



Linking mode of seed dispersal and climatic niche evolution in flowering plants

Thais Vasconcelos | James D. Boyko | Jeremy M. Beaulieu

Department of Biological Sciences,
 University of Arkansas, Fayetteville,
 Arkansas, USA

Correspondence

Thais Vasconcelos, Department of
 Biological Sciences, University of
 Arkansas, Fayetteville, AR 72701, USA.
 Email: tvasc@uark.edu

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Abstract

Aim: Due to the sessile nature of flowering plants, movements to new geographical areas occur mainly during seed dispersal. Frugivores tend to be efficient dispersers because animals move within the boundaries of their preferable niches, so seeds are more likely to be transported to environments that are similar to where the parent plant occurs. However, this efficiency can result in less opportunity for niche shifts over macroevolutionary time, ‘trapping’ plant lineages in particular climatic conditions. Here we test this hypothesis by analysing the role that the interaction with frugivores play in changing dynamics of climatic niche evolution in five clades of flowering plants.

Location: Global.

Taxon: The flowering plant families Apocynaceae, Ericaceae, Melastomataceae, Rosaceae and Solanaceae.

Methods: We model climatic niche evolution as a variable parameter Ornstein–Uhlenbeck process. However, rather than assuming regimes *a priori*, we use a hidden Markov model (HMM) to infer the complex evolutionary history associated with different modes of seed dispersal. In addition to allowing for a more accurate picture of the regimes, the use of HMMs allows partitioning the variance of climatic niche evolution to include dynamics independent of our focal character.

Results: Lineages dispersed by frugivores tend to have warmer and wetter climatic optima and are generally associated with areas where potential for vegetation growth is higher. However, lineages distributed in more mesic habitats, such as rainforests, are generally associated with slower rates of climatic niche evolution regardless of their mode of seed dispersal.

Main Conclusions: Characteristics of the abiotic environment may facilitate the evolution of some types of plant–animal interactions. Association with frugivores is an important modulator of how plants move in space, but its impact on their climatic niche evolution appears to be indirect. Seed dispersal by frugivores may facilitate the establishment of lineages in closed canopy biomes, but the general slower rates of climatic niche evolution in these habitats are possibly related to other general aspects of the ‘mesic syndrome’ rather than the behaviour of the animals that disperse their seeds.

KEY WORDS

Apocynaceae, climatic niche, Ericaceae, frugivory, hidden Markov models, Melastomataceae, Rosaceae, seed dispersal, Solanaceae, trait evolution



1 | INTRODUCTION

While angiosperms are colloquially known as the flowering plants, one may argue that it is in their fruits where some of their most striking adaptations are found. Fruits are not only important for reproduction but also crucial for how angiosperms diversify in space (Muñoz et al., 2019; Seidler & Plotkin, 2006). The sessile nature of flowering plants implies that their movement to new geographical areas occurs mainly during the phase of seed dispersal, when seeds are carried away from the parent plant into new sites (Levin et al., 2003). The way in which seeds are moved to new areas can therefore have a huge impact in determining where new individuals and populations of a species are established.

Adaptations for different modes of seed dispersal are usually responsible for changes in the whole morphology of the fruit (Gautier-Hion et al., 1985). Plants that depend on animals for seed dispersal usually produce fruits with fleshy pulp that attract and are consumed by frugivores (Eriksson, 2016; Jordano, 2000; Jordano et al., 2007). Convergent evolution is a sign of adaptation (Stearns, 1986), and many lineages of angiosperms converged to have traits that attract frugivores. Frugivores are mainly mammals and birds and their interaction with flowering plants through the process of seed dispersal is of special importance in diverse biomes such as subtropical and tropical rainforests (Jordano, 2000; Schupp, 1993). Adaptations for frugivore dispersal are particularly common in these biomes (e.g. Chen et al., 2017; Wang et al., 2021) and the interpretation for this pattern is usually linked to competition for light in warmer and wetter areas where trees tend to grow bigger, creating habitats that are shadier. These shady habitats impose strong selective pressure for the evolution of larger seeds due to the demand of storing nutrients for germination where sunlight is reduced (Foster & Janson, 1985; Leishman & Westoby, 1994). While the abundance of rainfall in these areas allow large trees to produce larger seeds, larger seeds also have a low dispersal potential on their own (Howe & Smallwood, 1982). Dispersal by animals becomes an advantage in this scenario because it increases the chances that seeds are carried away further

from the parent plant, avoiding competition for resources between generations of the same species (Westoby et al., 1996). Additionally, seed dispersal by frugivores tends to be more efficient because animals tend to move predictably in areas that are favourable for them (Sasal & Morales, 2013), so seeds are more likely to be carried to habitats that are similar to the parental plant (Schupp, 1993; see also Bolmgren & Eriksson, 2005).

The role of the interaction between fleshy fruits and frugivores in regulating how flowering plants move in space over time has been of particular interest to several branches of biogeography. For instance, dispersal by frugivores has been investigated for their effect on plant's range size (Reginato et al., 2020) or on the success of long-distance dispersal events (Onstein et al., 2019). However, a relatively unexplored venue is how different modes of seed dispersal may regulate the rate in which flowering plants overcome climatic barriers and adapt to different climatic conditions. Climate is one of the most important components of the abiotic environment and of special importance for sessile organisms (Huntley, 1991). On a macroevolutionary scale, lineages tend to keep track of their preferred climatic conditions, with the probability of shifts in habitat being modulated by, among other factors, exposure to different environments over time (Donoghue & Edwards, 2014). Given that seeds dispersed by frugivores may be more likely to be taken to the same biome as the parental plant (e.g. Janzen, 1971), there may also be less opportunity for them to move to different niches. Abiotic factors such as wind or water, on the other hand, are thought to disperse seeds in a more erratic fashion (Van der Pijl, 1982), leading seeds to both favourable and unfavourable niches and potentially promoting selective opportunities for rapid changes in climatic niche over time (Stebbins, 1974). Note that, in this context, the probability of dispersal to a suitable site for germination is independent of distance of dispersal.

By combining these ideas, one can hypothesize that the evolution of endozoochory, and the consequent association with frugivores for seed dispersal, may lead some lineages to become 'trapped' in particular climatic niches (Figure 1). That is, this interaction can

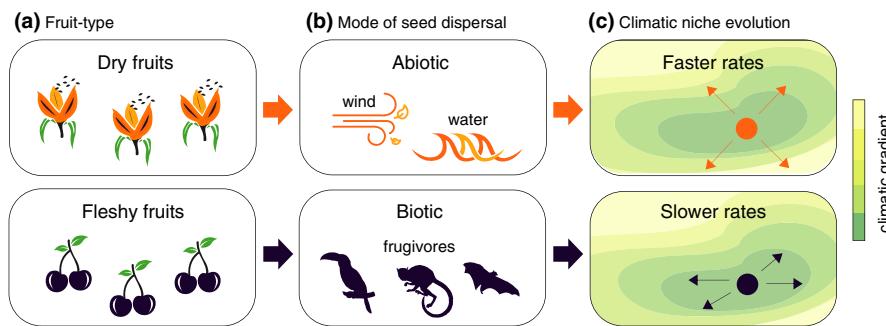


FIGURE 1 Reasoning behind the hypotheses tested in this study. (a) Dispersal syndrome is the plant trait representing discrete regimes, and each species is scored as having either fleshy or dry fruits. (b) Dry fruits are used as a proxy for abiotic seed dispersal, whereas fleshy fruits are used as a proxy for biotic seed dispersal (i.e. endozoochory, see Methods section). (c) Different modes of seed dispersal are expected to impact rates of climatic niche evolution in flowering plants differently, based on the assumption that abiotic factors promote erratic dispersal and increased opportunity for niche shifts through time (silhouettes adapted from phylopic.org and vecteezy.com)



lead flowering plant lineages to have relatively lower rates of climatic niche evolution, higher selective pressure for keeping a particular climatic niche through time or both. Adaptation to future predicted climate changes is thought to require much higher rates of climatic niche evolution than the observed in many lineages of organisms (e.g. Quintero & Wiens, 2013). The possibility that lineages dispersed by frugivores are less adaptable to new climatic conditions is worrying because it means that these lineages can be under severe threat from both climate change and defaunation, both of which are of particular concern in hotspots of biodiversity where these lineages are most diverse (Huntley, 1991; Pérez-Méndez et al., 2016). It is therefore crucial that the link between mode of seed dispersal and climatic niche evolution is well understood in flowering plants.

In this study, we take advantage of multiple trait evolution models to test three hypotheses related to how the interaction with frugivores may impact climatic niche evolution in flowering plants: (1) lineages with different modes of seed dispersal have different climatic niche optima, with those lineages that depend on frugivores shifting to mesic optima (i.e. higher potential for vegetation growth) and those that do not to xeric optima (i.e. lower potential for vegetation growth); (2) lineages that do not depend on an animal vector for seed dispersal have faster rates of climatic niche evolution over time, because erratic dispersal leads to more opportunities for occupying different niches; and conversely (3) lineages where seed dispersal depends on animal vectors tend to be more climatically conserved over time, under the assumption that frugivores animals themselves also experience niche conservatism and tend to move within the boundaries of their preferred niches. To test these hypotheses, we analysed climatic niche evolution in relation to fruit type in five diverse families of flowering plants of global distribution. We explore how fruit types affect climatic niche evolution in each of them and discuss generalities that can be applicable more broadly to all flowering plants.

2 | MATERIALS AND METHODS

Unless otherwise stated, all analyses described below were performed in R (R Development Core Team, 2021). All dataset and relevant code are available at github.com/tncvasconcelos/seed_dispersal.

2.1 | Phylogenetic trees and fruit type data

The flowering plant families Apocynaceae, Ericaceae, Melastomataceae (in addition to its species-poorer sister clade in Myrtales, the Crypteroniaceae–Alzateaceae–Peneaceae [CAP] clade, Maurin et al., 2021), Rosaceae and Solanaceae were chosen because they combine a set of desirable characteristics to investigate the link between frugivory and climatic niche evolution in flowering plants. First, they represent different branches of the angiosperm tree of life (Apocynaceae, Ericaceae and Solanaceae are asterids, whereas Melastomataceae and Rosaceae are rosids; Stevens, 2001 onwards).

Second, all the five clades are generally cosmopolitan, albeit in different kinds of habitats (e.g. Melastomataceae are particularly diverse in the tropics, whereas Rosaceae are mainly distributed in temperate areas of the Northern Hemisphere). Third, the five clades present variation in seed dispersal mode with multiple evolutionary shifts between endozoochory and other syndromes of seed dispersal (e.g. Knapp, 2002; Reginato et al., 2020; Stevens et al., 2004; Xiang et al., 2017), making them ideal to test the hypotheses of this study.

We assembled the latest phylogenies of the five clades from the literature. No phylogenetic inference analysis was performed by us; nexus or newick files for the five phylogenies were downloaded directly from the supplementary data of the original papers (in Reginato et al., 2020; Särkinen et al., 2013; Schwery et al., 2015; Sun et al., 2020) or sent by the corresponding author of the original paper upon request (in Fishbein et al., 2018). Together, the five phylogenetic trees encompass 5564 species of flowering plants and all present at least 10% of their species diversity sampled in the tree (Apocynaceae 1041 species, 23%; Ericaceae 478 species, 11%; Melastomataceae 1716 species, 34%; Rosaceae 1253 species, 44%; Solanaceae 1076 species, 39%). Each phylogenetic tree was analysed separately and constitute a natural replicate in our analyses.

We then scored the mode of seed dispersal for species sampled in the five phylogenetic trees following the literature of each group (see also Appendix 1). The five analysed flowering plant families present a wide variety of fruit morphologies, including drupes, berries, capsules, nutlets, achenes, pomes and fruit aggregates. Field observations of frugivore-mediated seed dispersal are not available for most of the analysed species and so, to score as many species as possible as being either dispersed by frugivores or not, we used the concept of dispersal syndrome (Valenta & Nevo, 2020). Syndromes are a combination of traits that are shared among unrelated species due to convergent evolution in response to similar selective pressures over time (Sinnott-Armstrong et al., 2021). In the context of seed dispersal, species that rely on frugivores to disperse their seeds typically present fruits that are fleshy and visually attractive when ripe, a syndrome called endozoochory (Gautier-Hion et al., 1985). We assigned each tip of each tree as being either endozoochorous (simplified as ‘fleshy fruited’ throughout the text) or non-endozoochorous (simplified as ‘dry fruited’ throughout the text), with the general assumption that the non-endozoochorous ones are mainly dispersed by abiotic factors.

These categories are simplified as ‘fleshy’ and ‘dry’ throughout the text, even though there are some endozoochorous fruits that are technically dry, such as those of *Gaultheria* (Ericaceae) which are dry, but have a fleshy persistent calyx that attract frugivores, or those of *Tabernaemontana* (Apocynaceae), which are also dry, but have fleshy arillate seeds and strong evidence of dispersal by frugivores (e.g. Villalobos-Chaves et al., 2020). Although the concept of dispersal syndrome is usually well supported in these five families, it did not avoid some challenges in scoring fruit type in groups where natural history observations are scarce and dispersal mode may vary in a continuum (e.g. berries in *Solanum*, Solanaceae, see Appendix 1) or in few cases where dry fruits may be also animal dispersed (e.g. epizoochory). For that reason, we



also remove from the analyses some species that had dubious interpretations regarding their mode of seed dispersal (e.g. the possibly epizoochorous *Acaena latebrosa* and *Acaena caesiglauca* in Rosaceae; Lee et al., 2001) or no information on fruit type at all (e.g. several species of *Solanum* in Solanaceae).

2.2 | Assemble and curation of occurrence data

We assembled distribution data for all the species sampled in each tree by first standardizing all tip names in the phylogenies according to the taxonomic backbone of the Global Biodiversity Information Facility (GBIF.org, 2020) using the package *taxize* (Chamberlain & Szöcs, 2013). We then used the package *rgbif* (Chamberlain et al., 2017) to download all occurrences available for these species that could be traced back to a preserved (i.e. herbarium) specimen (reference numbers of downloads are available in Appendix 1). A total of 914,496 records were compiled, including 133,278 for Apocynaceae, 138,209 for Ericaceae, 198,455 for Melastomataceae+CAP clade, 224,265 for Rosaceae and 220,289 for Solanaceae.

GBIF is the largest aggregate of natural history databases online, but species distribution data are often subject to issues including wrong coordinates and sampling bias (e.g. Colli-Silva et al., 2020; Maldonado et al., 2015). To alleviate some of these problems, we filtered all coordinates to address some of the most common problems encountered in these datasets using functions of the packages *raster*, *dismo* and *sp* (Hijmans et al., 2015, 2017; Bivand et al., 2013). We removed duplicated coordinates, points located in the sea, points with rounded latitude and longitude (i.e. without decimal places), points placed in countries other than those assigned in the specimen label and points that had 0 × 0 coordinates. We also removed outliers in distributions (defined as those whose minimum distance to the nearest three points was more than the mean total distance between all points) and species that occurred in more than two biogeographical realms (Olson et al., 2001), as a proxy for crops and invasive species. These filters are important to ensure high-quality data, but are also restrictive, and in the end 43% of species were removed from the dataset after the filtering process. These species were pruned from the trees before mapping regimes for modelling climatic niche evolution (see below).

2.3 | Measurements of climatic niche

We overlaid the filtered distribution points with the layers (rasters) of three environmental variables that were used to measure climatic niche for each species: aridity index, mean annual temperature and mean annual precipitation. Aridity index is a measurement of potential of vegetation growth (Trabucco & Zomer, 2018) and a good estimate for the distribution of closed canopy biomes across the globe. Aridity index is defined as Mean Annual Precipitation/Mean Annual Reference Evapo-Transpiration (ETO), while ETO is defined by the Penman-Monteith equation (Allen et al., 1998) which considers

variables of temperature, wind, solar radiation, soil temperature and vapour pressure (see Trabucco & Zomer, 2018). In general, the higher the aridity index the more mesic (i.e. humid) the biome is, so henceforward we will refer to this variable in the text simply as 'humidity'.

Humidity is probably the climatic variable that best fit the context of our first hypothesis since it describes potential of vegetation growth and thus how likely it is for a habitat to have closed canopy. However, we also analysed mean annual temperature and mean annual precipitation (respectively BIO01 and BIO12 from CHELSA; Karger et al., 2017) to make our results comparable to other studies that use these variables in the same context (e.g. Rolland et al., 2018). These two variables are henceforward referred simply as 'temperature' and 'precipitation' throughout the text. Though results with all three variables are reported, we note that humidity is strongly correlated with precipitation ($R^2 = 0.87$ in our dataset) and poorly correlated with temperature ($R^2 = 0.02$), whereas temperature is poorly correlated with precipitation ($R^2 = 0.12$). An additional advantage of analysing temperature is that this variable generally correlates with altitude, so it also captures reasonably well the climatic niche of lineages that are typically montane, such as Ericaceae (Schwery et al., 2015). All layers were analysed in their highest resolution of 30 arc-second (1 km at the equator). Note that because our measurement of niche is based on distribution data only, this may be best considered a measurement of realized niche, that is, the set of climatic variables where the species occur rather than fundamental niche (Qu & Wiens, 2020; Soberón, 2007).

We used functions of the R packages *sp* and *raster* to extract the values of each climatic variable in each distribution point. To reduce the bias associated with overcollecting in particular areas, we then filtered the distribution of every species with two or more valid points to consider only one occurrence in each 1 × 1 degree cell. The value of each remaining point was then log transformed before further analyses to make sure that climatic niche conformed with Brownian motion evolution (O'Meara et al., 2006). A proxy for the climatic niche of each species was then calculated as the mean of the log values of each environmental variable in each point. Note, however, that each species is a composition of populations that may also vary in their climatic tolerances. For that reason, we also incorporated uncertainty in the measurements of niche by calculating the within species variance, defined as the sample-size-weighted average of the individual species variance: σ_w^2/n_p , where: $\sigma_w^2 = \sum_i \sigma_{wi}^2 (n_i - 1)/\sum_i (n_i - 1)$, and σ_{wi}^2 is the sample variance of species i and n_i is the sample size of species i (see Labra et al., 2009). This error measurement was incorporated in all subsequent analyses of climatic niche evolution described below.

2.4 | Modelling climatic niche evolution in relation to fruit type

To model the evolution of climatic niche in relation to fruit type, we relied on the continuous trait evolution models available in the package *OUwie* (Beaulieu et al., 2012). *OUwie* uses a maximum likelihood



framework to fit models where a trait is expected to evolve according to either a Brownian motion (BM) or Ornstein–Uhlenbeck (OU) process. An OU process is modelled according to the differential equation:

$$dX_i(t) = \alpha [\theta_i(t) - X_i(t)] dt + \sigma dB_i(t),$$

which describes how a continuous trait X_i evolves as a function of time t towards some optimum value described by θ_i (see also Beaulieu et al., 2012; Hansen, 1997; O'Meara & Beaulieu, 2014). The parameter σ^2 represents the rate in which the value of the trait randomly fluctuates around θ_i and α describes the rate in which values are pulled back towards the optimum. A BM is a special case of OU where $\alpha = 0$, so only σ^2 is estimated.

It is particularly appealing to test our hypotheses using this framework for two reasons. First, OUwie allows parameters to vary according to discrete regimes mapped on the branches of a phylogenetic tree (Beaulieu et al., 2012). The regimes, in this case, are the two different states of fruit type (dry and fleshy; Figure 1a) and we assume that climatic niche (Figure 1c), the continuous trait, may take different parameter estimates while evolving under these two distinctive regimes.

Second, our questions can be neatly translated into the different parameters of BM and OU models (or transformations of those) (Table 1). Our first hypothesis, for example, would be simply corroborated in any scenario where $\theta_{\text{dry}} < \theta_{\text{fleshy}}$ for any of our climatic variables. To test our second and third hypotheses, on the other hand, we used transformations of the σ^2 and α parameters to facilitate unit interpretation. Stationary variance around the optimum, calculated by the formula $V = \sigma^2/2\alpha$, was interpreted as a measurement of rates of climatic niche evolution. A higher stationary variance would imply higher rates of evolution and less restrictive optima (i.e. high σ^2 in relation to low α). Higher rates of climatic niche evolution are hypothesized to be a consequence of erratic seed dispersal in dry fruits, so we would corroborate the second hypothesis in any scenario where $V_{\text{dry}} > V_{\text{fleshy}}$. Phylogenetic half-life, calculated as $t_{1/2} = \log(2)/\alpha$, expresses how long a trait takes to move halfway between the ancestral state and the optimum value of the trait and it was here used as a proxy of niche conservatism. As α takes larger values, $t_{1/2}$ decreases

and a $t_{1/2} = 0$ is ultimately equivalent to an instantaneous movement (or adaptation) from an ancestral state towards the optimum value of a trait, implying stronger niche conservatism. A scenario where $t_{1/2 \text{ dry}} > t_{1/2 \text{ fleshy}}$ would then be consistent with our third hypothesis, which predicts that dispersal by frugivores in lineages with fleshy fruit increases niche conservatism over time. Note that, under BM ($\alpha = 0$), $V = \text{NaN}$, in which case we will report values of σ^2 instead of V for rate of climatic niche evolution (see also Toljagić et al., 2018). Note also that θ is given in the unit trait, whereas V represents the variation scaled by the rate of adaptation. Half-life ($t_{1/2}$) is usually given in million years, but to make comparisons among different clades easier we present half-life in proportion to total tree height (i.e. $t_{1/2}/\text{total tree height}$, see Ho & Ané, 2014).

It is often revealed that the optimal value estimated for a trait is not observed in any extant taxa of that lineage (e.g. Toljagić et al., 2018). That can be a result of a long phylogenetic half-life (i.e. due to high niche conservatism, lineages move very slowly to their optima), low rates of niche evolution or recent evolution of a particular regime (Hansen, 2014). For that reason, we also compared the observed mean of each climatic variable with their theoretical optima for each fruit type. Based on preliminary results and to further support our discussion, we also performed a simple linear regression between theoretical optima and stationary variance for each climatic variable in different fruit types.

We tested the fit of seven evolutionary models of increasing complexities, which constrain or allow parameters to vary between fruit types: BM (a simple BM where $\sigma_{\text{dry}}^2 = \sigma_{\text{fleshy}}^2$), BMS (a multi-rate BM where $\sigma_{\text{dry}}^2 \neq \sigma_{\text{fleshy}}^2$), OU1 (an OU with a single optimum for both regimes, where $\theta_{\text{dry}} = \theta_{\text{fleshy}}$, $\sigma_{\text{dry}}^2 = \sigma_{\text{fleshy}}^2$ and $a_{\text{dry}} = a_{\text{fleshy}} > 0$), OUM (a multi-peak OU where $\theta_{\text{dry}} \neq \theta_{\text{fleshy}}$, but $\sigma_{\text{dry}}^2 = \sigma_{\text{fleshy}}^2$ and $a_{\text{dry}} = a_{\text{fleshy}} > 0$), OUMA (a multi-peak OU with variable adaptive rates, where $\theta_{\text{dry}} \neq \theta_{\text{fleshy}}$, $\sigma_{\text{dry}}^2 = \sigma_{\text{fleshy}}^2$ and $a_{\text{dry}} \neq a_{\text{fleshy}} > 0$), OUMV (a multi-peak and multi-rate OU where $\theta_{\text{dry}} \neq \theta_{\text{fleshy}}$, $\sigma_{\text{dry}}^2 \neq \sigma_{\text{fleshy}}^2$ and $a_{\text{dry}} = a_{\text{fleshy}} > 0$) and OUMVA (a multi-peak and multi-rate OU with variable adaptive rates, where $\theta_{\text{dry}} \neq \theta_{\text{fleshy}}$, $\sigma_{\text{dry}}^2 \neq \sigma_{\text{fleshy}}^2$ and $a_{\text{dry}} \neq a_{\text{fleshy}} > 0$). It is important to note that BM and OU models will assume that the underlying regimes are completely known. However, often regimes will have

TABLE 1 Hypotheses, predictions based on Brownian motion and Ornstein–Uhlenbeck parameters of climatic niche, and interpretation of predictions related to the link between mode of seed dispersal and climatic niche evolution tested in this study

Hypothesis	Parameter	Prediction	Interpretation
H1: Lineages that depend on frugivores for seed dispersal shift to mesic climatic optima	θ (adaptive optimum)	$\theta_{\text{dry}} < \theta_{\text{fleshy}}$	When water is abundant, competition for light leads to larger plants and shadier habitats. Shadier habitats require larger seeds, which in turn are more efficiently dispersed by animals
H2: Lineages that do not depend on frugivores for seed dispersal have faster rates of climatic niche evolution over time	V (stationary variance)	$V_{\text{dry}} > V_{\text{fleshy}}$	Abiotic dispersal is more erratic and leads to more opportunities for shifts in climatic niche over time in plant lineages with seeds dispersed by abiotic factors
H3: Lineages where seed dispersal depends on frugivores tend to have stronger climatic niche conservatism	$t_{1/2}$ (half-life)	$t_{1/2 \text{ dry}} > t_{1/2 \text{ fleshy}}$	Animals also experience climatic niche conservatism and tend to move within the boundaries of their preferred climatic niche. This behaviour can lead to stronger climatic niche conservatism for plant lineages with seeds dispersed by frugivores



a complex evolutionary history and if the underlying regimes of an OU model are incorrectly estimated, the fit of the OU model could also be impacted (Ho & Ané, 2014). Furthermore, in larger, older clades the same character states can result from different evolutionary processes through convergence, and we expect that transition rates vary in different parts of the tree. For instance, dry fruits in Solanaceae can be capsules (e.g. in *Nicotiana*) or dry berries (e.g. 'trample-burr' in some species of *Solanum*; see Knapp, 2002), whereas fleshy fruits in Rosaceae can be pomes (e.g. peaches in *Prunus*) or modified achenetum (e.g. strawberries in *Fragaria*; see Xiang et al., 2017). In other words, it may be advantageous to allow transition rates to vary in different parts of the phylogenetic tree, because it is unlikely that a simple binarization of fruit types represents the true rate variation underlying the discrete trait (see also Beaulieu et al., 2013; Boyko & Beaulieu, 2021). Finally, phylogenetic comparative methods can often find support for overly complex models because a model which includes some amount of heterogeneity in the evolutionary process is likely to be closer to the truth than a model which presumes little or no change (Beaulieu & O'Meara, 2016). In other words, it is possible to find that climatic niche evolution is associated with fruit type in circumstances where climatic niche evolution has been heterogeneous through time even if the evolution of climatic niche and mode of seed dispersal are unlinked.

To overcome these problems, we used package *corHMM* to generate stochastic maps based on several Markov and hidden Markov models (HMM; Beaulieu et al., 2013; Bollback, 2006; Boyko & Beaulieu, 2021). *corHMM* uses a maximum likelihood framework to fit discrete trait evolution models of varying complexity, allowing transition rates to vary in different parts of the tree. We used *corHMM* to fit a set of eight different models, each representing a different combination of time homogeneous and hidden rate classes (See Appendix 2). To account for uncertainty in model selection (Burnham & Anderson, 2002) and mitigate the risk of an incorrect regime assignment, we produced up to 1000 stochastic maps (simmmaps) in proportion to the AIC_c weight of each *corHMM* model (e.g. an AIC_c weight of 0.5 would correspond to 500 simmaps reconstructed with that model). Our hidden rate models (HMMs) include four rate categories: R1_{Dry}, R1_{Fleshy}, R2_{Dry} and R2_{Fleshy} (Appendix 2). If a simmap was produced under an HMM, it was summarized to be (1) hidden-rate-only (i.e. character independent; CID, where only rates 'R1' and 'R2' are defined), (2) observed-state-only (i.e. character dependent; CD, where only rates 'Dry' and 'Fleshy' are defined) and (3) as is with four rate categories (i.e. a hybrid model; HYB, where variation can exist dependent or independent of the focal character).

There are two reasons for the inclusion of character independent and character dependent models. First, there are many

variables that may affect climatic niche evolution outside of type of seed dispersal. If our modelling set were simply to compare a model where climatic niche evolution depends on mode of seed dispersal to a model where climatic niche evolution is homogeneous through time, we might conflate support for a heterogeneous process with support for fruit-type-dependent climatic niche evolution. Second, although the hybrid model can account for this hidden variation, the additional parameters compared to the character independent model may not be supported by the signal in the data. Thus, rather than forcing an overly complex model that has the potential to be poorly fit, we include the simpler nested models (CD and CID; Boyko & Beaulieu, 2021; Grundler & Rabosky, 2020).

We then fit our set of OUwie models to the simmaps generated using the HYB, CID and CD models (a total of 21 OU models, 7 OU models per simmap class). Once again, we need to account for model selection uncertainty in our OU modelling. To do this, we model averaged our parameter estimates based on the AIC_c weight of each of the 21 OU models. The final parameter estimates presented are the tip-averaged means and standard errors under each regime (fleshy and dry fruit) in each clade after removing 5% of the tail on either side of the parameter distributions. Tip averages are calculated by weighting the model-averaged OU parameter estimates (e.g. $\theta R - 1_{\text{Fleshy}} \theta R 2_{\text{Fleshy}} \theta R 1_{\text{Dry}} \theta R 2_{\text{Dry}}$) by probability that an extant species was in that particular state. The marginal probability that a tip is in a particular state was calculated using *corHMM*'s ancestral state reconstruction function which also provides estimates of extant species being in a particular hidden state.

3 | RESULTS

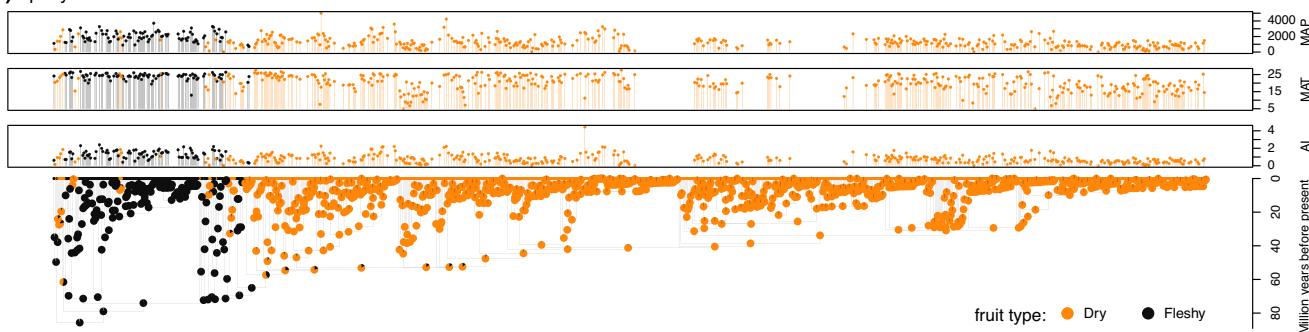
3.1 | Modelling fruit type and climatic niche evolution

Models with hidden rates received consistently higher support (lower AIC_c) in all clades with over 500 tips (all except Ericaceae), meaning that rates of fruit type evolution generally vary across the trees and within each of the observed fruit type states (Appendix 3). In most of the above-mentioned clades, the AIC_c weight for models with homogeneous rates was almost negligible, so the vast majority of the 1000 simmaps were based on HMMs. Transition rates tended to be low (<1 events per million year) in all clades, except in Rosaceae where transition rates were as high as 3.4 events per million year in highly supported models (Appendix 4). Regardless of the model, there was also a strong tendency for dry fruits as the ancestral states at the roots of all clades, with the exception of Apocynaceae (Figure 2a–e'i, Appendix 4).

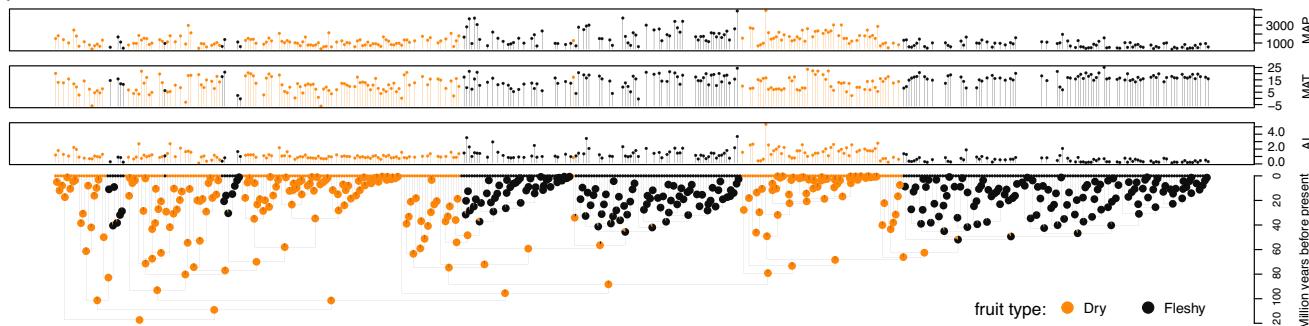
FIGURE 2 Ancestral state reconstructions of the averaged *corHMM* models and climatic niche means for species of (a) Apocynaceae, (b) Ericaceae, (c) Melastomataceae+CAP clade, (d) Rosaceae and (e) Solanaceae. Gaps represent tips with no climatic information that were pruned from the tree prior to OUwie analyses. AI, humidity, MAT, temperature, MAP, precipitation



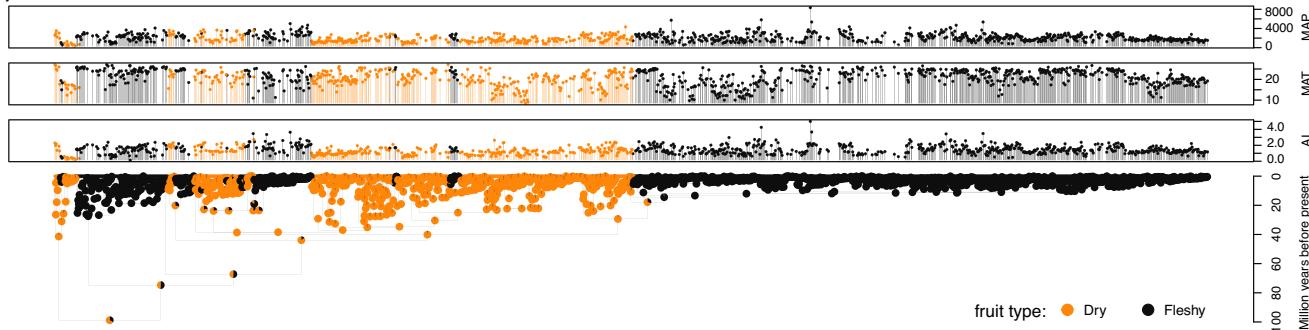
(a) Apocynaceae



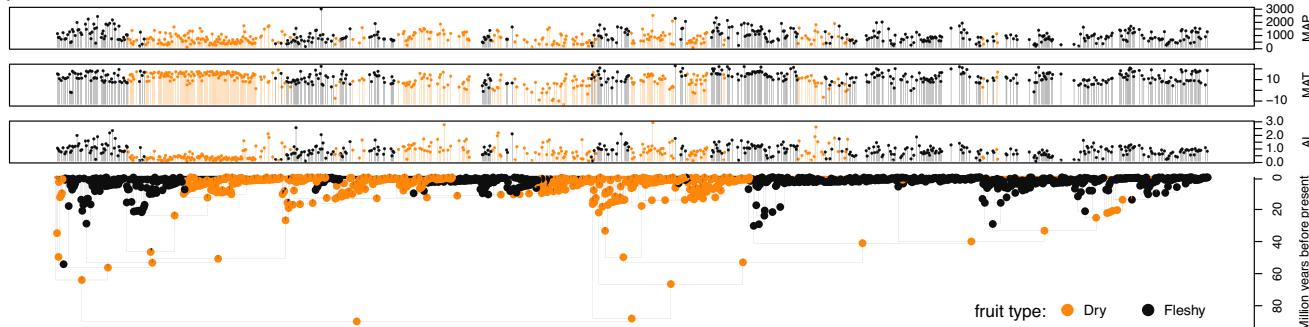
(b) Ericaceae



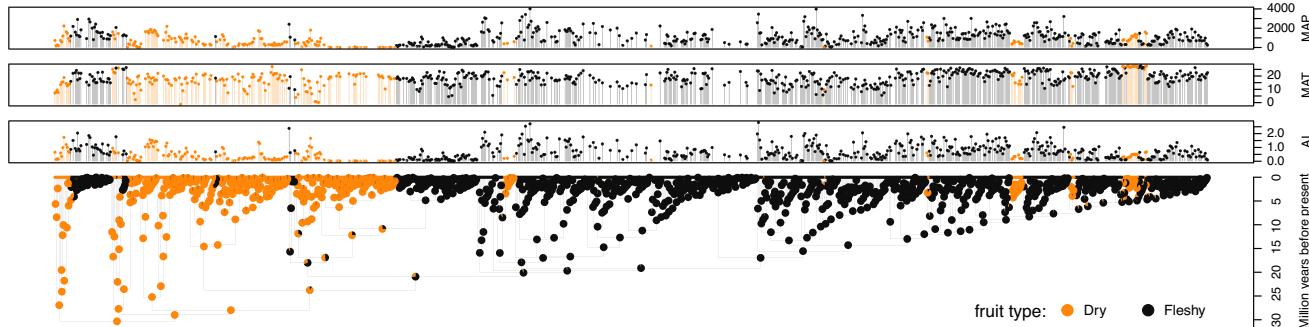
(c) Melastomataceae + CAP clade



(d) Rosaceae



(e) Solanaceae



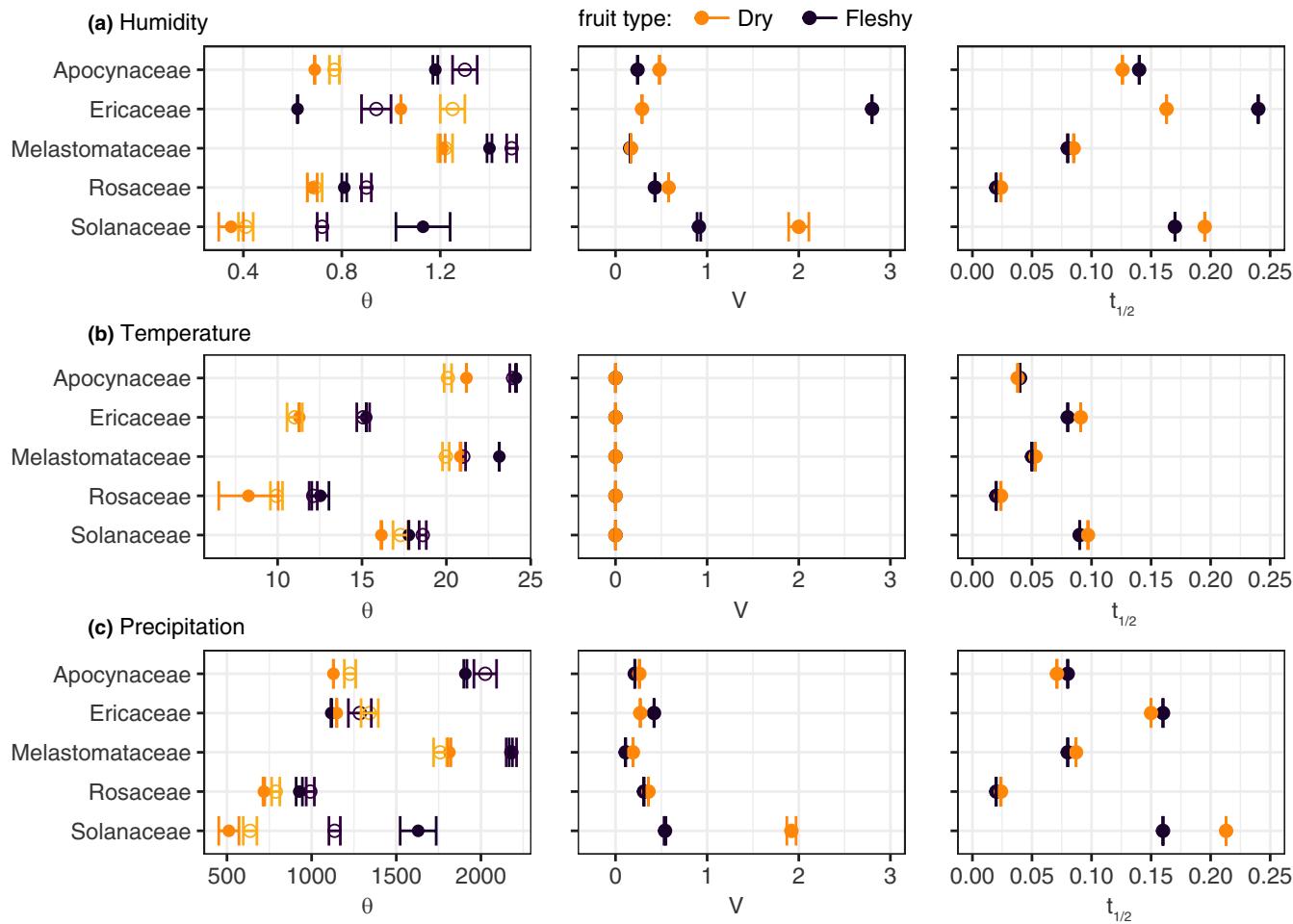


FIGURE 3 Parameter estimates from OUwie analyses of climatic niche evolution summarized by variable, clade and fruit type. Values reported represent the means of the tips of each fruit type across all analysed simeamps for each clade. Optima (θ) are given in the unit of the climatic variable and half-lives are given in proportion to tree height. Open circles in lighter colors in first column represent the actual mean of each climatic variable in each clade. Error bars indicate standard error. θ , climatic optimum, V, stationary variance, $t_{1/2}$, half-life

In all clades, OU models explained climatic niche evolution better than BM models (Appendix 3a-e'ii'), supporting an $\alpha > 0$ and thus a general trend to climatic niche conservatism in all lineages. Although our focus is mainly on parameter estimates and not on model fit, we note that the generally higher AIC_c weights for models that predict different climatic optima and rates of climate niche evolution in lineages with distinct fruit types (OUma, OUMv and OUMva) indicate a link between mode of seed dispersal and how flowering plants explore their climatic niche through evolutionary time. Parameters estimated through averaging the set of OUwie models according to their AIC_c are discussed below (Figure 3; Appendix 5). Although the difference in parameter estimates between lineages with dry and fleshy fruits is slight in some clades, standard errors of most estimates do not overlap. The small standard errors associated with each parameter indicate that variance among parameter estimates at the tips in different states is low, even when considering the rate heterogeneity provided by the HMMs.

3.2 | Generalities that link seed dispersal and climatic niche in flowering plants

A generality emerges across all clades examined where lineages with fleshy fruits tend to have warmer climatic optima and lineages with dry fruits shift to colder climatic optima ($\theta_{\text{dry}} < \theta_{\text{fleshy}}$; Figure 3b, first column). Though this difference is minimal in Solanaceae, it can be up to 3°C in Melastomataceae and Apocynaceae and 4°C in Ericaceae and Rosaceae. All clades, except Ericaceae, also present higher optima for humidity and precipitation in fleshy fruited lineages (Figure 3a,c, first column). In general, these results indicate a correlation between evolution of endozoochorous fruits and distribution in warmer and wetter habitats, in line with our first hypothesis.

Another generality observed in our results is the tendency of stationary variance to be higher in dry fruited lineages when compared to fleshy fruited lineages ($V_{\text{dry}} > V_{\text{fleshy}}$) for humidity and precipitation (Figure 3a,c, second column). This result is observed in all clades except, again, for Ericaceae. Stationary variance for temperature

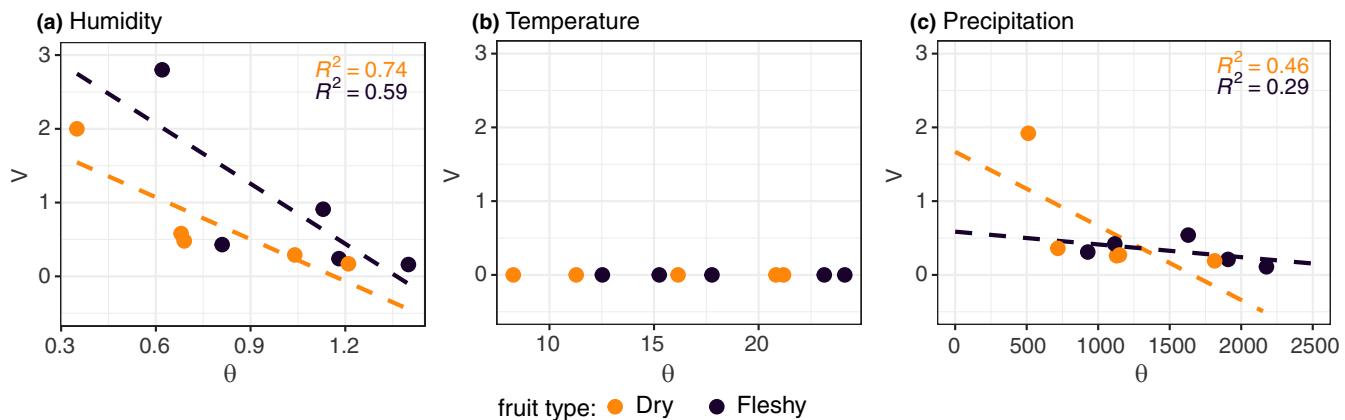


FIGURE 4 Simple linear regression between stationary variance (V) and climatic optima (θ) for (a) humidity, (b) temperature and (c) precipitation. Colours represent different fruit types. Data points used in correlations are those presented in Appendix 5. Optima (θ) are given in the unit of the climatic variable. θ , climatic optimum, V , stationary variance

(Figure 3b, second column) was very low (i.e. 0) regardless of clade and fruit type and there was no substantial difference in temperature half-life between fleshy and dry fruited lineages in any clade. Overall, these results indicate that (1) lineages with dry fruits tend to shift climatic niches more often than fleshy-fruited lineages and (2) thermal niche evolution is slow in all clades, regardless of fruit type. Although these results are generally in line with our second hypothesis, it is also interesting to note that stationary variance and climatic optima appear to be strongly negatively correlated for humidity, regardless of fruit type (Figure 4a). This correlation is weak for precipitation (Figure 4c) and nonexistent for temperature (Figure 4b), where all clades have a stationary variance of 0. This trend was not predicted by our initial hypotheses, but it may indicate that lineages in more humid environments have slower rates of climatic niche evolution regardless of their ecological interactions with frugivores.

Finally, no trend was observed when comparing half-lives of the three climatic variables in lineages with different fruit types (Figure 3, third column). In fact, we found all possible ways that differences in phylogenetic half-life could be related to fruit type, suggesting little support for our third hypotheses ($t_{1/2 \text{ dry}} > t_{1/2 \text{ fleshy}}$). In Melastomataceae and Rosaceae, different fruit types led to slight differences in phylogenetic half-life; in Ericaceae and Apocynaceae, fleshy fruited lineages show longer half-life; and in Solanaceae fleshy fruits were correlated with shorter half-lives (Figure 3; Appendix 5). Thus, the only clade that consistently followed our third hypothesis was Solanaceae. However, it is interesting to note that half-lives are generally shorter when related to temperature compared to other climatic variables in all clades, again possibly indicating a strong climatic niche conservatism related to this variable in comparison to the others.

3.3 | Contrasting climatic mean with theoretical optima

We observed similarities between mean values of climatic variables and their theoretical optima (θ) in most comparisons (Figure 3, first

column). An interesting trend is the relatively higher mean of humidity and precipitation in relation to the optima of these variables in all clades and fruit types. That is, the estimated optima tend to be more humid than the mean observed in all clades. A notable exception is Solanaceae with fleshy fruits, where the humidity and precipitation optima are much higher than the means observed in the group (0.72 vs. 1.13 and 1135.91 mm vs. 1629.4 mm). We note also that the theoretical optima of humidity for fleshy fruited lineages are not observed in any clade.

4 | DISCUSSION

4.1 | Generality 1: Frugivory is correlated with transitions to warmer and wetter habitats

We present a detailed comparative analysis to test whether different modes of seed dispersal impact dynamics of climatic niche evolution in flowering plants. Endozoochorous fruits appear generally associated with warmer and wetter environments, where potential for vegetation growth and formation of closed canopy biomes is higher, as predicted by our first hypothesis. A correlation between fleshy fruits and warmer habitats had been previously demonstrated by studies focused on spatial analyses along a latitudinal gradient within a continent (Chen et al., 2017; Correa et al., 2015). However, our results suggest that lineages with endozoochorous fruits were associated with warmer climatic optima in all clades, each of which vary in evolutionary history and/or geographical distribution. For instance, both the temperate Rosaceae (Chin et al., 2014; Li et al., 2017; Sun et al., 2020) and the tropical Apocynaceae (Fishbein et al., 2018) present lineages with endozoochorous fruits in warmer habitats, despite the first being restricted to mean annual temperatures below 13°C and the second above 20°C (Figure 3).

These results add evidence to the fact that characteristics of the abiotic environment may facilitate the evolution of some types of plant-animal interactions. Other studies showing that certain reproductive and vegetative syndromes are significantly more common in



a particular type of habitat include, for instance, pollination by vertebrates in higher altitudes, where bees do not fly well (Dellinger et al., 2021), and defensive traits such as spines in open habitats where grazing is more frequent (Charles-Dominique et al., 2016). Our study found an evolutionary correlation between endozoochory and mesic biomes, which may indicate either (1) a pre-adaptation (e.g. Alzate et al., 2020), where the evolution of fleshy fruits facilitate lineages to enter mesic habitats and outcompete local species in the dispersal of larger seeds; or alternatively (2) the mesic habitat favours the evolution of fleshy fruit, given the advantage of this trait in dispersing large seeds where presence of frugivores animals and abundant rainfall are not limiting factors. Movement of pre-adapted lineages or local adaptation is, however, difficult to disentangle (Donoghue, 2008) and probably both scenarios contribute in different proportions to the pattern observed in the five analysed clades.

4.2 | Generality 2: Slower rates of climatic niche evolution in mesic habitats

Our parameter estimates are consistent with our second hypothesis that lineages with dry fruits have faster rates of climatic niche evolution ($V_{dry} > V_{fleshy}$) for humidity and precipitation in four out of the five analysed clades. The negligible values of stationary variance for temperature (Figure 4b) compared to the other climatic variables (Figure 4a,c) strongly indicate that lineages are in general tightly adapted to their thermal optima (Araújo et al., 2013; Qu & Wiens, 2020), regardless of their ecological interactions. Although fruit type does seem to have an impact on the value of the optimal temperature of a lineage, shifting fleshy fruited lineages towards warmer habitats (Figure 3b), it does not seem to affect the rate in which lineages are pulled away or towards their thermal optima over time.

In Ericaceae, the opposite pattern was found where lineages with dry fruits have lower stationary variance around the precipitation optima than their relatives with fleshy fruits. In this particular case, the pattern is perhaps driven by the distribution of *Dracophyllum*, a large genus with dry fruits that is distributed in some of the wettest areas in the world (Wagstaff et al., 2010). In fact, when this genus is removed from the calculation of climatic means, dry fruited lineages shift from 1.25 (± 0.05) to 1.11 (± 0.04) in mean aridity index, approaching the standard error of fleshy fruited lineages (0.94 ± 0.06). Second, although *Dracophyllum* does not have fruits with classic endozoochorous syndrome, there is some evidence that this genus may represent an exception to the rule and be actually dispersed by birds (Wagstaff et al., 2010). Third, *Dracophyllum* has a characteristic insular distribution, and island radiations are often characterized by unusual biologies when compared to continental lineages (Losos & Ricklefs, 2009).

Additionally, Ericaceae is also the only clade where the climatic optima of dry fruited lineages are wetter than that of fleshy fruited lineage (i.e. higher humidity and precipitation; Figure 3a,c). In other words, an alternative interpretation of this result is that there may be a general pattern related to rates of climatic niche evolution in lineages distributed in more humid environments

regardless of their mode of seed dispersal. If such a result was generally applicable, it would suggest that lineages in more mesic habitats, where potential for vegetation growth is higher, will have slower rates of climatic niche evolution independent of fruit type (Figure 4). There are several potential explanations for this pattern. First, when plants grow bigger (as expected where aridity index is higher), they also tend to have longer generation times (Petit & Hampe, 2006), which in turn leads to slower rates of climatic niche evolution and stronger niche conservatism (Smith & Beaulieu, 2009). Second, lineages in more humid regions, including many of the dry-fruited lineages of Ericaceae, are also distributed in areas that are relatively climatically stable on a global scale, such as some tropical rainforests (Stebbins, 1974). Longer generations and less changes in climate over time could then result in slower rates of climatic evolution in these lineages (Araújo et al., 2013; Qu & Wiens, 2020).

We therefore propose an extension to our original hypotheses: we suggest that the impact of frugivory on the evolution of climatic niche evolution in flowering plants is indirect. Slower rates of climatic niche evolution may not be a direct result from the behaviour of frugivores during seed dispersal. Instead, biotic dispersal may facilitate lineages to establish in areas where climatic niche evolves slower for other reasons, such as where a 'mesic syndrome', that is, a set of traits related to life in humid habitats, is prevalent.

4.3 | No correlation between mode of seed dispersal and climatic niche conservatism

We found no trend for how climatic niche conservatism related to dispersal type as most clades presented similar half-lives in both fleshy and dry fruited lineages for all climatic variables. Overall, these results show a weak support for the role of frugivory-mediated seed dispersal on climatic niche conservatism, unless particularities of the clades are considered in the interpretation. For example, Solanaceae was the only clade consistent with our third hypothesis, where fleshy fruited lineages do present stronger niche conservatism when compared to relatives with dry fruits ($t_{1/2\ dry} > t_{1/2\ fleshy}$). Curiously, lineages with fleshy fruits in Solanaceae also appear far from their climatic optima in relation to both humidity and precipitation (Figure 3). In both of these climatic variables, the true mean of fleshy fruited lineages is found in a much drier environment (lower humidity and precipitation) than the climatic optima estimated for them. Solanaceae is also the youngest of all analysed clades and half-lives are longer relative to the age of the clade compared to other groups (Appendix 5). It may be the case that there has been less time for Solanaceae lineages to reach the climatic optimum after evolving fleshy fruits. The possibility of a lag in Solanaceae is supported by the observation that fleshy fruits in Apocynaceae and Melastomataceae appeared earlier in evolutionary time and had smaller half-lives (Figure 2; Fishbein et al., 2018; Reginato et al., 2020). Fleshy fruits in these three families can attract the same guilds of frugivores in some areas (e.g. Bello et al., 2017), and so a possible explanation for the lag



between observed mean and optima in fleshy fruited Solanaceae is competition with other lineages that evolved fleshy fruits earlier in more humid areas. However, more work on the role of competition for seed dispersers in modulating the distribution of plant lineages is required to corroborate this hypothesis.

4.4 | Conclusions and caveats

The mode of seed dispersal is important for how flowering plants move in space but linking this process to how plants adapt to different environmental circumstances over long time-scales can be less straightforward. Our results suggest that distribution in mesic habitats and presence of endozoochory are evolutionary correlated. However, the way in which endozoochory impacts climatic niche evolution over time may be incidental. Fleshy fruits may have facilitated lineages to enter mesic habitats by allowing them to outcompete others in the dispersal of large seeds, and, once in these habitats, lineages may present slower rates of climatic niche evolution for other reasons. In that way, it is probably not the behaviour of frugivores that 'trap' flowering plants to their preferable niches, nor the erratic dispersal of dry fruits that make them shift biomes more often. Rather, slower rates of climatic niche evolution are possibly a consequence of other traits that are also linked with mesic habitats, such as woody habit and longer generation times. As caveats, we note that (1) The methodologies described herein can only indicate correlation, whereas inferences of causation are given by the interpretation of the patterns in their biological context (as summarized in Figure 1). (2) Although we focused on endozoochory, the same expectation in relation to animal movement during seed dispersal should be applicable to epizoochory. There is, unfortunately, much less information regarding this syndrome than there is for endozoochory, and for that reason we did not consider epizoochory here. While we removed the few species that could present epizoochory from the analyses, future studies should focus on better understanding this syndrome and its impact on biogeography and the climatic niche evolution of flowering plants. Finally, we also emphasize that the particularities of each lineage matter when studying climatic niche evolution, but this makes it all the more remarkable that such profound generalities can also exist. Each of the clades we analysed presented a unique evolutionary and biogeographical history. Nonetheless, we found repeated patterns of climatic niche evolution related to shared environmental characteristics (humidity, temperature and precipitation) and convergent phenotypes (mode of seed dispersal).

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CONFLICT OF INTEREST

The authors declare no conflict of interests.

DATA AVAILABILITY STATEMENT

All datasets and code required to replicate the analyses of this study are available at github.com/tncvasconcelos/seed_dispersal. Vasconcelos, Thais; Boyko, James; Beaulieu, Jeremy (2021), Linking mode of seed dispersal and climatic niche evolution in flowering plants, Dryad, Dataset, <https://doi.org/10.5061/dryad.h76hdrhf>

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BIOSKETCH

T.V., J.D.B. and J.M.B. are evolutionary biologists devoted to understanding how plants have become so diverse. Central to their approach is deciphering and using phylogenies, as well as the development of new statistical approaches, to intersect many aspects of plant biology, ranging from trait evolution, biogeography, diversification, conservation and genomics.



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