trait-dependent diversification in the group. In future studies it may be useful to consider those states that are present in the study group and have been consistently shown to be linked to diversification in this review (e.g. epiphytism or self-incompatibility), or those that have already been shown to be influential in the clade of interest in prior work, alongside the chosen study traits. This would allow one to determine whether the effect of the original variable remains and attribute any 'noise' to a known trait alongside any potential hidden states.

Another aspect of evolutionary context we found to be important was when the trait of interest evolved relative to the chosen study clade. Previous work based has shown that at relatively low transition rates the root state most often had lower speciation rates [42] and that root state assumptions have substantial impacts on simulated macroevolutionary scenarios [75]. It appears that similar patterns may have made their way into empirical results. Putative root state was among the most important categorical variables when predicting trait-dependent diversification (Fig. 5). Choosing where the root of your tree is may seem an arbitrary and unimportant choice made during data collection or study design, but our results indicate that it is associated with downstream results as when trait-dependent diversification is detected, net diversification rates are most often higher (73% of cases) for a derived state. Likewise, we

found that the proportion of trait-dependent diversification varied with the taxonomic scale of the study with studies investigating families or clades above the order level most often yielding significant associations (Fig. S3). When conducting a study of trait-dependent diversification it may therefore be worth considering how altering the scope of an SSE study would affect the ancestral state, and whether this would have any downstream effect on inferences. All of these different factors point towards a need for careful consideration of evolutionary context when designing a study of trait-dependent diversification, with no simple explanation as to the best approach.

## Clade-driven vs hypothesis-driven approaches

The lack of any clear, general trend emerging from our literature survey can also be linked to the heterogeneity in the focus and objectives of published studies, or different levels of ascertainment bias related to how study clades and traits are chosen [76]. Some studies were clearly aimed at testing traits predicted, *a priori*, to affect diversification, and clades were chosen for their relevance to the tested hypothesis. In contrast, other studies focused on a clade of interest (i.e. 'phylogenetic natural history' [77]), for which many traits can be opportunistically tested depending on the available data. This may explain, for example, why geographic range is so often tested - even if associations with diversification rate are found relatively rarely the data on a taxon's geographic distribution is typically easy to find. This pattern is particularly evident when we compare the frequency of trait-dependent diversification in extrinsic (probably easier to measure or more readily available) and intrinsic (less easy to measure) traits, where intrinsic traits (e.g. vegetative traits) more often than not have published evidence of trait-dependent diversification while in the majority of cases extrinsic traits (e.g. biogeography) do not (Fig. 2). One potential consequence of these two different approaches to conducting a study of trait-dependent diversification is that opportunistically tested traits may have blurred any general patterns based on how consistently a particular trait is linked to diversification.

There is clearly a continuum between hypothesis-driven and clade-driven approaches so it is difficult to categorise studies based on this criterion but with our collated data on the number of clades and traits investigated per study we can make an attempt. For example, there were 131 studies (86% of the total) focusing on a single clade. With the expectation that studies that look at vastly different traits (those in different categories at trait level 2 (Table S1)) in a single group

are clade-driven, around 30% could be considered this way. This is an approximation - there may be studies that tested several different traits, each driven by strong hypotheses or studies where many traits were tested opportunistically but just a single result reported. Nevertheless, there is division in the way that trait-dependent studies are conducted and effort should be made by authors to be clear on which of these approaches was taken. Another useful aim would be to try to merge these two approaches so that clear hypotheses are outlined in multiple, well-known clades, particularly if we want to understand large-scale patterns.

## Biases in empirical results

When synthesising the literature, only data from published studies are available, which presents several issues when trying to infer general patterns in nature. It is undoubtedly easier to publish a clear, significant effect of a trait on diversification than a lack of effect. Yet determining the latter is critical to our understanding of how traits influence angiosperm diversification. A trait type that often leads to trait-dependent diversification e.g. fruit morphology (Fig. 2a) may be over-valued because its consistency is due to publication bias rather than its role in generating angiosperm diversity. Much evidence that could change these kinds of general patterns likely remains unpublished, or unreported in publications. Furthermore, if we assume that it is easier to publish a finding of trait-dependent than one where no effect is found, this could also affect the results of the machine learning approach used here as the proportions of trait-dependent results may be over-inflated.

One of the major criticisms of early SSE models was the propensity to infer false positives [41, 42] and the difficulty in determining whether focal trait itself is the driver of diversification [9]. This could be a potential explanation for the inconsistency of the effects of traits across clades - it may be that false positives caused by lineage-specific factors correlated with the shared focal trait are driving the disparate patterns. SSE models including hidden states and their associated null models allow researchers to disentangle the effects of unmeasured traits and the possibility of trait-independent diversification, to be more confident in their results. If such biases were affecting the conclusions we make here, we might expect different results from models with and without hidden states. We re-plotted Figure 2, with only results from models that contain hidden states (Fig. S16). We found that the proportion of trait-dependent outcomes increased for slightly reproduction and significantly for biogeography and decreased slightly for vegetative

and more substantially habitat. This might suggest that introduction of hidden states to SSE modelling had more of an effect on the results inferred using extrinsic traits, though we note that these analyses are based on a drastically reduced data set (21 studies). Even if complex patterns should remain, there is hope to get a clearer picture of diversification processes in angiosperms from well-designed datasets and more careful analyses with models that can limit the potential for false positives.

## Best practices for SSE model use and result reporting

Though a number of recommendations have been made on the requirements for accurate inference with SSE models, most empirical studies do not meet them. Using strict thresholds (50% taxon sampling, 300 tips and minor tip state frequency of 10%) we find that just ten studies meet all of these criteria. Perhaps the most concerning criterion is sampling fraction - the majority of recent studies use phylogenetic trees representing less than 50% of the known, extant species in their study groups. The apparent relationship between sampling fraction and inference of trait-dependent diversification (Fig 4) might suggest that studies with low sampling fraction are leading to more false positives. It could also be that with a high sampling fraction it's easier to publish any kind of result as it is deemed to be representative of the true relationship between the trait and diversification. Whereas with low sampling fraction it may be more difficult to publish when there is no effect of a trait because lack of power can easily be invoked as a caveat to the inference, ultimately over-inflating the number of positive results at lower sampling fractions. A special effort should be made towards disentangling the relationship between sampling fraction and results of SSE models, through the use of simulations to identify underlying causes. In addition we urge researchers to stick to thresholds that have been put forward [42, 57, 59] to ensure that biases are not introduced by using inadequate data sets. If recommendations cannot be followed, because of natural limitations in clade size, for example, these should be stated clearly as caveats.

In most studies, not all of the information we wanted to collect was available and it was sometimes difficult to access. Collecting data for many properties (e.g. samples per state) required us to count from figures or extract statistics from archived raw data, which were not always freely available. For example, information about the putative root state was retrievable in less than half (47.3%) of studies and in many of these cases it had to be inferred based on sources

of information outside of the study itself. Another key piece of information that we were unable to extract and use here was the number of independent origins of each character state. Robust estimates of associations between traits and diversification rates necessitate multiple independent origins (but not too many [42]) and corresponding rate changes [59] so an idea of this value per study, inferred using ancestral state reconstructions, would be useful for interpretation of the robustness of results. Another way this could be done is by combining stochastic mapping of traits and an SSE model [78], which would allow ancestral states to be reconstructed while taking into account diversification rate differences among states, and would facilitate comparisons across studies. Likewise, diversification and transition rates were often not reported in an easily-accessible and standardized manner, or in some cases, not at all. These should be reported, and if possible, confidence metrics around rate estimates should be reported e.g. bootstrap or Bayesian credible intervals. Louca & Pennell [79] recently pointed out how diversification rate estimation can be susceptible to issues of unidentifiability. SSE methods are not directly affected by these issues due to their assumptions of time-independent rates (i.e. diversification does not vary over time) [80]. However, this does not mean that there will not be other, related issues we uncover in the future. One way to reduce the potential for unidentifiability would be to avoid reporting and assessing speciation and extinction rates separately, focusing instead on compound parameters such as net diversification rate $(\lambda - \mu)$, turnover rate $(\lambda + \mu)$ and extinction fraction $(\mu/\lambda)$ that are typically used in more recent SSE models (e.g. HiSSE).

We have shown that dataset properties are closely linked to SSE model results, so it is paramount that they are reported in a consistent manner. To encourage standardized result reporting we propose an initial set of characteristics that should be made available in all future studies using SSE models (See Supplementary Data 1). This will allow researchers to better understand their own results, and to better interpret the work of others. Furthermore, this standardized data availability will improve our capacity to synthesize major trends in empirical results, not just in plants but in other groups as well. Thorough results reporting in studies that follow established recommendations will help to facilitate more rapid progress, in both knowledge of past diversification and methodological innovation.

As we argue above, evolutionary context appears to be important for understanding trait-dependent diversification. So how to best choose a trait and clade to study? First, we recommend having, or collaborating with someone who has an intimate knowledge of the biology of the study

group(s). This will help unlock more difficult to study, yet perhaps more influential, intrinsic trait types. It will also help to inform hypothesis generation and better account for other traits that may be related to the focal trait. Preliminary knowledge of the phylogenetic tree and ancestral state reconstruction should be used to ensure the derived state(s) arose multiple times and that the ratio among different states is not extreme (<10:1). In terms of choosing a clade, it is first important to adhere, as best as possible, to the recommendations for using SSE models e.g. avoid clades much smaller than 300 taxa and focus on those that are well sampled (>50%). Working at a much larger scale, e.g. angiosperm-level analyses, is certainly appealing but creates a range of issues related to confounding factors that current models will find difficult to disentangle. To better learn about the factors that influence angiosperm diversity we therefore suggest a focus on intermediate-sized clades i.e. large genera, families or tractable orders. If these clades are well-sampled they would approach the limit of our current computational feasibility (but see [81]). Some good example studies that are similar to the guidelines proposed here are Fernández-Mazuecos, et al. [82], who examine how a classic key innovation, floral nectar spurs, affects diversification in the tribe Antirrhineae (including toadflaxes), or Han et al. [54] who show that polyploidy driven by habitat shifts is associated with increased diversification rate in the speciose genus *Allium* (including garlic and relatives). If trait-dependent diversification is to be investigated a larger scale, it may be wiser to test the same hypotheses in several different, intermediate-sized clades while accounting for the unique and shared aspects of their biology (e.g. through the use of hidden states or trait combinations), then combining results [42] to uncover general patterns.

## Knowledge gaps and future avenues

We found that there is a strong correlation between the number of studies dedicated to a clade and its species richness. The groups most often studied belong to large families such as Orchidaceae as well as other speciose and economically-important families such as Poaceae (Fig. S2). Clades with relatively few species such as Gunnerales or Ulmaceae (containing the elms) are implicitly difficult to study as they do not contain the number of species required to generate reliable inferences of diversification patterns. These may need to be grouped with other closely related clades if their macroevolutionary history is to be explored. Our review also identified groups that are understudied. One of the most obvious is Asteraceae, species-rich yet subject to

relatively few trait-based diversification studies (Fig. S2), or Alismatales, an order that has more than 4,500 species (Fig. S1) but just a single study on their trait-based diversification [83]. In addition, some families with more than 1,000 species, such as Phyllanthaceae or Orobanchaceae have yet to be studied in this way. Such groups provide good focal points for future research and their study will provide a more well-rounded picture of flowering plant macroevolutionary dynamics.

High-quality phylogenetic trees are not the only ingredient for SSE studies; trait data also need to be available. We found that traits were studied at different intensities and highlight traits related to lifespan, dispersal and symbiosis as ripe avenues for new studies that have potential to unearth important patterns in trait-dependent diversification. However, apart from a few traits such as geographical range or climatic preferences, gathering high-quality data for large numbers of species is a time-consuming activity. A first step towards broadening the availability of trait data is the practice of publishing trait data as appendices to a scientific study, which is now standard. Then, to test for context-dependent effects of traits and to uncover what traits hide in the hidden-state approaches, one needs to consider several traits together. Using data from previous SSE studies is difficult because species included in different studies usually have only small overlaps. One solution is to encourage the integration of trait data generated from any study into large, global trait databases such as eFLOWER [84], TRY [85] or more focused databases e.g. AusTraits [86]. These differ in the level of curation and completeness: some databases focus on specific taxa and put special effort in gathering as many traits as possible for all (eFLOWER, AusTraits), while others are less restrictive about trait completeness and thus allow to integrate data of many more taxa (TRY). Both types of approaches have their strengths and weaknesses, and users will have to take these into account, just like the quality of the phylogenetic trees.

A strength, but also a limit, of macroevolutionary methods is that they encapsulate many mechanisms into aggregated parameters that may appear as statistical (and conceptual) black boxes. Another potential avenue for further work would be to try to better link macroevolutionary patterns from diversification analyses to other sources of evidence. If a trait is predicted to affect speciation and extinction it is through various ecological and genetic processes that can also be put to the test. For example, by comparing sister species with contrasted mating systems (selfing vs. outcrossing), Park et al. (2018) [87] showed that niche breath was initially

similar between species but tended to decline over time in selfing lineages, in agreement with the dead-end scenario proposed for this trait and detected in macroevolutionary analyses [33, 88]. This highlights how trends from macroevolutionary studies could be tested from ecological or population genetic studies. Yet the reverse approach is also possible. We can identify traits that potentially have a strong effect on ecological and genetic mechanisms that primarily control speciation and extinction, such as traits affecting coexistence and niche partitioning [89] (e.g. specific ~~Leaf Area~~ or seed mass), genetic differentiation between populations [90] (e.g. pollination mode, mating system, growth form) or those associated with commonness and rarity [91] (e.g. seed production). Such traits could be ideal candidates for macroevolutionary studies exploring their effect in diversification and provide *a priori* hypotheses and help to avoid opportunistic studies that may dilute real trends.

# Conclusions

When bringing together the last 12 years of study on trait-dependent diversification in angiosperms, it is the inconsistent effects of traits that stand out, rather than the importance of a particular set of universal drivers. Generally, intrinsic traits were linked to diversification more often than extrinsic traits yet almost all traits with more than a small amount of research effort had studies with inconsistent results. This points towards an important role for the evolutionary context of a clade in determining how a particular trait affects diversification. Questions posed and hypotheses tested should take such context into account when using trait-dependent models of diversification. Furthermore, the nature of the data itself, relating to factors such as how well-sampled or large a clade is, was shown to have a greater influence on practical SSE model use than previously thought and must be considered carefully. The accelerating production of large, high-quality phylogenetic trees and innovation in the means to create them [92–94] provides unprecedented potential and power to uncover the origins of angiosperm diversity. The guidelines we set out in this review will help to improve how we use trait-dependent models and our template for reporting results will facilitate future synthesis as SSE models continue to be used and developed. Overall, we have only touched the surface of what we can learn about trait-dependent diversification in angiosperms. Will results from novel studies on trait-dependent diversification in angiosperms change the trends we observe here? Given the production of new datasets that meet recommendations for robust inference, future methodological developments enabling studies at wider scopes and the potential for new discoveries in understudied traits and clades, we think it is certainly possible. Though our study focused on flowering plants the conclusions we draw about consistency, context dependence and SSE model use will apply to studies of trait-dependent diversification across the entire tree of life.

# Acknowledgements

# Supplementary Material

Code associated with this manuscript is available from `http:/github.com/ajhelmstetter/sseReview`. PapieRmache can be found at `http:/github.com/ajhelmstetter/papieRmache`.

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