

RESEARCH PAPER

WILEY

Global Ecology
and BiogeographyA Journal of
Macroecology

Why is fruit colour so variable? Phylogenetic analyses reveal relationships between fruit-colour evolution, biogeography and diversification

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CAS Strategic Priority Research Program, Grant/Award Number: XDB31000000; National Natural Science Foundation China, Grant/Award Number: 41671052, 31100163, 31270272, 31320103919 and U1502261; Applied Fundamental Research Foundation of Yunnan Province, Grant/Award Number: 2017FB072; the Hundred-Talent Program of Kunming Medical University, Grant/Award Number: 60117190444 and 60118090109; the U.S. National Science Foundation, Grant/Award Number: DEB-0717711, DEB-0717744 and DEB-1655690; the National Geographic Society, Grant/Award Number: 4-03-9329; the CAS President's International Fellowship Initiative, Grant/Award Number: 2010T2S05 and 2017VCA0024; ARC DECRA fellowship, Grant/Award Number: DE150101773; Marsden grants, Grant/Award Number: 16-UOA-277 and 18-UOA-034

Editor: Shai Meiri

Abstract**Aim:** Are different fruit colours related to large-scale patterns of dispersal, distribution and diversification? Here, we investigate this question for the first time, using phylogenetic approaches in the tribe Gaultherieae (Ericaceae). We test relationships between fruit colour and (a) biogeographic dispersal, (b) elevational and latitudinal species distributions and (c) rates of diversification.**Location:** Global.**Time period:** Recent to 30 million years ago.**Major taxa studied:** The plant tribe Gaultherieae in the family Ericaceae (blueberries and relatives).**Methods:** We estimated a new time-calibrated phylogeny for Gaultherieae. Data on fruit colours and geographic distributions for each species were compiled from published sources and field observations. Using phylogenetic methods, we estimated major dispersal events across the tree and the most likely fruit colour associated with each dispersal event, and tested whether dispersal between major biogeographic regions was equally likely for different fruit colours, and whether dispersal distances were larger for certain colours. We then tested the relationships between fruit colours and geographic variables (latitude, elevation) and diversification rates.**Results:** Large-scale dispersal events were significantly associated with red-fruited lineages, even though red-fruited species were relatively uncommon. Further, different fruit colours were associated with different elevations and latitudes (e.g. red at lower elevations, violet at lower latitudes, white at higher elevations). Violet colour was related to increased diversification rates, leading to more violet-fruited species globally.

Main conclusions: Overall, we show that different fruit colours can significantly impact the large-scale dispersal, distribution and diversification of plant clades. Furthermore, the interplay between biogeography and fruit-colour evolution seems to generate “taxon cycles” in fruit colour that may drive variation in fruit colour over macroevolutionary time-scales.

KEYWORDS

biogeography, dispersal, diversification, Ericaceae, fruit, Gaultherieae, phylogeny

1 | INTRODUCTION

Fruit is a crucial food source for humans and other animals and may be a major driver of large-scale patterns of plant diversity (e.g. Bolmgren & Eriksson, 2005; Herrera, 1989). However, the significance of particular fruit colours for plant evolution and distribution remains unclear. The chief ecological function of fleshy fruit is to facilitate seed dispersal by attracting and nutritionally rewarding frugivorous animals (Bolmgren & Eriksson, 2005; Lee, 2010; Willson & Whelan, 1990). Using ecological approaches, many studies have analysed associations between frugivore preferences and the frequency of different fruit colours in different regions (e.g. Duan, Goodale, & Quan, 2014; Herrera, 1989; Janson, 1983; Lomáscolo & Schaefer, 2010; Schaefer, Valido, & Jordano, 2014; Voigt et al., 2004; Willson, Irvine, & Walsh, 1989). However, few studies (if any) have used a phylogenetic approach to test whether different fruit colours affect large-scale patterns of plant dispersal and distribution.

For example, certain fruit colours might promote long-distance dispersal among regions. Ecological studies suggest that birds often prefer red fruit (e.g. Duan et al., 2014; Shanahan, So, Gompton, & Gorlett, 2001) or darker coloured fruit (Schaefer et al., 2014). In a phylogenetic study of *Coprosma* (Rubiaceae), the authors noted that many dispersal events were by red-fruited lineages, and they suggested that this pattern might be related to bird dispersal (Cantley, Markey, Swenson, & Keeley, 2016). However, they did not test for a statistical association between fruit colour and dispersal. Moreover, most species in the genus had red fruit, such that more dispersal by red-fruited lineages would be expected by chance, even if there were no causal relationships between fruit colour and dispersal.

Fruit-colour evolution may also be influenced by other abiotic and biotic factors besides biotic dispersal. These include seed predation (Mack, 2000), pathogens (Cazetta, Schaefer, & Galetti, 2008), solar radiation (Burns, 2015; Lee, 2010; Willson & Whelan, 1990) and other abiotic factors (Willson et al., 1989). Geographic gradients related to climate (e.g. latitude, elevation) might be especially important, but remain infrequently studied. Nakanishi (1996) found that in Japan, black fruits were most common in warm temperate areas and red in cooler areas. Yet, Burns, Cazetta, Galetti, Valido, and Schaefer (2009) tested for geographic patterns in fruit colour using data from 232 species from Europe, and North and South America, but found no evidence for associations between fruit colour and geographic gradients. Nevertheless, variation in flavonoid

and anthocyanin biosynthesis in fruit was found across latitudinal and elevational ranges (Lätti, Riihinen, & Kainulainen, 2007; Zoratti, Karppinen, Luengo Escobar, Häggman, & Jaakola, 2014).

An association between fruit colour and conditions across a clade's geographic range might help to explain why fruit colour varies so extensively within and between clades. An analysis of fruit-colour evolution across angiosperms found little phylogenetic conservatism (i.e. no phylogenetic signal; Stournaras et al., 2013). Nonetheless, it is unclear why fruit colour should be so variable. For example, if certain fruit colours are more attractive to frugivores (e.g. Duan et al., 2014; Schaefer et al., 2014; Shanahan et al., 2001), it may be disadvantageous to switch to a different colour that frugivores generally find less conspicuous or attractive. Yet, if different fruit colours are favoured in different environments (e.g. climates, latitudes, background colours), this might help drive variation in fruit colour within clades.

Different fruit colours may also be associated with different diversification rates (e.g. Beaulieu & Donoghue, 2013; Stebbins, 1974; Tiffney & Mazer, 1995). Diversification is the accumulation of species over time within a clade, or the speciation rate minus the extinction rate (Magallón & Sanderson, 2001). However, the mechanisms by which particular fruit colours might influence speciation and extinction remain uncertain (Herrera, 1989). We speculate that certain fruit colours may be favoured in environments that promote rapid diversification (e.g. montane tropical regions; Hughes & Eastwood, 2006; Hutter, Lambert, & Wiens, 2017; Spriggs et al., 2015). Thus, fruit colour itself may not directly drive diversification, but there might be a synergy between fruit colour and geographic distribution that affects diversification. To our knowledge, this hypothesis has not been explicitly tested.

Here, we test the impact of different fruit colours on patterns of dispersal, distribution and diversification in the tribe Gaultherieae (family Ericaceae). Their diverse fruit types and broad geographic distribution make them an excellent model system for this question. Gaultherieae includes c. 280 species (Fritsch et al., 2011; Wang et al., 2015) and spans many continents (Asia, Australia, Europe, North and South America), latitudes (75° to -52°) and elevations (0–4,700 m; Supporting Information Tables S1, S2). They also have a diversity of fruit types (Figure 1). Fruits in Gaultherieae are considered “dry” or “fleshy”. Fleshy fruits have various colours (Figure 1), including white, red or “violet” (blue to purplish black; Supporting Information Figure S1a–e; see Methods). Note that our focus here is

on the potential implications of these fruit phenotypes for the dispersal, distribution and diversification of plant species, regardless of whether the various animal species that might eat these fruits see these colours the same or differently relative to humans. Therefore, we follow standard practice in the plant literature in characterizing fruit colours. However, perceptual biases might be relevant (e.g. Kemp et al., 2015), especially if we fail to find significant patterns using human-based characterization of fruit colours.

In this paper, we integrate data on fruit colour, geographic distribution and phylogeny to address the following questions. (a) Are certain fruit colours non-randomly associated with large-scale biogeographic dispersal events? (b) Does fruit colour vary geographically (i.e. with latitude and elevation)? (c) Are some fruit colours associated with accelerated diversification rates? (4) Can relationships between fruit colour and geographic distribution explain the associations between fruit colour and diversification? We find significant relationships between fruit colour, biogeography and diversification in Gaultherieae, and suggest that similar patterns may be widespread in angiosperms.

2 | MATERIALS AND METHODS

2.1 | Phylogeny estimation

We estimated a new time-calibrated phylogeny for Gaultherieae (Figure 1). Detailed methods, data and results are provided in Supporting Information Appendices S1–S3, Datasets S1–S6 and Figures S1–S6. The new phylogeny included eight species (of 128 total) not included in earlier large-scale trees, but was otherwise similar to previous estimates (e.g. Fritsch et al., 2011). We also reconstructed a tree for Ericaceae to better estimate clade ages within Gaultherieae. For comparative analyses, we used the majority-rule consensus tree estimated by BEAST (Drummond, Suchard, Xie, & Rambaut, 2012), and also 10 trees selected at evenly spaced intervals (every 10 million generations) from the posterior distribution of post-burn-in trees. We used these 10 trees to address the sensitivity of the results to uncertainty in the topology and branch lengths. Although 10 is not a large number, taking the mean result from hundreds or thousands of trees should simply return the same result as using the majority-rule tree.

2.2 | Trait data

Data on fruit types and geographic distributions were compiled from many sources including published floristic and taxonomic treatments, herbarium records and online databases (Supporting Information Tables S1–S2). These references included the most recent monographs and revisions for these species at the time of analysis, including records from herbaria around the world. Fruit data were available for 218 species (and 123 of 128 in the tree). However, most species lacking fruit data (47/69) belonged to *Diplycosia* (121 species) in which most known species share the same fruit type (Supporting Information Table S2). Species were

classified into four fruit-type categories: dry (versus fleshy), and fleshy with red, white or violet colour (we refer only to colours hereafter). Following standard practice (e.g. Traveset, Willson, & Verdú, 2004), we used “violet” to encompass a broad range of colours at that end of the visible colour spectrum (purple, blue and blackish purple), given that intermediates between them are common (Supporting Information Figure S1a–e). We included dry fruit as another state of the character “fruit type” as there were transitions between dry fruit and different fruit colours (Figure 1), and so excluding taxa with dry fruit would potentially bias estimation of transitions between fruit colour types. We also wanted to know if dry fruit impacted dispersal, distribution or diversification of species with this fruit type.

The latitudinal and elevational ranges and midpoints for each species were estimated from the references mentioned above (Supporting Information Table S2). Data were typically based on many localities per species. For example, for the Neotropics and East Asia there was collectively an average of 26 localities/species (range = 1–307). However, some species are known from few localities because they apparently have small geographic ranges. We obtained elevational data directly from these references but estimated broad-scale latitudes using Google Earth Pro (Sullivan, 2009).

2.3 | Testing relationships between fruit colours and dispersal

Overview. We then tested whether the frequency or rate of dispersal between major biogeographic regions differed among fruit colours. This primarily involved the following steps: (a) estimating the biogeographic history of the clade to infer dispersal events on specific branches, (b) estimating the evolution of fruit colour across the tree to infer which fruit colours were associated with these dispersal events and (c) testing whether dispersal was non-randomly associated with certain fruit colours. We also used a likelihood approach that simultaneously estimated biogeographic history and character evolution and tested if models in which dispersal depended on fruit colour had better fit to the data than models in which dispersal was independent of fruit colour.

Estimating dispersal. For the biogeographic analyses, the distribution of Gaultherieae was divided into eight regions (Supporting Information Table S3) that largely followed Bremer (1992): (1) temperate East Asia (65° N to the Tropic of Cancer, c. 70 to 170° E); (2) tropical East Asia (including New Guinea; tropics of Cancer to Capricorn, c. 95 to 150° E); (3) Australia (including Tasmania); (4) New Zealand; (5) temperate South America (65° S to Tropic of Capricorn); (6) Neotropics (tropics of Cancer to Capricorn); (7) temperate North America (65° N to Tropic of Cancer); and (8) the other cool temperate and subarctic regions of the Northern Hemisphere (65 to 70° N, including western Asia and Europe).

We then estimated dispersal events among these regions across the tree. Biogeographic analyses were conducted with the time-calibrated tree and the dispersal–extinction–cladogenesis (DEC) model with the R package *BioGeoBEARS*, version 0.2.1 (Matzke, 2013). The

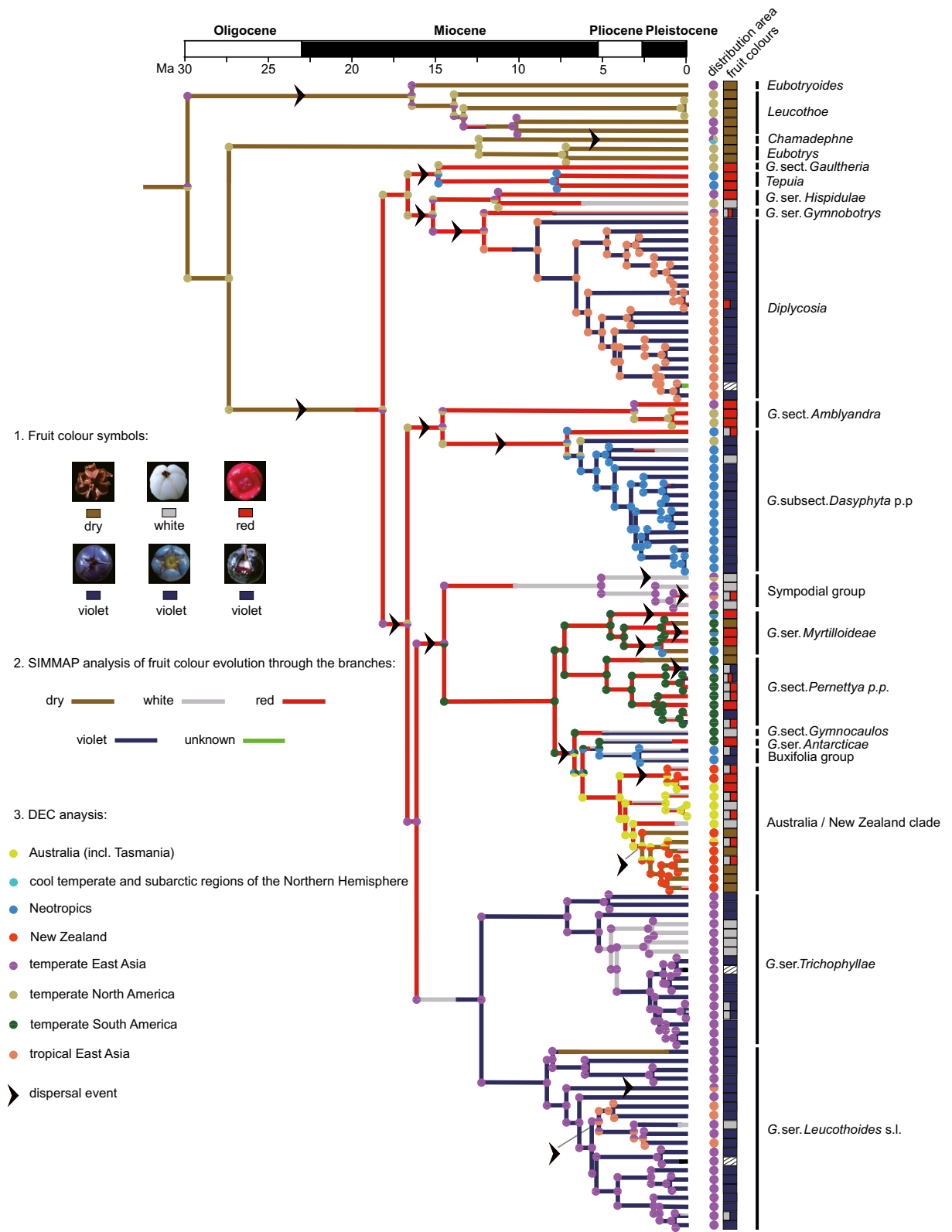


FIGURE 1 The evolution of fruit colours and biogeographic dispersal in the tribe Gaulterieae. Ancestral-area reconstructions (coloured circles at nodes) and inferred dispersal events (arrows) are summarized from biogeographic analyses with the dispersal–extinction–cladogenesis (DEC) model. The coloured branches indicate the reconstructed fruit colour on each branch based on SIMMAP analyses. The column of coloured circles at the tree tips indicates the present distribution area(s) for each species. The column of rectangles indicates each species’ fruit colour(s). Colours of regions and fruit types are given in the legend (bottom left). Images of representative fruit colours are given above the legend. The tree shown is the consensus tree from BEAST analyses

maximum number of ancestral areas allowed at internal nodes must be set for these analyses. We compared the Akaike information criterion (AIC; Burnham & Anderson, 2002) of models with different maximum numbers of areas (3, 4, 5). We found that 3 had slightly lower AIC values than 4 or 5 (consensus tree: 3 = 320.72, 4 = 322.16, 5 = 322.10). Three is also the maximum number of regions in which extant species occur, making this the most realistic value. Dispersal events were inferred on branches where the region with the highest proportional likelihood differed between adjacent nodes.

Estimating fruit-colour evolution. To infer the most likely fruit state associated with each dispersal event, we then estimated the evolution of fruit colours across the tree. We primarily used stochastic character mapping (SIMMAP; Bollback, 2006) using the R package *phytools* (Revell, 2012). We also used the BayesMultistate model (Pagel & Meade, 2006; Pagel, Meade, & Barker, 2004) in BAYESTRAITS 3.0 (<http://www.evolution.rdg.ac.uk/SoftwareMain.html>) to visualize fruit evolution across the tree (see Supporting Information Figure S3 legend for details). Each species was classified into one of four fruit-type categories (states in a multistate character), as described above. Species with more than one fruit type were coded as polymorphic in *phytools* and BAYESTRAITS.

For the stochastic mapping analyses, we first found the best-fitting model to use for reconstructions. We used the “ace” function in the R package APE (Paradis, Claude, & Strimmer, 2004) to compare the equal-rates (ER; a single rate for all possible transitions between states), symmetrical (SYM; a different transition rate between all pairs of states, but the same rate for both possible transitions between each pair; e.g. the red-to-white rate equals the white-to-red rate) and all-rates-different (ARD; a different rate for each possible transition between states) models. The best-fit model was determined using the AIC score for each model for each tree. The ER model had the best fit (consensus tree: ER = 369.25, SYM = 393.22, ARD = 418.82, mean of 10 trees: ER = 375.97, SYM = 398.80, ARD = 424.99). Therefore, the ER model was used. We then used the *make.simmap* function (in *phytools*) with 100 generations to generate a posterior probability distribution of character histories for each tree. The posterior distribution of character-state histories for each branch was then summarized using the *describe.simmap* function.

Testing frequencies of fruit types. Given the reconstructed dispersal events and fruit types across the tree, we tested whether dispersal events were equally distributed among the four fruit types, or more frequent for certain fruit types. However, dispersal events may be most frequent among whichever fruit type is most common among all species in the group, or most common among species in the tree. Therefore, we first performed chi-square tests (in R; R Core Team, 2013) to evaluate whether numbers of species with each fruit type were significantly different among all species with known fruit types, and whether these numbers differed significantly among species included in the tree (Supporting Information Table S4). We also performed two-tailed tests of equal proportions (“prop.test” in R) to evaluate whether proportions of species of each fruit type differed among all known species relative to those in the tree (Supporting Information Table S4).

Linking fruit colour and dispersal. We then tested which fruit colour was most frequently involved in dispersal events. We assigned a colour to each dispersal event based on which colour was reconstructed on the branch on which the dispersal event was inferred. In some cases, > 1 colour was reconstructed on a branch with a dispersal event. A colour was given a weight of 1.00 if it was the only one reconstructed on that branch, 0.50 if two were reconstructed on the branch and 0.33 if three were reconstructed on that branch (no more than three were inferred for any branch). Weighted values were summed across dispersal events to give an overall value for each colour for each tree (Supporting Information Tables S5, S6). For each tree, we performed Friedman nonparametric tests to determine whether dispersal events were equally distributed among the four colours based on the set of weighted values. We used the Friedman test because we used weighted values rather than the raw counts used in the chi-squared test. Furthermore, the weighted values were not normally distributed based on Shapiro–Wilk tests (Supporting Information Table S5), requiring a nonparametric test.

We also specifically tested if red fruit (which had the highest frequency of dispersal) can influence dispersal. We estimated the proportion of all dispersal events assigned to each of the four fruit types, and then tested if red fruit had a proportion significantly different from 0.25, using a binomial test in R. Assignment of colour changes to particular dispersal events could be incorrect if both changes occurred on the same branch (as it would be difficult to infer which change came first). Our downweighting of dispersal events associated with branches with two or more reconstructed colours (when assigning dispersal events to colours) should reduce the potential impact of errors related to this problem.

Likelihood-based approach. We also compared the likelihood of models in which dispersal is independent of fruit colour (null model) to models in which dispersal is dependent on fruit colour (specifically, red fruit). We used a trait-based dispersal approach (Matos-Maravi et al., 2018; Matzke, 2016) now implemented in BioGeoBEARS, version 1.1 (<https://github.com/nmatzke/BioGeoBEARS>). These analyses required binary (two-state) coding of fruit colours. We used two approaches to deal with intraspecific variation. First, species were coded as either (Supporting Information Dataset S5): never red (species having any colour but red) versus red (species with red, or red and another colour). Second, species were coded as either (Supporting Information Dataset S6): not consistently red (species not having red or only sometimes having red) versus consistently red (species having only red).

This trait-based dispersal approach also considers distance as potentially impacting the probability of dispersal between regions. However, inferring exact distances associated with each dispersal event is impossible. Instead, a matrix of relative distances between each pair of regions was approximated based on the distance between their geographic centres (midpoints of latitudinal and longitudinal ranges) using GOOGLE EARTH PRO (Supporting Information Tables S3, S5–S7).

We compared 24 likelihood models, including combinations of standard biogeographic models (DEC, DIVALIKE, BAYAREALIKE;

Matzke, 2013, 2014), a distance-dependent model, fruit colour-dependent models and models with a multiplier on dispersal probability for non-red lineages. We then compared the log-likelihoods and AIC weights of trait-independent models to trait-based dispersal models using the sample size-corrected AIC (AICc). The analysis of each model was run twice to check for convergence.

Dispersal distances and fruit colours. We also tested whether dispersal distances among regions tended to be larger for certain colours. We calculated the mean dispersal distance for each colour for each tree (summed dispersal distances for each colour divided by number of dispersal events; Supporting Information Table S6). We used Kruskal–Wallis one-way analysis of variance to evaluate whether dispersal distances differed significantly among colours (distances in Supporting Information Table S5), given that the data were not normally distributed (based on a Shapiro–Wilk test).

Non-phylogenetic tests. We acknowledge that some of these tests are not phylogenetic. However, the dispersal events analysed are phylogenetically independent, reducing the need for a phylogenetic correction. Furthermore, because most analyses involve internal branches of the phylogeny, there is no straightforward phylogenetic correction.

2.4 | Testing relationships among fruit colour, geographic distribution and diversification rate

We then tested the relationship between fruit colour and geographic distribution (latitude, elevation), and between colours, geographic variables and diversification rates. We focused primarily on clade-based analyses, utilizing 20 well-supported clades that are morphologically and geographically distinct (Fritsch et al., 2011; Middleton, 1991), and that encompass all 280 species in the tribe (Supporting Information Table S1). We describe species-based and region-based analyses (both methods and results) in Supporting Information Appendix S4. We performed regression analyses using phylogenetic generalized least squares (PGLS; Martins & Hansen, 1997) with the R package *caper*, version 0.5.2 (Orme et al., 2013). Following standard practice, branch lengths were transformed with the estimated maximum likelihood value of lambda ($\lambda = \text{“ML”}$), and kappa and

delta fixed at 1 (default values). Given the many analyses, we exclusively used the consensus tree.

These analyses used the proportion of species in each clade having each colour, encompassing all species with known colours in each clade (Supporting Information Table S8). We coded polymorphic species assuming equal proportions of colours within species (e.g. a species with both red and white was counted as 0.5 for each). Geographic variables were coded based on the mean values of all species within each clade. Estimation of diversification rates is described below.

For clade-level analyses, we tested (a) each fruit colour versus each geographic variable (or combination of variables), (b) diversification rate versus each colour and (c) diversification rate versus each geographic variable. Based on these initial results, we performed multiple regression analyses that included significant variables ($p < 0.05$) from the preceding analyses. The best-fitting model had the lowest AIC score. For multiple regression analyses of diversification rate (for $\epsilon = 0.5$, see below), we also calculated standardized partial regression coefficients (SPRC) to evaluate the relative contribution of each independent variable to the best-fitting regression model that included geographic and colour variables, following Moen and Wiens (2017). Note that state-dependent speciation–extinction (SSE) models would only allow us to test for a significant effect of one variable at a time, and would not address how much variation in diversification rates was explained by each variable (nor the relative contributions of each variable in a multiple regression model).

We acknowledge that we performed many tests, raising concerns that some low p -values may occur by chance. However, we selected regression models based on AIC scores, and evaluated the strength of relationships based on r^2 (i.e. not using p -values). Even if unimportant variables were included in some models because of spuriously low p -values, use of the AIC should eliminate models with unnecessary parameters. We did not perform standard Bonferroni correction, as this approach is controversial (Nakagawa, 2004). Furthermore, even advocates of this correction generally support its application to individual tables, not every test in a given study (e.g. Rice, 1989). Nevertheless, we applied a sequential Bonferroni correction (see Rice, 1989) across the best-fitting models within Tables 1 and 2.

Variables	r^2	Relationship	p -values
white ~ mean el. midpoint + mean lat. midpoint + mean el. range + mean lat. range	0.6749	Positive Positive Positive Negative	0.0002
red ~ mean el. midpoint	0.3555	Negative	0.0033
violet ~ mean lat. midpoint	0.5037	Negative	0.0003

TABLE 1 Summary of results of clade-based phylogenetic generalized least squares (PGLS) analyses of fruit types and geographic attributes, showing the best-fitting model for each fruit type [lowest Akaike information criterion (AIC)]

Note. Only results with p -values < 0.05 are shown. Full results are in Supporting Information Table S15. “Elevational” is abbreviated as “el.” and “latitudinal” is abbreviated as “lat”. The results shown are significant after a sequential Bonferroni correction for this table.

TABLE 2 Relationships between diversification rates, fruit colour and geographic variables

Variables	r^2	Relationship	p -values	AIC
div. rate ~ violet	0.3597	Positive	0.0031	-31.8367
div. rate ~ mean lat. midpoint	0.3074	Negative	0.0066	-30.2688
div. rate ~ mean lat. range	0.1671	Negative	0.0416	-26.5789
div. rate ~ mean lat. midpoint + mean lat. range	0.3196	Negative Negative	0.0147	-29.7669
div. rate ~ mean el. midpoint + mean lat. midpoint	0.2670	Negative Negative	0.0277	-28.2763
div. rate ~ mean lat. midpoint + mean lat. range + violet	0.4010	Negative Negative Positive	0.0104	-31.5258

Note. Diversification rate (div. rate, epsilon = 0.5) is the dependent variable and violet fruit colour and geographic variables are independent variables. Only results with p -values < 0.05 are shown. Full results are in Supporting Information Table S15; violet fruit is the only colour that shows any significant relationship with diversification rates. The best-fitting model [lowest Akaike information criterion (AIC)] is in bold. "Elevational" is abbreviated as "el". and "latitudinal" is abbreviated as "lat". The best-fitting model is significant after a sequential Bonferroni correction across this table.

2.5 | Estimating diversification rates

To estimate diversification rates we used the method-of-moments estimator for stem-group ages (MS estimator; Magallón & Sanderson, 2001), with the R package *GEIGER 2.0.6* (Harmon et al., 2015). Following standard practice, three relative extinction fractions ($\epsilon = 0, 0.5, 0.9$) were applied to all clades in three separate analyses. However, different values have limited impact on relationships between true and estimated rates for stem-group estimates (Meyer & Wiens, 2018), and we primarily used the intermediate value (0.5). The stem-group estimator is generally more accurate and more robust to incomplete species sampling, whereas the crown-group estimator can yield biased rates with incomplete sampling (Meyer & Wiens, 2018). Rates for each clade are summarized in Supporting Information Table S9. Simulations show that the MS estimators are relatively accurate, and do not require positive relationships between clade age and richness (Kozak & Wiens, 2016), nor constant rates within clades (Meyer, Roman-Palacios, & Wiens, 2018; Meyer & Wiens, 2018). We did not use *BAMM* (Rabosky, 2014), as it underestimates rate variation across trees and yields weaker relationships between true and estimated rates (Meyer et al., 2018; Meyer & Wiens, 2018).

3 | RESULTS

3.1 | Relationship between fruit colour and biogeographic dispersal

The number of species of each fruit colour differed significantly, both among all species with known colours and also among those species sampled in the tree (based on chi-squared tests, both $p < 0.0001$; Supporting Information Table S4). The proportion of species of each fruit type was similar between these two datasets, and only violet

differed significantly ($p = 0.022$; $p > 0.111$ for all others). Violet was the most common overall (66%) and among species in the tree (53%; Supporting Information Table S4). Red and white were less common (c. 15% each) and dry fruit was the least common (8% overall, 14% in the tree). Reconstruction of fruit colours using SIMMAP also favoured violet as the most common on a per branch basis (Figure 1): violet was reconstructed on 141.5 branches, red on 77, dry on 35 and white on 34.5.

Given these frequencies alone, one would expect most dispersal events to be associated with violet-fruited lineages. In contrast to this expectation, most dispersal events were by red-fruited lineages (Figures 1, 2; Supporting Information Tables S5, S6). Biogeographic analyses inferred 21 dispersal events among the eight regions (20–24 among the 10 trees). The dispersal frequency among fruit colours differed significantly (Friedman test: $p < 0.0001$, for the consensus tree and mean $p = 0.012 \pm 0.03$ with range = $3.74e-05$ –0.80 among the 10 trees; Supporting Information Table S11). Frequencies of red fruit were generally significantly higher (Supporting Information Table S11, and boxplots of dispersal frequencies in Supporting Information Figures S4–S6). For the consensus tree (Supporting Information Table S6), red was the most likely fruit state reconstructed on branches on which dispersal events were inferred (14), followed by dry (3), violet (2.5) and white (1.5). Values were similar among the 10 trees (means for dry = 3.36, white = 2.09, red = 12.34 and violet = 4.31, Supporting Information Table S6).

This bias does not simply reflect a large number of dispersals of red-fruited species at a particular time period or from a region with many red-fruited species. Dividing the history of the tribe into 5-Myr time intervals (starting with 25–20 Ma) and assigning dispersal events to intervals based on the midpoint age of branches on which dispersal was inferred, red is associated with the most dispersal events for the majority of time intervals: 25–20 Ma: dry = 1.5, red

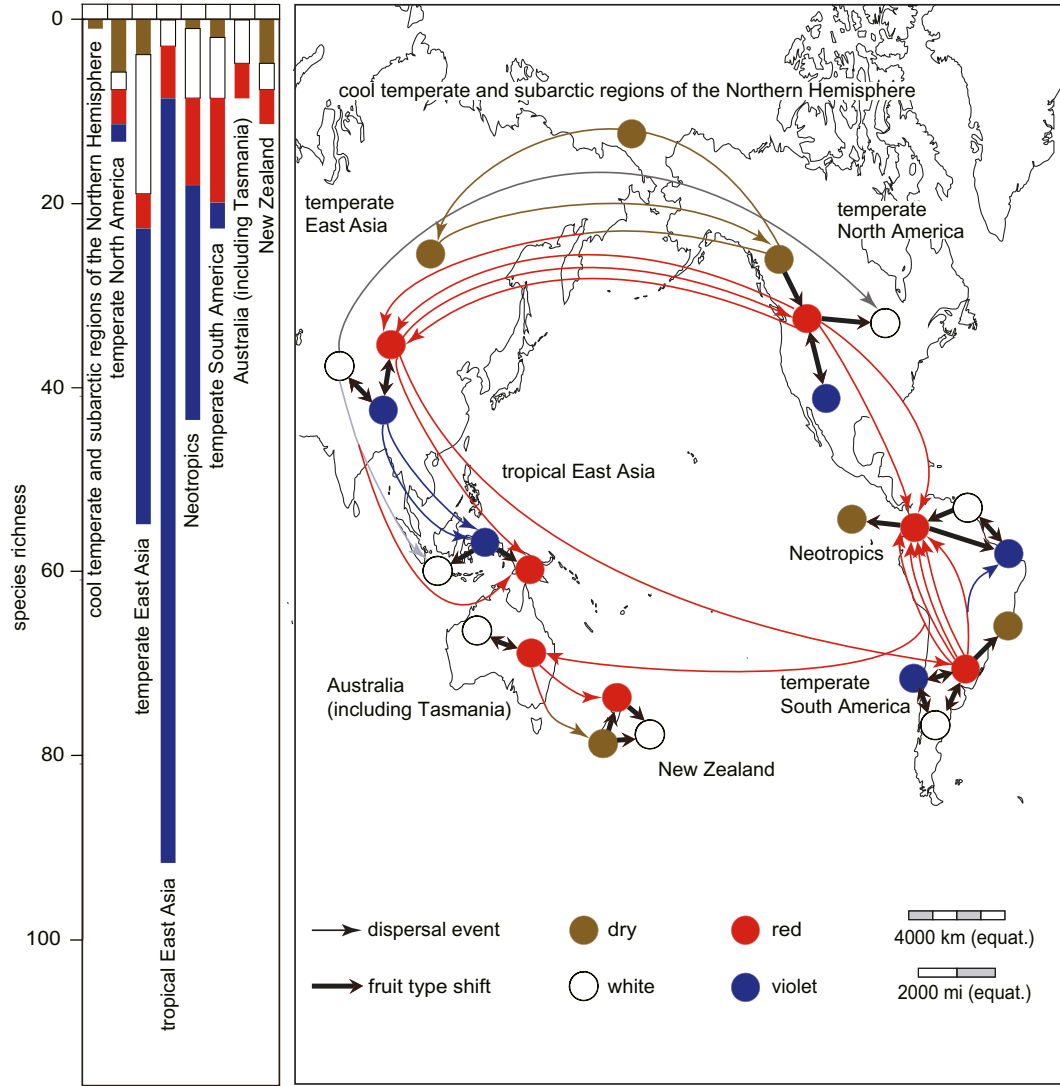


FIGURE 2 Patterns of species richness, dispersal and evolution of fruit colour within and among eight biogeographic regions. Analyses are based on the BEAST consensus tree for the tribe Gaultherieae. On the left, the number of species having each fruit colour in each region is summarized (Supporting Information Table S2). On the right, the fruit colour associated with each dispersal event between regions is indicated by thin coloured lines connecting regions, based on dispersal-extinction-cladogenesis (DEC) analyses for ancestral areas (Figure 1) and reconstructions of fruit-colour evolution (Figure 1, Supporting Information Table S5). Evolutionary changes in fruit colour in each region are also summarized (thick lines), based on combining Bayesian ancestral state reconstructions for fruit types in BAYESTRAITS (Supporting Information Figure S3) and ancestral-area reconstructions (Figure 1).

= 0.5; 20–15: red = 1; 15–10: red = 6; 10–5: dry = 1, red = 1, violet = 1; 5–0: dry = 0.5, white = 1.5, red = 5.5, violet = 1.5. Most importantly, red dispersal is most frequent (by > 3-fold) during the most recent time slice, when red is relatively uncommon. The high number of red-fruit dispersal events from 15–10 Ma is also striking, because the absolute number of extant red-fruited species that could potentially disperse was presumably much lower then, even if red-fruited species were more common relative to other colours (Figure 1). Furthermore, there is no significant relationship between the number or proportion of red-fruited species in a region and the number of dispersal events from that region by red-fruited lineages (number: $r^2 = 0.005$; $p = 0.878$; proportion: $r^2 = 0.142$; $p = 0.405$; $n = 7$ regions with red-fruited species; data summarized in Supporting Information Table S5 legend).

Using BioGeoBEARS, likelihood models linking fruit colour and dispersal accrued 100% of the AICc model weights for both fruit-colour coding schemes (Supporting Information Tables S12–S13). The best-fitting dispersal model included distance-dependent dispersal and fruit colour, suggesting that both significantly influenced dispersal. The multiplier on dispersal for non-red is 0.036 (Supporting Information Dataset S5) or 0.048 (Supporting Information Dataset S6), depending on the coding scheme. Thus, the dispersal probability for non-red fruit is only 3.6% or 4.8% of that for red fruit.

Dispersal distances were also significantly different among fruit colours [Kruskal–Wallis: $p < 0.0001$ for the consensus tree and mean $p = 0.004 \pm 0.01$ (range = $6.68e-07 - 0.028$) for 10 trees; Supporting Information Table S14], and distances for red were generally significantly higher (see mean ranks in Supporting Information Table

S14 and boxplots of dispersal distances in Supporting Information Figures S4, S6). Mean dispersal distances tended to be larger for red fruit (consensus tree = 6,679 km, mean of 10 trees = 6,318 km; Supporting Information Table S6), followed closely by dry (6,466, 6,244) and then white (5,835, 3,995) and violet (3,604, 3,880).

3.2 | Relationships among fruit colour, geographic distributions and diversification rates

In the clade-based PGLS analyses (Table 1, Supporting Information Table S15), white was positively associated with the combination of mean elevational and latitudinal midpoints and ranges ($r^2 = 0.67$), red was negatively associated with mean elevational midpoint ($r^2 = 0.36$) and violet was negatively associated with mean latitudinal midpoints ($r^2 = 0.50$). Diversification rates of clades were significantly related to their proportion of species with violet fruit ($r^2 = 0.3597$, $p = 0.0031$, AIC = -31.8367), but not other fruit types (Table 2, Supporting Information Table S15). However, diversification rates were also significantly related to mean latitudinal midpoint and range ($r^2 = 0.3196$, $p = 0.0147$, AIC = -29.7669). Adding violet colour to this model increased model fit (AIC = -31.5258). The standardized partial regression coefficients (SPRC) for this latter model suggest that most variation in diversification rates is explained by violet colour (SPRC = 0.54), and not latitudinal midpoint (0.12) or range (0.33). Overall, the diversification analyses help explain why violet is the most common fruit colour overall, especially in the Neotropics and in Asia (Figure 2).

Fruit colours showed one or more significant relationships with geographic variables in most other analyses, including global species-based analyses, species-based analyses within each biogeographic region and region-based analyses (Supporting Information Appendix S4, Tables S16–S19).

4 | DISCUSSION

In this paper, we use a phylogenetic approach to test relationships between fruit colour and large-scale dispersal, species' elevational and latitudinal distributions and diversification rates. We show for the first time that red fruit is significantly associated with large-scale biogeographic dispersal among regions. We also show significant relationships between fruit colours and patterns of latitudinal and elevational distributions (Table 1), including associations between red fruit and lower elevations, white and higher elevations and violet and lower latitudes. We also find higher diversification rates associated with violet fruit (as in Spriggs et al., 2015). We discuss these results in turn below. We also propose that fruit colours may show repeated "taxon cycles" within and among biogeographic regions (Figure 2), with one colour associated with dispersal between regions (i.e. red) that then evolves other colour/types within each region that are associated with different elevations and latitudes (dry, violet, white), and one colour associated with increased diversification

and richness (violet). These geographic fruit-colour cycles may help explain the extreme variability in fruit colours across angiosperm phylogeny.

We recognize that some readers may dismiss our results because we analysed only one group of plants. However, we provide evidence below suggesting that these patterns could be quite general. Furthermore, many of these patterns might be difficult to address with broad-scale analyses with less complete taxon sampling among closely related species. Thus, we suggest that the generality of the patterns found here should be tested with detailed, species-level studies in other plant groups.

4.1 | Fruit colour and large-scale dispersal

We found that red fruit is significantly associated with large-scale dispersal events, and that dispersal associated with red fruit tends to involve longer distances. To our knowledge, ours is the first study to document these patterns from a combined phylogenetic and biogeographic perspective. A study on *Coprosma* (Rubiaceae) suggested that red fruit was frequently associated with long-distance dispersal (Cantley et al., 2016), but without statistical analyses (or accounting for the preponderance of red-fruited species in the genus). Nevertheless, the similar patterns between *Coprosma* and Gaultherieae are consistent with the idea that these patterns may be general.

Previous ecological studies offer potential mechanistic explanations for these large-scale patterns. Several studies have reported that red fruit is associated with avian foraging, which may facilitate long-distance and overwater dispersal among regions (Janson, 1983; Wheelwright, 1988; Wheelwright & Janson, 1985; Willson et al., 1989). For example, Duan et al. (2014) found that artificial red fruits were especially attractive to and favoured by birds more than other fruit colours. Similarly, animals (birds, primates) with colour vision tend to eat red figs due to their conspicuousness in green foliage (Shanahan et al., 2001). However, darker fruits (including red and violet) were found to be favoured by various bird frugivores (Schaefer et al., 2014; Willson, Graff, & Whelan, 1990). Clearly, this is an area in need of further research, and our phylogenetic results should provide greater impetus to explore these patterns with detailed ecological data.

Fruit dispersal has been documented in 18 species of Gaultherieae, representing all fruit colours (Supporting Information Table S20). Most species are predominantly or exclusively bird-dispersed, including two species with only red fruit, six with both red and white fruit, two with white fruit, two with white, red and violet fruit and one with dry fruit. Among the four with violet fruit, three are bird-dispersed and one is wind-dispersed and the one species with both white and violet fruit is also wind-dispersed. An important area for future studies may be to focus on which bird taxa are involved in dispersing these fruits, and whether species that consume red fruits engage in long-distance migration and dispersal more than those consuming species with other fruit colours. This could be studied in Gaultherieae and more broadly across angiosperms.

4.2 | Fruit types and geographic distributions

We also found that different fruit types were associated with different latitudinal and elevational distributions. These geographic variables can explain considerable variation in fruit colour among clades (Table 1). Similar patterns were also seen at the species level (Supporting Information Table S16) and among regions (Supporting Information Table S19). We are not aware of similar patterns in previous studies. Thus, there are few pre-existing hypotheses to explain these patterns. Nevertheless, we present some ideas below.

We found that red fruit is often associated with lower elevations and violet with lower latitudes (Table 1). Higher frequencies of frugivory have been documented at lower elevations and higher latitudes (e.g. Nishi & Tsuyuzaki, 2004; Van Dersal, 1938; Willson, Sabag, Figueroa, Armesto, & Caviedes, 1996; Young, Kelly, & Nelson, 2012). This might help explain associations between red fruit and these habitats, but this will require further study. Interestingly, habitats at relatively high elevations and low latitudes have higher UV radiation compared to lower elevations and higher latitudes (Daniels, 1959), which might help explain associations between dark (violet) fruit and these habitats. Furthermore, it has been suggested that delphinidin (involved in violet anthocyanin production), evolved first in gymnosperms in high-elevation habitats in the Carboniferous, and helps protect against more intense UV radiation in these habitats (Campanella, Smalley, & Dempsey, 2014). Gloger's (1833) rule suggests that darker animals live closer to the equator due to changing selective pressures (e.g. UV irradiance; Cuthill, 2015). Latitudinal gradients in colouration occur in diverse organisms (humans: Jablonski & Chaplin, 2010; lichen-forming Teloschistaceae: Gaya et al., 2015; the plant *Argentina anserina*, Koski & Ashman, 2015). Increases in violet-fruited species with increasing elevation parallels the pattern of darker skin colour in montane populations of humans (Tibetans; Zhang, Li, Zhang, Wang, & Yu, 2012) and the lizard *Psammodomus algirus* (Reguera, Zamora-Camacho, & Moreno-Rueda, 2014). Both were hypothesized to be adaptations to greater UV radiation at higher elevations. Future studies should conduct tests of UV sensitivity for different fruit colour types among closely related species of Gaultherieae.

However, UV sensitivity may not help explain increases in white-fruited species at higher elevations (Table 1). Based on our field experience, we speculate that white-fruited species might occur more frequently in shady microenvironments, such as forest understorey. In these darker environments, white fruits might be far more conspicuous than violet fruits. Testing this hypothesis will require detailed ecological studies.

Although not a fruit colour, we also found an increase in dry-fruited species at higher latitudes (Supporting Information Tables S17, S19), as in earlier studies (Chen, Cornwell, Zhang, & Moles, 2016; Willson et al., 1989). This pattern may be explained by lower moisture availability at higher latitudes, and an association between fleshy fruits and greater moisture availability (Chen et al., 2016; Willson et al., 1989).

4.3 | Fruit types, geographic distribution and diversification rates

Our results support the idea that certain fruit colours increase diversification rates. However, they also show how such relationships might sometimes be indirect. We found a strong relationship between violet fruit and diversification (Table 2). Intriguingly, Spriggs et al. (2015) found a similar pattern in *Viburnum* (Adoxaceae), with purple fruits (equivalent to violet) having increased diversification relative to red fruits. Thus, fruit colour might impact diversification in similar ways across different clades. In theory, the apparent relationship between fruit colour and diversification might be a by-product of a relationship between colour and geographic distributions. Violet fruit is related to lower latitudes, as are increased diversification rates (Table 2). It is well known that low-latitude habitats can accelerate diversification (e.g. Jansson & Davies, 2008; Pyron & Wiens, 2013; Rolland, Condamine, Jiguet, & Morlon, 2014), especially high-elevation tropical habitats (e.g. Hughes & Eastwood, 2006; Hutter, Guayasamin, & Wiens, 2013; Hutter et al., 2017). However, in our results (Table 2), the best-fitting model to explain variation in diversification rates includes violet colour alone. Moreover, a multiple regression model including both geographic variables and fruit colour suggests that diversification rates are dominated by violet colour alone, but with some contributions from geographic variables (based on standardized partial regression coefficients).

Why should violet fruit colour promote diversification? We speculate that violet colour may confer greater protection from UV radiation at high elevations and low latitudes in Gaultherieae. Thus, white- and red-fruited species may be more confined to shady areas at various elevations, which might limit their ability to survive, spread and subsequently speciate in these habitats. If supported by future ecological studies, this pattern might help explain the greater frequency of violet-fruited lineages in these habitats, and their higher diversification rates there.

4.4 | Are there taxon cycles in fruit colour?

Our results suggest that patterns of variation in fruit colour may follow a process similar to a taxon cycle (Wilson, 1961). In the most general terms, a taxon cycle involves a repeated progression of dispersal and phenotypic evolution among islands or other regions, where certain phenotypes promote dispersal and others evolve after colonization. We found that one colour (red) seems to promote dispersal among regions (despite being relatively uncommon), but tends to be associated with lowland habitats (Table 1). In contrast, two other colours (violet, white) were less likely to spread among regions but typically evolved independently from red-fruited species within each region (Figure 2). They often spread into high-elevation habitats (Table 1). Violet then showed accelerated diversification and high species richness, especially in tropical habitats (Table 2). Thus, violet-fruited species predominate in Asia, the Neotropics, and globally (Figure 2), despite their more limited dispersal ability. There are also higher frequencies of dry-fruited species in high-latitude

habitats (Figure 2) and repeated evolution there (e.g. New Zealand, temperate South America). Overall, these patterns are repeated across multiple regions, as shown by our biogeographic reconstructions and analyses of fruit colour evolution (Figure 2), parallel relationships between geographic factors and fruit colours on different continents (Supporting Information Table S17) and similar patterns of species richness among fruit types on different continents (Figure 2). These patterns might apply to other angiosperm groups, because they may be related to mechanisms that could apply quite broadly, as described above (e.g. avian preference for red fruits, possible selection for darker fruit at higher elevations and dry fruit in drier habitats, higher diversification rates in violet fruit). Thus, we speculate that similar taxon cycles might be important in driving fruit-colour evolution and variation across angiosperms. In short, we suggest that repeated changes in fruit colour within and among biogeographic regions may help explain why fruit colour is so variable among species (e.g. Stourenas et al., 2013).

5 | CONCLUSIONS

In this study, we show that different fruit colours are associated with biogeographic dispersal, latitudinal and elevational distribution patterns and patterns of diversification. Taken together, these different correlates associated with different fruit colours suggest that there might be taxon cycles driving patterns of fruit colour within and among geographic regions. Such cycles might help explain patterns of fruit colour variation across angiosperms. Conversely, the results illustrate how different fruit colours may help to drive large-scale patterns of plant dispersal, distribution and diversification.

ACKNOWLEDGMENTS

The authors thank Hai-Dong Li, Wei Wang, Hai-Fei Yan, Jun-Bo Yang and Yong-Biao Zhang for laboratory advice and assistance, and Peter Raven, Peter Bernhardt, Vanessa Handley and Catherine Bush for suggestions on the manuscript. This study was supported by grants from Chinese Academy of Sciences Strategic Priority Research Program of Chinese Academy of Sciences (XDB31000000 to D.-Z.L. and H.W.), National Natural Science Foundation China (41671052, 31270272, 31100163 to L.L.), Applied Fundamental Research Foundation of Yunnan Province (2017FB072 to L.L.), the Hundred-Talent Program of Kunming Medical University (60117190444, 60118090109 to L.L.), Joint Fund of the National Natural Science Foundation of China-Yunnan Province (U1502261 to H.W.), Major International Joint Research Project of National Science Foundation China (31320103919 to H.W.), the U.S. National Science Foundation (DEB-0717711 to P.W.F., DEB-0717744 to K.A.K., DEB-1655690 to J.J.W.), the National Geographic Society (4-03-9329 to P.W.F. and L.L.), the CAS President's International Fellowship Initiative (PIFI, 2010T2S05 to PWF, 2017VCA0024 to J.J.W.), an Australian Research Council DECRA (Discovery Early Career Researcher

Award) fellowship (DE150101773 to N.J.M.) and Marsden grants (16-UOA-277, 18-UOA-034 to N.J.M.).

CONFLICTS OF INTEREST

The authors declare no conflict of interest.

AUTHOR CONTRIBUTION

J.J.W., D.-Z.L., L.L., P.W.F. and H.W. designed the study; L.L., J.J.W., P.W.F. and K.A.K. wrote the paper; L.L. and N.J.M. performed the analyses.

DATA ACCESSIBILITY

All data, including molecular datasets, BEAST majority rule consensus tree and Markov chain Monte Carlo (MCMC) trees, fruit-trait data, geographic data and results from all analyses are available as Supporting Information.

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BIOSKETCH

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

How to cite this article: Lu L, Fritsch PW, Matzke NJ, et al. Why is fruit colour so variable? Phylogenetic analyses reveal relationships between fruit-colour evolution, biogeography and diversification. *Global Ecol Biogeogr*. 2019;00:1–13. <https://doi.org/10.1111/geb.12900>