DOI: 10.1111/ele.13753

LETTER

ECOLOGY LETTERS WILEY

Dispersers and environment drive global variation in fruit colour syndromes

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Revised: 10 March 2021

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Funding information

National Science Foundation, Grant/ Award Number: DGE-1122492 and DEB-1441634

Editor: José Maria Gomez

INTRODUCTION

Many plants depend on animals for seed dispersal (Willson et al., 1989). In this mutualistic interaction, plants provide a nutritious reward to animals that eat their fruits and disperse the seeds (van der Pijl, 1969). Animal dispersal requires that plants advertise their fleshy fruits and, consequently, the relationship between fruit colours and animal dispersers has long been of interest. The primary hypothesis, the disperser syndrome hypothesis (DSH), attributes fruit colour to selection by animals in accordance with their perceptual abil-

ities, resulting in syndromes of traits corresponding to major disperser guilds (van der Pijl, 1969; Ridley, 1930). According to the DSH, bird-dispersed fruits are small with contrastive colours while mammal-dispersed fruits are large with cryptic colours and an odour, to appeal to mammals with good olfaction but poor vision (Janson, 1983; Valenta & Nevo, 2020).

attributed to selection by animal dispersers, despite weak evidence for this hypothesis. Here, we test the relative importance of biotic (bird and mammal frugivory) and abiotic (wet season temperatures, growing season length and UV-B radiation) factors in determining fruit colour syndrome in 3163 species of fleshy-fruited plants. We find that both dispersers and environment are important, and they interact. In warm areas, contrastive, bird-associated fruit colours increase with relative bird frugivore prevalence, whereas in cold places these colours dominate even where mammalian dispersers are prevalent. We present near-global maps of predicted fruit colour syndrome based on our species-level model and our newly developed characterisations of relative importance of bird and mammal frugivores.

The colours of fleshy fruits play a critical role in plant dispersal by advertising

ripe fruits to consumers. Fruit colours have long been classified into syndromes

KEYWORDS

Abstract

animal dispersal, disperser syndrome hypothesis, fruit colour, global patterns, seed dispersal

Evidence for bird and mammal syndromes is mixed. Birds and mammals are frequently observed consuming a wide variety of colours (Kitamura et al., 2002; Knight & Siegfried, 1983; Wheelwright & Janson, 1985). Innate preferences for bird-associated colours among birds have been reported, but these tend to be weak, inconsistent over time and variable within individuals (Duan et al., 2014; Duan & Quan, 2013; McPherson, 1988; Willson, 1994). Both birds and mammals are extraordinarily diverse, and include obligate and facultative frugivores such as cassowaries (Bradford et al., 2008), hornbills (Kitamura et al., 2004), passerines (Willson, 1994), lemurs (Valenta et al., 2015), bats (Hodgkison et al., 2003), elephants (Gautier-Hion et al., 1985) and bears (Hwang et al., 2002; Rodríguez et al., 2021), among many other groups. Despite this diversity, many studies acknowledge differences between dispersers yet continue to group fruits into broad "bird" and "mammal" categories (Brodie, 2017; Cazetta et al., 2008; Lomáscolo et al.,

2008; Masaki et al., 2012; Ferreira do Nascimento et al., 2020; Valenta et al., 2018a; Valido et al., 2011).

Weak evidence in support of the DSH indicates that other factors may be important in determining fruit colouration. Several alternative hypotheses have been proposed but have not received the attention of the DSH. For example, pigment synthesis is influenced by environmental conditions which could underlie evolutionary transitions in fruit colour. Anthocyanins-which produce black, blue, purple or red colours-typically increase after exposure to UV-B radiation, possibly to prevent photoinhibition (Chalker-Scott, 1999; Gould, 2004; Steyn et al., 2002). Photosynthesis in fruits can contribute roughly half of the carbon required for their development, so protecting the photosynthetic apparatus during development may be important to reproductive success (Cipollini & Levey, 1991; Todd et al., 1961). Cold temperatures also trigger anthocyanin synthesis (Lätti et al., 2008; Steyn et al., 2002, 2009). Contrastive colours (black, blue and red), produced by greater quantities of anthocyanins, absorb more radiation, which could increase the temperature of fruits and limit damage from cold (Bogert, 1949). Evolutionary transitions in fruit colour could result from these physiological responses if fruits are more successful because birds prefer fruits with higher anthocyanin content (Schaefer et al., 2008) or because anthocyanin-rich fruits survive better under stressful environmental conditions.

Non-physiological alternatives have also been proposed. For instance, short growing seasons may drive evolution towards fruit colours that occur earlier in development (i.e. paedomorphic evolution). Many fruits display a sequence of colours during development (green, yellow, red and/or black) over the course of several months (Sinnott-Armstrong et al., 2020; Willson & Thompson, 1982). Where growing seasons are short, plants may not have time to complete multiple colour changes, and consumption of immature fruits by dispersers may initiate an evolutionary transition from later-stage colours (black/red, more contrastive) to earlier-stage colours (green/yellow, more cryptic) (Sinnott-Armstrong et al., 2018). Alternatively, selection could favour distinctive colours (Willson & Whelan, 1990), honest signals of nutritional content (Albrecht et al., 2018; Schaefer et al., 2008, 2014; Sinnott-Armstrong et al., 2020) or mimicry of higher quality fruits (Galetti, 2002; Stournaras et al., 2015).

Here, we take a hypothesis-testing approach to assessing the DSH alongside alternative explanations. We select a set of predictor variables designed to reflect, as closely as possible, each of the four hypotheses that we test. Historically, studies of macroecological drivers have tended to use an agnostic approach of testing a wide variety of environmental predictor variables, e.g., a suite of bioclimatic variables, without requiring an explicit link to hypotheses. This approach can be useful for hypothesis *generation* when little is known about a particular ecological pattern or mechanism. However, explicit hypothesis testing, with predictor variables developed to address particular hypotheses, is becoming more common (e.g. Dalrymple et al., 2020; Law et al., 2020; Velasco et al., 2020). This latter approach is advantageous because a variable developed explicitly to address a particular mechanism can offer a more direct statistical interpretation. Recent efforts to expand the set of global-scale predictors beyond traditional bioclimatic variables have contributed enormously to our ability to test biological hypotheses on a global scale (e.g. UV-B radiation, Beckmann et al., 2014; growing season length, Garonna et al., 2016; cloud cover, Wilson & Jetz, 2016).

We follow this rationale, and here develop custom predictors designed to address four hypotheses to explain fruit colour variation. We divide fruits into two categories. "Contrastive" colours have historically been associated with bird dispersal (e.g. black, blue and red) and generally result from concentrated pigments, chiefly anthocyanins. "Cryptic" colours have historically been associated with mammal dispersal (e.g. green, brown and vellow) and are comparatively pigment poor. We test the following four hypotheses: (1) the DSH, that contrastive colours are correlated with bird dispersers, and cryptic colours with mammalian dispersers; (2) that contrastive colours occur where UV-B radiation is higher; (3) that contrastive colours occur where wet season temperatures are colder and (4) that contrastive colours occur where growing seasons are longer.

MATERIALS AND METHODS

Plant species and fruit traits

We used the dataset from Sinnott-Armstrong et al. (2018) to prepare an initial list of species and fruit colours. For the purposes of this study, we followed Janson (1983) and classified fruits into contrastive colours associated with bird dispersal ("Type A" = black, blue, red and white) and cryptic colours associated with mammal dispersal ("Type B" = green, yellow, brown and orange). Species recorded as having fruit colours spanning the two syndromes were removed. We used the Taxonomic Name Resolution Service to synonymise names and record taxonomic family and order (Boyle et al., 2013). For these analyses, we retain white and orange because they are classified by Janson (1983) into his types.

We downloaded occurrence records for each species from the Global Biodiversity Information Facility, retaining preserved specimens and research-grade human observations (GBIF; data https://doi.org/10.15468/ dl.dksmco). Using the R package *CoordinateCleaner*, we removed records with zero coordinates, and equal latitude and longitude (Zizka et al., 2019). We eliminated points over oceans, at country capitals, country centroids, biodiversity institutions and the GBIF headquarters. The remaining occurrence points were rasterised to an equal area grid consisting of 360×114 grid cells, i.e., c. 110 km on the side near the equator (Hurlbert & Jetz, 2007). We reduced the dataset to a single occurrence per grid cell per species, and removed species occupying fewer than 20 grid cells. Overall, we retained 3163 plant species (Table S1).

Although we have data on >3000 fleshy-fruited species, this is a small fraction of global seed plant diversity (~350,000 species; Smith & Brown, 2018) and estimating the representativeness of our data is challenging. That said, our data span broad geographic space and phylogenetic diversity, representing 195 families from 59 orders (Tables S2 and S3). The number of species in each family in our dataset broadly corresponds to preliminary estimates of the total number of fleshy-fruited species per family (Sinnott-Armstrong & Donoghue, in prep.). For instance, seven of the top 10 most species-rich families in our dataset (Rubiaceae, Rosaceae, Melastomataceae, Myrtaceae, Araceae, Lauraceae and Piperaceae) are also among the 10 families with the most fleshy-fruited species. Some large clades include only fleshy-fruited species, such as Lauraceae (2900 species), Araceae (3400) and Piperaceae (3700). Although these clades are relatively well represented in our dataset, we have only a small percentage of their species (e.g. 89 Lauraceae, 86 Araceae and 83 Piperaceae). While our data are incomplete, we do not see how biases in its representation would alter the results.

Biotic predictor

We chose a single predictor to represent each of our four hypotheses. For the DSH, we created a spatial predictor variable, "relative bird frugivore prevalence", to represent the relative richness of frugivorous birds and mammals weighted by their dietary reliance on fruit. We obtained maps of breeding ranges for landbirds from Jetz et al. (2012) and for mammals from the IUCN (IUCN, 2016), and intersected them with the aforementioned 110-km resolution grid to obtain species lists for each grid cell. For each species, we obtained diet data from EltonTraits 1.0 (Wilman et al., 2014), which describes diet on a scale from 0.0 to 1.0 at 0.1 intervals, where 0.0 indicates no consumption of fruit and 1.0 indicates complete reliance on fruit. We next calculated absolute frugivore prevalence of birds and mammals for each grid cell, by summing the frugivore scores for all members of an assemblage. A grid cell with absolute bird frugivore prevalence of 10 could thus arise from, e.g., 10 species with frugivore scores of 1.0 each, or from 100 species that each have scores of 0.1. Finally, we calculated relative bird frugivore prevalence as: absolute bird frugivore prevalence/(absolute bird frugivore prevalence + absolute mammal frugivore prevalence). Higher values of this index indicate greater frugivory potential from birds, while lower values signal that mammal frugivory predominates.

The variable as described above represents the assemblage-level relative frugivore prevalence at any individual grid cell (Figure 1a). However, there is an alternative, species-level formulation of this variable, where each disperser species is additionally weighted by its range size (Jetz et al., 2012; Figure S1). In this



FIGURE 1 Biogeographic prevalence of fleshy-fruited plant species that display contrastive colours. (a) Range-weighted proportion of plant species displaying contrastive colours. Data are mapped at a grain size of 110 km at the equator and values of 1 (purple) correspond to more contrastive colours while lower values (yellow) correspond to a higher frequency of cryptic colours. The unequal representation of species due to differing range sizes is addressed via subsampling (see methods). (b) Distribution of fruit colours in environmental space, with Whittaker biomes plotted as an overlay. Whittaker biomes are numbered as follows: 1 = tropical rainforest, 2 = tropical seasonal forest, 3 = subtropical desert, 4 = temperate rainforest, 5 = temperate seasonal forest, 6 = woodland/shrubland, 7 = temperate grassland, 8 = boreal forest, 9 = tundra. Each grid cell spans 1° of temperature by 10 cm of precipitation. Points in the inset illustrate the average species value for mean annual temperature and mean annual precipitation. The same scale bar applies to both panels

alternative formulation, which is explored in more detail in the Supplemental Material, all species contribute equally to the index regardless of their range size. In the assemblage-level formulation, wide-ranging species have a strong influence on the spatial patterns due to their contributions to many more grid cells than narrow-ranging species. Which formulation to select depends on the exact question asked, and there are advantages and disadvantages to both (see Supplemental Material). Here, we emphasise the results from the assemblage-level formulation of this variable (i.e. without range-weighting), but we provide the results of the species-level (range-weighted) variable in the supplement and discuss the results here.

Abiotic predictors

To test the relative importance of our biotic predictor compared with competing abiotic hypotheses, we used raster layers for each abiotic hypothesis. For growing season length, we computed the mean *growing season length* per grid cell averaged across 2003–2012 using data from Garonna et al. (2016).

To test the cold temperatures hypothesis, we used the CHELSA climatic layer "mean temperature of the wettest quarter" (Karger et al., 2017). Mean temperature of the wettest quarter incorporates both the long time periods needed for fruit development, and precipitation. Many fruits develop over the span of several months (e.g. Camargo et al., 2013; Willson & Thompson, 1982), and fleshy, animal-dispersed fruits are more common where precipitation is higher (Almeida-Neto et al., 2008; Howe & Smallwood, 1982). We call this variable "wet season temperature".

We initially tested the UV hypothesis with UV-B layers from Beckmann et al. (2014). However, UV radiation was highly (negatively) collinear with *wet season temperature*. When we included UV in our models, it emerged as a strong predictor that was negatively correlated with contrastive colouration (the opposite of our hypothesis). Based on this finding, we concluded that our data show no support for the UV hypothesis and we omitted this variable from the final analyses.

All predictors were centred and scaled, except *relative bird frugivore prevalence* which ranged between 0 and 1. All predictors were resampled to an equal area projection with 360×114 grid cells (excluding Antarctica), in line with the expected reliable spatial resolution of the bird and mammal range maps (Hurlbert & Jetz, 2007).

Spatial and environmental patterns

To account for unequal representation across plant species due to differences in range size (number of grid cells occupied), we randomly generated 1000 subsamples of 10 occurrence points per species (following Quintero & Jetz, 2018). The proportion of species with contrastive/cryptic colours was then averaged across all subsamples, and the results are shown in Figure 1a. To estimate values per species for each predictor variable for our models, we extracted predictor values for each occurrence record and calculated the average value per species. We plot the location of each species in biome space in Figure 1b (Whittaker, 1975).

Modelling

We ran three types of models. First, we built a phylogenetic multi-predictor model for the 3163 species in our dataset, with fruit colour syndrome as a binary response (contrastive or cryptic). We started with all interactions between *relative bird frugivore prevalence* (either assemblage- or species-level), wet season temperature and growing season length. We performed phylogenetic logistic regression using the R package phylolm (Ho & Ané, 2014) and a recent phylogeny of angiosperms (Smith & Brown, 2018) which we subsetted to the species in our dataset. We then performed model averaging (Dormann et al., 2018) in order to determine the suite of equivalently good models (based on AICc) and the relative importance of each predictor (the sum of AICc weights of the models in which that term appears).

In addition, we repeated the logistic regression but instead of a phylogeny we included nested taxonomic levels (order, family) as random effects in a mixed effects model and employed model averaging to determine the best-fitting models and predictors. Finally, we performed phylogenetic path analysis (using the same, pruned phylogeny as above) in the R package *phylopath* (Bijl, 2018; von Hardenberg & Gonzalez-Voyer, 2013). For the path analysis, we focused on the question of whether abiotic variables directly influence fruit colouration, or whether they influence fruit colouration indirectly through *relative bird frugivore prevalence*. The full set of models included in the path analysis can be found in Figure S2.

Here, we focus on the results of the phylogenetic logistic regression and note where the mixed effects models and path analyses differed. We ran each of these models with assemblage-level (presented in the text) and species-level (presented in the supplement) *relative bird frugivore prevalence*, for a total of six modelby-predictor combinations. We additionally ran the phylogenetic logistic regressions and mixed effects models including a variable for eastern vs. western ("Old World" vs. "New World") *hemisphere*; because hemisphere is highly correlated with the taxonomy of both plants and animals, we present these results in the supplement and focus on the results without *hemi-sphere* in the text.

Predicting global patterns

We used the preferred model from model averaging to predict both species-level and grid-cell-level spatial variation in fruit colour syndrome, following the approach in Jetz and Rubenstein (2011). To account for differences in species range sizes affecting variation in fruit colours across grid cells, we randomly subsampled the grid cell occurrences for each species down to 10. For each of 1000 subsamples, we re-ran the model to obtain new estimates of the coefficients of the model terms, which we then used to predict the probability of bird colour for each species and each subsample of occurrences. Finally, we calculated the average proportion of species with contrastive colours for each grid cell across all 1000 predictions. We assessed the accuracy of our predictions by calculating the area under the ROC curve (AUC) of observed and predicted fruit colour syndromes for each species.

Prediction of fruit colour syndrome across grid cells enabled us to make predictions for regions of the world where we do not have fruit colour data. To expand these species-level predictions to global predictions, we used a generalised linear model with the same predictor terms as the preferred model, but without phylogenetic information. We followed the same procedure as above, randomly subsampling occurrence records and re-running models to obtain a distribution of model coefficients. For each iteration, we predicted the proportion contrastive colours per grid cell using the grid-cell values of each predictor. We then averaged the resulting 1000 maps from our subsamples and models. We assessed the accuracy of observed and predicted grid-cell proportion of contrastive colours using Spearman's rank correlation (*rho*).

RESULTS

Geography of fruit colour syndromes

The proportion contrastive colours varies broadly across space (Figure 1a). Tropical biomes exhibit relatively low frequencies of contrastive colours (tropical rain forest, 63%–66%; and tropical seasonal forests, 65%–66%; Figure 1b). Colder biomes primarily display contrastive colours: boreal forest and tundra have 97% and 98% contrastive colours on average, and temperate seasonal forests have 83%, temperate rain forests 71% and woodlands and shrublands 80%.

Geography of relative bird frugivore prevalence

Relative bird frugivore prevalence varies strongly across the globe and is especially high in Australia, northern Africa and temperate zones with some exceptions, such as western North America. *Relative mammal frugivore prevalence* is higher in tropical regions (especially central Africa and the Indo-Pacific, but less so in the Amazon) as well as at boreal latitudes in the northern hemisphere (Figure 2a). In contrast to these clear spatial patterns, variation in *relative bird frugivore prevalence* in environmental space is less clear (Figure 2b). Tundra is dominated by mammal frugivory, with only 13.8% of frugivory by birds. Boreal forests and temperate grasslands also have low bird frugivore prevalence (47.6% and 30.2% respectively). In all other biomes, *relative bird frugivore prevalence* exceeds 50% (59–67%).



FIGURE 2 Observed *relative bird frugivore prevalence*. (a) *Relative bird frugivore prevalence*. Each grid cell is coloured by the proportion of frugivorous species that are birds (out of frugivorous birds and mammals), weighted by their dietary specialisation on fruit. (b) *Relative bird frugivore prevalence* in environmental space, with Whittaker biomes overlain. The inset illustrates the grid cell means aggregated in environmental space. For other details see Figure 1

Biotic and abiotic drivers

Of the possible models from model averaging of the phylogenetic logistic regressions, 13 received an AIC weight >0. The strongest model (AIC weight = 0.47; Figure 3a) included an interaction between wet season temperature and relative bird frugivore prevalence plus their main effects. These terms were part of most selected models (AIC weight > 0.99 for wet season temperature and rela*tive bird frugivore prevalence*; AIC weight = 0.52 for the interaction between wet season temperature and relative bird frugivore prevalence). Growing season length was not included in the best model but had moderate importance (AIC weight = 0.53). Using the species-level formulation of *relative bird frugivore prevalence*, the best model included interactions between both wet season temperaturet and growing season length with relative bird frugi*vore prevalence* (AIC weight = 0.72; all of these variables and interactions had variable importance > 0.50) (Figure S3).

Partial residuals plots, created using the *effects* R package (Fox, 2003), illustrate the effect of predictor variables on fruit colour (Figure 4). Where *relative bird*

frugivore prevalence is high, the probability of exhibiting a contrastive colour is always high, regardless of *wet season temperature*. However, when *relative bird frugivore prevalence* is low, colder *wet season temperature* is associated with more contrastive fruit colours and warmer *wet season temperature* with cryptic colours.

Results of the mixed effects model were qualitatively the same, and included an interaction between *wet season temperature* and *relative bird frugivore prevalence* (AIC weight > 0.99) while *growing season length* had only moderate importance (AIC weight = 0.56; Figure 3b).

Phylogenetic path analysis found that all three predictor variables directly influence fruit colour (Figure 3c), although the correlation is stronger with *relative bird frugivore prevalence* (0.20) and *wet season temperatures* (-0.24) than *growing season length* (0.08). Both abiotic variables influence *relative bird frugivore prevalence* and thus also have an indirect effect on fruit colour.

The results using species-level relative bird frugivore prevalence supported the importance of wet season temperatures and relative bird frugivore prevalence across all models (Figure S3). When including a variable for hemisphere, growing season length had relatively more



FIGURE 3 Model results using the assemblage-level *relative bird frugivore prevalence* for each model type. Relative AIC weights for predictor terms from model averaging of the (a) phylogenetic logistic regression and (b) mixed effects model. AIC weights ("importance") are calculated per predictor term by summing the AIC weight of each model containing that predictor. Higher importance values indicate that the predictor occurs in models with higher AIC weights. The predictor terms that occur in the best model are black, while gray bars indicate variables not included in the best model. The five best models with AIC weight > 0 are illustrated, with X marks indicating the predictor terms included in that model along with the model's AIC weight. *temp* = wet season temperatures, *birds* = relative bird frugivore prevalence, *gsl* = growing season length. (c) Results of the path analysis, including each predictor variable (interaction terms did not have weight in the results and thus are excluded from the visualisation). Blue arrows indicate positive correlations and red arrows indicate negative correlations. Numbers report the strength of each correlation



FIGURE 4 The interaction of biotic and abiotic drivers of among-species variation in contrastive (bird-associated) vs. cryptic (mammalassociated) fruit colour. (a) and (b) illustrate the distribution of raw data variation in colour syndrome in relation to two focal variables, (a) *wet season temperatures* and (b) *relative bird frugivore prevalence*. Each point refers to one species, and boxplots show the interquartile range (boxes), median (notched line) and upper and lower 25% (horizontal bars). (c and d) Partial residuals plots illustrating the effects of the interaction between *wet season temperature* and *relative bird frugivore prevalence* based on a model including both variables and their interaction. (c) Partial residuals of *wet season temperature* plotted under conditions of high (top 20%) and low (bottom 20%) *relative bird frugivore prevalence*. (d) Partial residuals of *relative bird frugivore prevalence* plotted under conditions of high (top 20%) and low (bottom 20%) *wet season temperature*. We chose thresholds of 20% for visualisation purposes, in order to balance having a sufficient sample size in the ends of the distributions and displaying the trends effectively. Coloured bands delineate 95% confidence intervals

importance than when *hemisphere* was not included (Figure S4).

Predictions across geographic space

When aggregated in geographic space, our species-level predictions broadly recapitulate the observed spatial patterns in fruit colour (Figure 5a). Observed and predicted proportions of contrastive colours per grid cell are correlated (Spearman's *rho* = 0.74, p < 0.001; Figure 5c). When comparing grid-cell proportions of contrastive colours without phylogenetic information, the quality of the predictions decreased (Spearman's *rho* = 0.68, p < 0.001; Figure 5c,d).

DISCUSSION

Contrary to the dominant hypothesis that variation in fruit colours is driven by selection by dispersers, we find consistent evidence across several types of models that abiotic variables are important. Although the exact results varied somewhat by model type and predictor (assemblage- vs. species-level *relative bird frugivore prevalence*), no model found that *relative bird frugivore prevalence* alone was sufficient to predict fruit colour variation. Most models support the importance of both wet season temperatures and relative bird frugivore prevalence, typically with an interaction between these two variables. The interaction between wet season temperature and relative bird frugivore prevalence suggests a possible explanation for inconsistent evidence in support of the DSH: mammalian frugivores may be necessary for the evolution and maintenance of cryptic colours, but not *sufficient*. Cryptic colours can be common, but only when temperatures are warm and *relative bird frugivore* prevalence is low (and, thus, relative mammal frugivore prevalence is high). Consequently, the prevalence of frugivores may be important only under certain climatic conditions; outside of those conditions, abiotic variables may have a stronger influence on fruit colour evolution. Path analysis suggests that these abiotic variables have direct and indirect effects on fruit colouration. Although there was some variation in results across different model and predictor combinations (especially with respect to the importance of growing season length), all results highlighted the importance of abiotic variables in fruit colour variation.

Analytical approach

We ran these three different types of models because each has advantages and disadvantages, and we sought to gauge the range and consistency of results in the



FIGURE 5 Predicted fruit colour syndrome (proportion contrastive fruit colours) across space. (a) Geographic variation in the predicted *species*-level syndrome of each species. Grid cells are coloured according to the average proportion contrastive fruit colours across all subsampled model coefficients, with taxonomic level incorporated as random effect. Values of 1 (purple) represent more contrastive colours while lower values (yellow) represent more cryptic colours. (b) Model predictions mimic the observed spatial variation (Spearman's *rho* = 0.74) when phylogenetic information is included. (c) Predicted *grid-cell*-level proportion contrastive fruit colours, no phylogenetic information. (d) The predictions lacking phylogeny did not perform as well as those that included phylogeny (Spearman's *rho* = 0.68). Diagonal lines (b, d) indicate a one-to-one relationship between predicted and observed proportion fruit colours. To produce these maps, we generated 1000 random samples of 10 occurrences per species for our fruit colour data, re-calculated the average of each predictor value per species derived from those subsamples and then modelled fruit colour using the covariates in our "best" model. To predict species-level patterns (a, b), we used our phylogenetic logistic regression; to predict grid-cell level patterns (c, d), we used a generalised linear model with the same covariates, but lacking the phylogenetic information. We then used the respective model coefficients to predict the proportion contrastive fruit colours across the globe for each species (a, b) or each grid cell (c, d) and averaged across all 1000 iterations

context of varied model specifications. Phylogenetic logistic regression is typically preferable to a taxonomybased model, but our confidence in our phylogenetic tree is low because it was pruned from a megaphylogeny of angiosperms which itself relied on taxonomy as a scaffold for constructing the tree (Smith & Brown, 2018). The mixed effects models may be appropriate given that fleshy fruits have evolved many times independently. These models thus avoid errors associated with reconstructing a highly homoplastic trait on a very sparsely sampled tree. Path analysis is best suited to providing information about whether predictors directly and/or indirectly influence the response variable. Consequently, utilising all three models allowed us to provide different perspectives on the relationship, if any, between predictor variables and response variables.

In addition to model type, the selection of predictor variables to represent specific hypotheses can also influence the power and specificity of the targeted hypothesis testing. Macroecological studies assessing biotic drivers have in the past used straightforward species counts, with limited quantitative data accounting for dietary preferences. Here, we developed a predictor that estimated the relative frugivore prevalence experienced by plant species as well as current evidence allows. We weighted potential disperser species by their dietary preference for fruit in developing the *relative bird frugivore prevalence* predictor. In addition, we explored assemblage-level (not weighted by range) and species-level (weighted by range) formulations of this metric. There are arguments in favour of both approaches: the assemblage-level variable might better reflect the average disperser presence

in any given community, while the species-level variable enables all disperser species to have equal weighting rather than being heavily biased towards wide-ranging dispersers. This important contrast is discussed in detail in the Supplemental Material. By matching the predictor variable as closely as possible to our focal hypothesis, and exploring different formulations of this predictor variable, we aimed to provide as general a global test as currently possible.

Spatial patterns in fruit colours

Latitudinal gradients in fruit colouration have been previously reported (Sinnott-Armstrong et al., 2018), but our analyses reveal longitudinal patterns as well. Europe and China have more cryptic colours than eastern North America and Japan. Western North America has a higher prevalence of contrastive colours compared to eastern North America, and a similar pattern seems to hold in Europe although we have little data from Eastern Europe. In Australia, more contrastive colours occur towards the west and more cryptic colours to the east.

Relative bird frugivore prevalence

The relative importance of bird dispersers is spatially heterogeneous (Figure 2a). Throughout most of the tropics, relative bird frugivore prevalence is low, indicating that mammal frugivores play a larger role. This is especially true in central Africa and the Indo-Pacific, while much of the Amazon basin has moderate relative bird frugivore prevalence. This is not surprising, given that the Amazon has one of the richest frugivorous bird communities in the world (Fleming et al., 1987; Kissling et al., 2009, 2011). Interestingly, our fruit colour data do not reflect the dominance of bird dispersers in the Amazon. Instead, Amazonian fruits display a high frequency of cryptic (mammal-associated) colours. If anything, cryptic colours are more common in tropical South America than in the Palaeotropics. Sampling biases may contribute to this pattern; for instance, we have little data on fruit colours from the Indo-Pacific (Figure S5).

How can we explain that Amazonian forests are dominated by bird frugivores (Fleming et al., 1987; Kissling et al., 2009, 2011) but by cryptic fruits traditionally associated with mammal dispersal? One possibility is that most palaeotropical primates have trichromatic colour vision, while neotropical primates are largely dichromatic, i.e., red–green colourblind (Dominy et al., 2003; Jacobs, 2009; Jacobs et al., 2017; Melin et al., 2017, 2019). However, if colour vision was a crucial factor, then we would expect neotropical plants to have an overabundance of contrastive fruit colours, which would be visually attractive to both birds and dichromatic primates. Amazonian birds are exceptionally diverse and highly

frugivorous (Kissling et al., 2009), and only 24% of neotropical frugivores are primates or bats as compared with 28% in Africa and 35% in Southeast Asia (Fleming et al., 1987). Abiotic factors may drive the prevalence of cryptic colours in the Amazon, irrespective of the importance of mammalian frugivores. Large fruit and seed size may evolve to provide nutrition and protection to the developing embryo in shaded environments (Mack, 2000; Salisbury, 1942), but large sizes may incur high metabolic costs associated with high anthocyanin production in large fruits (Willson & Whelan, 1990). Thus, large, cryptic-coloured fruits could be adapted to shaded, tropical rainforests rather than to mammalian frugivores. Similar abiotic environments between Amazonian and palaeotropical forests may explain their similarity in fruit traits despite different relative bird frugivore prevalence.

Another unusual location is Madagascar, where mammals (especially lemurs) have long been thought to play a much larger role in seed dispersal than in most other regions of the world (Fleming et al., 1987; Valenta et al., 2018b; Wright et al., 2005). Our results generally support this idea, though we note that Madagascar does not appear to be as unique in the importance of mammals as is often claimed. *Relative bird frugivore prevalence* is low on the island, but this is true of most of the Palaeotropics and in some higher latitude regions.

Mammals provide an unexpectedly high proportion of frugivory at high latitudes in boreal to Arctic habitats (Figure 2). This is especially apparent in northern North America (*relative bird frugivore prevalence* <60%). High latitudes have much lower frugivore diversity than the tropics. In temperate zones, bears, foxes and mustelids play an important role in seed dispersal (Bustamante et al., 1992; Koike et al., 2008; Rodríguez et al., 2021; Takahashi et al., 2008; Zhou et al., 2008a, 2008b), and in southern Spain the seeds of 40% of the fleshy-fruited plant species have been found, undamaged, in the scat of carnivoran mammals (Herrera, 1989). Our somewhat counter-intuitive results for areas like western North America highlight the need for more studies of high latitude mammalian frugivores.

As described above, an additional consideration is that *relative bird frugivore prevalence* does not incorporate certain characteristics that may influence seed dispersal effectiveness, such as abundance, biomass or body size. Differing modes of foraging introduce another complication. Large mammals may consume more fruits at a time than small birds, but also deposit seeds in larger clusters (Howe, 1986). Birds may not disperse seeds as far due to shorter retention times in the gut (Traveset, 1998). These biotic factors illustrate the challenge in adequately describing the expected relationship between dispersers and fruits: selection on fruit colour cannot be purely a function of disperser identity, but also relates to how many fruits a disperser consumes, where it deposits the seeds, and the degree to which it prefers certain colours over others (Jordano, 1987; Schupp et al., 2010; Valenta et al., 2018b). Furthermore, omnivorous birds that only consume a small amount of fruit in their diet can nonetheless have a strong impact by increasing the dispersal of rare plant species (Carlo & Morales, 2016; Morán-López et al., 2018).

Abiotic hypotheses

We found that wet season temperature is an important factor explaining fruit colour syndrome, and that growing season length may be moderately important. Colder wet season temperatures are strongly associated with increased contrastive colouration, in agreement with our hypothesis. Growing season length may not be as strong of a driver of fruit colour evolution as we have proposed here and elsewhere (Lo et al., 2011; Sinnott-Armstrong et al., 2018), or its importance may be clade specific. For growing season length to affect the evolution of fruit colour, a species would need to produce immature colours, experience a change in the length of the growing season, have viable seeds prior to fruit maturity and experience consistent selection by dispersers across its range. These conditions may be met only in a subset of clades. Alternatively, the influence of growing season length may be more apparent within the contrastive and cryptic categories (e.g. paedomorphic evolution from black-fruited ancestors to red fruit colour, rather than from black/red to yellow/green). This latter possibility is not captured by our models. Overall, abiotic variables clearly influence fruit colouration, and the role of growing season length and paedomorphic evolution should be further investigated.

Predictions

We based our predictions on our best-performing phylogenetic logistic regression (which included an interaction between relative bird frugivore prevalence and wet season temperature). Predictions based on this model are moderately accurate at predicting fruit colour syndrome, and capture both broad patterns (more contrastive colours at high latitudes than in the tropics) and finer-scale differences (such as the higher frequency of cryptic colours in eastern Asia than eastern North America) (Figure 5). This latter pattern may arise from the continued presence of monkeys in eastern Asia, which are lacking in eastern North America (Eyde, 1985). There are also regions of mismatch between our predictions and observed fruit syndrome patterns. For instance, cryptic colours are predicted to dominate in Australia and the northsouth axis of Africa to a greater degree than we observe. In addition, we note that the inclusion of phylogenetic relatedness results in better predictions. The degree to

which fruit colours are phylogenetically conserved has been a matter of debate (Jordano, 1995; Stournaras et al., 2013; Valenta et al., 2018a). Here, incorporating phylogeny enables us to better understand the factors that underlie fruit colour variability, and also to better predict fruit colour syndromes in new species and new places.

CONCLUSIONS

What factors contribute to the evolution and geography of fruit colour syndromes? We find that both biotic and abiotic variables are important. Fruits displaying cryptic colours largely occur in warm environments where relative bird frugivore prevalence is low. When wet season temperatures are cool and/or relative bird frugivore preva*lence* is high, most fruits display contrastive colours. The finding that dispersers are important is not surprising. But our finding that abiotic variables are necessary to explain fruit syndromes highlights that future studies examining alternative hypotheses will be critical to advancing our understanding of fruit colour. In addition, we highlight the need for explicit hypothesis testing in macroecological modelling, and the careful selection of predictor variables designed to test those explicit hypotheses. We provide two new, publicly available predictor layers, one with an assemblage-level and a second with a species-level characterisation of relative bird frugivore prevalence.

ACKNOWLEDGEMENTS

This research was supported by an NSF Graduate Research Fellowship (DGE-1122492, DEB-1441634) to M.S.A. W.J. gratefully acknowledges support from NSF DEB-1441634 for the VertLife project. Pedro Jordano, Rick Prum and members of the Donoghue laboratory provided discussions and comments that greatly improved the manuscript. We are further grateful to three anonymous reviewers for their insightful comments, and to the innumerable natural historians whose observations, monographs and datasets enable macroecological research.

AUTHORSHIP

M.S.A., M.J.D. and W.J. designed the study. M.S.A. performed the statistical analyses, and all authors interpreted the results. M.S.A. wrote the first draft of the manuscript, and all authors contributed substantially to revisions.

PEER REVIEW

The peer review history for this article is available at https://publons.com/publon/10.1111/ele.13753.

DATA AVAILABILITY STATEMENT

All data are publicly available on Data Dryad (https://doi.org/10.5061/dryad.hmgqnk9gf).

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REFERENCES

- Albrecht, J., Hagge, J., Schabo, D.G., Schaefer, H.M. & Farwig, N. (2018) Reward regulation in plant-frugivore networks requires only weak cues. *Nature Communications*, 9, 4838.
- Almeida-Neto, M., Campassi, F., Galetti, M., Jordano, P. & Oliveirafilho, A. (2008) Vertebrate dispersal syndromes along the Atlantic forest: Broad-scale patterns and macroecological correlates. *Global Ecology and Biogeography*, 17, 503–513.
- Beckmann, M., Václavík, T., Manceur, A.M., Šprtová, L., von Wehrden, H., Welk, E. et al. (2014) glUV: A global UV-B radiation data set for macroecological studies. *Methods in Ecology* and Evolution, 5, 372–383.
- Bijl, W.V.D. (2018) phylopath: Easy phylogenetic path analysis in R. *PeerJ*, 6, e4718.
- Bogert, C.M. (1949) Thermoregulation in reptiles, a factor in evolution. Int. J. Org. Evol., 3, 195–211.
- Boyle, B., Hopkins, N., Lu, Z., Raygoza Garay, J.A., Mozzherin, D., Rees, T. et al. (2013) The taxonomic name resolution service: An online tool for automated standardization of plant names. *BMC Bioinformatics*, 14, 1–14.
- Bradford, M.G., Dennis, A.J. & Westcott, D.A. (2008) Diet and dietary preferences of the southern cassowary (*Casuarius casuarius*) in North Queensland, Australia. *Biotropica*, 40, 338–343.
- Brodie, J.F. (2017) Evolutionary cascades induced by large frugivores. Proceedings of the National Academy of Sciences of the United States of America, 114, 11998–12002.
- Bustamante, R.O., Simonetti, J.A. & Mella, J.E. (1992) Are foxes legitimate and efficient dispersers? A field test. Acta Oecologica, 13, 203–208.
- Camargo, M.G.G., Cazetta, E., Schaefer, H.M. & Morellato, L.P.C. (2013) Fruit color and contrast in seasonal habitats – A case study from a cerrado savanna. *Oikos*, 122, 1335–1342.
- Carlo, T. & Morales, J.M. (2016) Generalist birds promote tropical forest regeneration and increase plant diversity via rare-biased seed dispersal. *Ecology*, 97, 1819–1831.
- Cazetta, E., Schaefer, H.M. & Galetti, M. (2008) Does attraction to frugivores or defense against pathogens shape fruit pulp composition? *Oecologia*, 155, 277–286.
- Chalker-Scott, L. (1999) Environmental significance of anthocyanins in plant stress responses. *Photochemistry and Photobiology*, 70, 1–9.
- Cipollini, M.L. & Levey, D.J. (1991) Why some fruits are green when they are ripe: Carbon balance in fleshy fruits. *Oecologia*, 88, 371–377.
- Dalrymple, R.L., Kemp, D.J., Flores-Moreno, H., Laffan, S.W., White, T.E., Hemmings, F.A. et al. (2020) Macroecological patterns in flower colour are shaped by both biotic and abiotic factors. *New Phytologist*, 228, 1972–1985.
- Dominy, N.J., Svenning, J.-C. & Li, W.-H. (2003) Historical contingency in the evolution of primate color vision. *Journal of Human Evolution*, 44, 25–45.
- Dormann, C.F., Calabrese, J.M., Guillera-Arroita, G., Matechou, E., Bahn, V., Bartoń, K. et al. (2018) Model averaging in ecology: A review of Bayesian, information-theoretic, and tactical approaches for predictive inference. *Ecological Monographs*, 88, 485–504.
- Duan, Q., Goodale, E. & Quan, R. (2014) Bird fruit preferences match the frequency of fruit colours in tropical Asia. *Scientific Reports*, 4, 5627.
- Duan, Q. & Quan, R.-C. (2013) The effect of color on fruit selection in six tropical Asian birds. *Condor*, 115, 623–629.
- Eyde, R.H. (1985) The case for monkey-mediated evolution in bigbracted dogwoods. *Arnoldia*, 45, 3–9.

- Fleming, T.H., Breitwisch, R. & Whitesides, G.H. (1987) Patterns of tropical vertebrate frugivore diversity. *Annual Review of Ecology* and Systematics, 18, 91–109.
- Fox, J. (2003) Effect displays in R for generalised linear models. *Journal of Statistical Software*, 8, 1–18.
- Galetti, M. (2002) Seed dispersal of mimetic fruits: Parasitism, mutualism, aposematism or exaptation? In: Levey, D.J., Silva, W.R. & Galetti, M. (Eds.), Seed dispersal and frugivory: Ecology, evolution and conservation. Oxon, UK: CABI Publishing, pp. 177–191.
- Garonna, I., de Jong, R. & Schaepman, M.E. (2016) Variability and evolution of global land surface phenology over the past three decades (1982–2012). *Global Change Biology*, 22, 1456–1468.
- Gautier-Hion, A., Duplantier, J.-M., Quris, R., Feer, F., Sourd, C., Decoux, J.-P. et al. (1985) Fruit characters as a basis of fruit choice and seed dispersal in a tropical forest vertebrate community. *Oecologia*, 65, 324–337.
- Gould, K.S. (2004) Nature's swiss army knife: The diverse protective roles of anthocyanins in leaves. *Journal of Biomedicine & Biotechnology*, 5, 314–320.
- Herrera, C.M. (1989) Frugivory and seed dispersal by carnivorous mammals, and associated fruit characteristics, in undisturbed Mediterranean habitats. *Oikos*, 55, 250–262.
- Ho, L.S.T. & Ané, C. (2014) A linear-time algorithm for Gaussian and non-Gaussian trait evolution models. *Systematic Biology*, 63, 397–408.
- Hodgkison, R., Balding, S.T., Zubaid, A. & Kunz, T.H. (2003) Fruit bats (Chiroptera: Pteropodidae) as seed dispersers and pollinators in a lowland Malaysian rain forest. *Biotropica*, 35, 491–502.
- Howe, H.F. (1986) Seed dispersal by fruit-eating birds and mammals. In: Murray, D.R. (Ed.), *Seed dispersal*. New York, NY: Academic Press, pp. 123–189.
- Howe, H.F. & Smallwood, J. (1982) Ecology of seed dispersal. Annual Review of Ecology and Systematics, 13, 201–228.
- Hurlbert, A.H. & Jetz, W. (2007) Species richness, hotspots, and the scale dependence of range maps in ecology and conservation. *Proceedings of the National Academy of Sciences of the United States of America*, 104, 13384–13389.
- Hwang, M.-H., Garshelis, D.L. & Wang, Y. (2002) Diets of Asiatic black bears in Taiwan, with methodological and geographical comparisons. Ursus, 13, 111–125.
- IUCN. (2016) The IUCN Red List of Threatened Species, Version 2016–1. Available from: http://www.iucnredlist.org [Accessed 15th December 2018].
- Jacobs, G.H. (2009) Evolution of colour vision in mammals. Philosophical Transactions of the Royal Society of London. Series B, 364, 2957–2967.
- Jacobs, R.L., MacFie, T.S., Spriggs, A.N., Baden, A.L., Morelli, T.L., Irwin, M.T. et al. (2017) Novel opsin gene variation in largebodied, diurnal lemurs. *Biology Letters*, 13, 20170050.
- Janson, C.H. (1983) Adaptation of fruit morphology to dispersal agents in a Neotropical forest. *Science*, 219, 187–189.
- Jetz, W. & Rubenstein, D.R. (2011) Environmental uncertainty and the global biogeography of cooperative breeding in birds. *Current Biology*, 21, 72–78.
- Jetz, W., Thomas, G.H., Joy, J.B., Hartmann, K. & Mooers, A.O. (2012) The global diversity of birds in space and time. *Nature*, 491, 444–448.
- Jordano, P. (1987) Avian fruit removal: Effects of fruit variation, crop size, and insect damage. *Ecology*, 68, 1711–1723.
- Jordano, P. (1995) Angiosperm fleshy fruits and seed dispersers: A comparative analysis of adaptation and constraints in plantanimal interactions. *The American Naturalist*, 145, 163–191.
- Karger, D.N., Conrad, O., Böhner, J., Kawohl, T., Kreft, H., Soria-Auza, R.W. et al. (2017) Data from: Climatologies at high resolution for the earth's land surface areas. *Dryad Digital Repository*. https://doi.org/10.5061/dryad.kd1d4

- Kissling, W.D., Böhning-Gaese, K. & Jetz, W. (2009) The global distribution of frugivory in birds. *Global Ecology and Biogeography*, 18, 150–162.
- Kissling, W.D., Sekercioglu, C.H. & Jetz, W. (2011) Bird dietary guild richness across latitudes, environments and biogeographic regions. *Global Ecology and Biogeography*, 21, 328–340.
- Kitamura, S., Yumoto, T., Poonswad, P., Chuailua, P. & Plongmai, K. (2004) Characteristics of hornbill-dispersed fruits in a tropical seasonal forest in Thailand. *Bird Conservation International*, 14, S81–S88.
- Kitamura, S., Yumoto, T., Poonswad, P., Chuailua, P., Plongmai, K., Maruhashi, T. et al. (2002) Interactions between fleshy fruits and frugivores in a tropical seasonal forest in Thailand. *Oecologia*, 133, 559–572.
- Knight, R.S. & Siegfried, W.R. (1983) Inter-relationships between type, size and colour of fruits and dispersal in southern African trees. *Oecologia*, 56, 405–412.
- Koike, S., Morimoto, H., Goto, Y., Kozakai, C. & Yamazaki, K. (2008) Frugivory of carnivores and seed dispersal of fleshy fruits in cool-temperate deciduous forests. *Journal of Forest Research*, 13, 215–222.
- Lätti, A.K., Riihinen, K.R. & Kainulainen, P.S. (2008) Analysis of anthocyanin variation in wild populations of bilberry (Vaccinium myrtillus L.) in Finland. Journal of Agriculture and Food Chemistry, 56, 190–196.
- Law, S.J., Bishop, T.R., Eggleton, P., Griffiths, H., Ashton, L. & Parr, C. (2020) Darker ants dominate the canopy: Testing macroecological hypotheses for patterns in colour along a microclimatic gradient. *Journal of Animal Ecology*, 89, 347–359.
- Lo, E.Y.Y., Stournaras, K.E., Schaefer, H.M., Oliver, J., Edwards, E.J., Donoghue, M.J. et al. (2011) A possible global pattern in the distribution of fruit colors. Contrib. talk Present. Evol. Conf., Norman, OK.
- Lomáscolo, S.B., Speranza, P. & Kimball, R.T. (2008) Correlated evolution of fig size and color supports the dispersal syndromes hypothesis. *Oecologia*, 156, 783–796.
- Mack, A.L. (2000) Did fleshy fruit pulp evolve as a defence against seed loss rather than as a dispersal mechanism? *Journal of Biosciences*, 25, 93–97.
- Masaki, T., Takahashi, K., Sawa, A., Kado, T., Naoe, S., Koike, S. et al. (2012) Fleshy fruit characteristics in a temperate deciduous forest of Japan: How unique are they? *Journal of Plant Research*, 125, 103–114.
- McPherson, J.M. (1988) Preferences of cedar waxwings in the laboratory for fruit species, colour and size: A comparison with field observations. *Animal Behavior*, 36, 961–969.
- Melin, A.D., Chiou, K.L., Walco, E.R., Bergstrom, M.L., Kawamura, S. & Fedigan, L.M. (2017) Trichromacy increases fruit intake rates of wild capuchins (*Cebus capucinus imitator*). Proceedings of the National Academy of Sciences of the United States of America, 114, 10402–10407.
- Melin, A.D., Nevo, O., Shirasu, M., Williamson, R.E., Garrett, E.C., Endo, M. et al. (2019) Fruit scent and observer colour vision shape food-selection strategies in wild capuchin monkeys. *Nature Communications*, 10, 1–9.
- Morán-lópez, T., Carlo, T.A. & Morales, J.M. (2018) The role of frugivory in plant diversity maintenance – A simulation approach. *Ecography (Cop.)*, 41, 24–31.
- Nascimento, L.F.D., Guimarães, P.R., Onstein, R.E., Kissling, W.D. & Pires, M.M. (2020) Associated evolution of fruit size, fruit colour and spines in Neotropical palms. *Journal of Evolutionary Biology*, 33, 858–868.
- Quintero, I. & Jetz, W. (2018) Global elevational diversity and diversification of birds. *Nature*, 555, 246–250.
- Ridley, H. (1930) *The Dispersal of Plants Throughout the World*. Kent, UK: Reeve and Ashford.
- Rodríguez, A.G., Albrecht, J., Szczutkowska, S., Valido, A., Farwig, N. & Selva, N. (2021) The role of the brown bear Ursus arctos

as a legitimate megafaunal seed disperser. *Scientific Reports*, 11, 1282.

- Salisbury, E.J. (1942) The reproductive capacity of plants. Studies in quantitative biology. London: G. Bell & Sons.
- Schaefer, H.M., McGraw, K. & Catoni, C. (2008) Birds use fruit colour as honest signal of dietary antioxidant rewards. *Functional Ecology*, 22, 303–310.
- Schaefer, H.M., Valido, A. & Jordano, P. (2014) Birds see the true colours of fruits to live off the fat of the land. *Proceedings of the Royal Society B: Biological Sciences*, 281, 20132516.
- Schupp, E.W., Jordano, P. & Gómez, J.M. (2010) Seed dispersal effectiveness revisited: A conceptual review. *New Phytologist*, 188, 333–353. https://doi.org/10.1111/j.1469-8137.2010.03402.x
- Sinnott-Armstrong, M. & Donoghue, M.J. (n.d.). How many fleshyfruited plants are there?
- Sinnott-Armstrong, M., Downie, A.E., Federman, S., Valido, A., Jordano, P. & Donoghue, M.J. (2018) Global geographic patterns in fruit colors and related traits. *Global Ecology and Biogeography*, 27, 1339–1351.
- Sinnott-Armstrong, M., Lee, C.M., Clement, W.L. & Donoghue, M.J. (2020) Fruit syndromes in Viburnum: Correlated evolution of color, nutritional content, and morphology in fleshy birddispersed fruits. *BMC Evolutionary Biology*, 1, 1–19.
- Smith, S.A. & Brown, J.W. (2018) Constructing a broadly inclusive seed plant phylogeny. *American Journal of Botany*, 105, 302–314.
- Steyn, W.J., Wand, S.J.E., Holcroft, D.M. & Jacobs, G. (2002) Anthocyanins in vegetative tissues: A proposed unified function in photoprotection. *New Phytologist*, 155, 349–361.
- Steyn, W.J., Wand, S.J.E., Jacobs, G., Rosecrance, R.C. & Roberts, S.C. (2009) Evidence for a photoprotective function of lowtemperature-induced anthocyanin accumulation in apple and pear peel. *Physiologia Plantarum*, 136, 461–472.
- Stournaras, K.E., Lo, E., Böhning-Gaese, K., Cazetta, E., Matthias Dehling, D., Schleuning, M. et al. (2013) How colorful are fruits? Limited color diversity in fleshy fruits on local and global scales. *New Phytologist*, 198, 617–629.
- Stournaras, K.E., Prum, R.O. & Schaefer, H.M. (2015) Fruit advertisement strategies in two Neotropical plant-seed disperser markets. *Evolutionary Ecology*, 29, 489–509.
- Takahashi, K., Shiota, T., Tamatani, H., Koyama, M. & Washitani, I. (2008) Seasonal variation in fleshy fruit use and seed dispersal by the Japanese black bear (Ursus thibetanus japonicus). Ecological Research, 23, 471–478.
- Todd, G.W., Bean, R.C. & Propst, B. (1961) Photosynthesis & respiration in developing fruits. II. Comparative rates at various stages of development. *Plant Physiology*, 36, 69–73.
- Traveset, A. (1998) Effect of seed passage through vertebrate frugivores' guts on germination: A review. *Perspectives in Plant Ecology, Evolution and Systematics*, 1(2), 151–190.
- Valenta, K., Brown, K.A., Rafaliarison, R.R., Styler, S.A., Jackson, D., Lehman, S.M. et al. (2015) Sensory integration during foraging: The importance of fruit hardness, colour, and odour to brown lemurs. *Behavioral Ecology and Sociobiology*, 69, 1855–1865.
- Valenta, K., Kalbitzer, U., Razafimandimby, D., Omeja, P., Ayasse, M., Chapman, C.A. et al. (2018a) The evolution of fruit colour: Phylogeny, abiotic factors and the role of mutualists. *Scientific Reports*, 8, 14302.
- Valenta, K. & Nevo, O. (2020) The dispersal syndrome hypothesis: How animals shaped fruit traits, and how they did not. *Functional Ecology*, 34, 1158–1169.
- Valenta, K., Nevo, O. & Chapman, C.A. (2018b) Primate fruit color: Useful concept or alluring myth? *International Journal of Primatology*, 39, 321–337.
- Valido, A., Schaefer, H.M. & Jordano, P. (2011) Colour, design and reward: Phenotypic integration of fleshy fruit displays. *Journal* of Evolutionary Biology, 24, 751–760.
- van der Pijl, L. (1969) Principles of dispersal in higher plants. Berlin: Springer.

- Velasco, J.A., Villalobos, F., Diniz-Filho, J.A.F., Poe, S. & Flores-Villela, O. (2020) Macroecology and macroevolution of body size in Anolis lizards. *Ecography (Cop.)*, 43, 812–822.
- von Hardenberg, A. & Gonzalez-Voyer, A. (2013) Disentangling evolutionary cause-effect relationships with phylogenetic confirmatory path analysis. *Evolution (N. Y.)*, 67, 378–387.
- Wheelwright, N.T. & Janson, C.H. (1985) Colors of fruit displays of bird-dispersed plants in two tropical forests. *The American Naturalist*, 126, 777–799.
- Whittaker, R.H. (1975) *Communities and ecosystems*. Macmillan Publishing Co., Inc.
- Willson, M.F. (1994) Fruit choices by captive American robins. Condor, 96, 494–502.
- Willson, M.F., Irvine, A.K. & Walsh, N.G. (1989) Vertebrate dispersal syndromes in some Australian and New Zealand plant communities, with geographic comparisons. *Biotropica*, 21, 133–147.
- Willson, M.F. & Thompson, J.N. (1982) Phenology and ecology of color in bird-dispersed fruits, or why some fruits are red when they are "green". *Canadian Journal of Botany*, 60, 701–713.
- Willson, M.F. & Whelan, C.J. (1990) The evolution of fruit color in fleshy-fruited plants. *The American Naturalist*, 136, 790.
- Wilman, H., Belmaker, J., Jennifer, S., de la Rosa, C., Rivadeneira, M.M. & Jetz, W. (2014) EltonTraits 1.0: Species-level foraging attributes of the world's birds and mammals. *Ecology*, 95, 2027.
- Wilson, A.M. & Jetz, W. (2016) Remotely sensed high-resolution global cloud dynamics for predicting ecosystem and biodiversity distributions. *PLoS Biology*, 14, 1–20.
- Wright, P.C., Razafindratsita, V.T., Pochron, S.T. & Jernvall, J. (2005) The key to Madagascar frugivores. In: Dew, J.L. & Boubli, J.P. (Eds.) *Tropical fruits and frugivores: The search for*

strong interactors. Dordrecht, The Netherlands: Springer, pp. 121–138.

- Zhou, Y.-B., Slade, E., Newman, C., Wang, X.-M. & Zhang, S.-Y. (2008a) Frugivory and seed dispersal by the yellow-throated marten, *Martes flavigula*, in a subtropical forest of China. *Journal of Tropical Ecology*, 24, 219–223.
- Zhou, Y.-B., Zhang, L., Kaneko, Y., Newman, C. & Wang, X.M. (2008b) Frugivory and seed dispersal by a small carnivore, the Chinese ferret-badger, *Melogale moschata*, in a fragmented subtropical forest of central China. *Forest Ecology and Management*, 255, 1595–1603.
- Zizka, A., Silvestro, D., Andermann, T., Azevedo, J., Ritter, C.D., Edler, D. et al. (2019) CoordinateCleaner: Standardized cleaning of occurrence records from biological collection databases. *Methods in Ecology and Evolution*, 10, 744–751.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

How to cite this article: Sinnott-Armstrong MA, Donoghue MJ, Jetz WJ. Dispersers and environment drive global variation in fruit colour syndromes. *Ecology Letters*. 2021;24:1387–1399. https://doi.org/10.1111/ele.13753