

# Global geographic patterns in the colours and sizes of animal-dispersed fruits

Miranda A. Sinnott-Armstrong<sup>1</sup>  | Alexander E. Downie<sup>1</sup> | Sarah Federman<sup>1</sup> |  
Alfredo Valido<sup>2</sup> | Pedro Jordano<sup>2</sup> | Michael J. Donoghue<sup>1</sup>

<sup>1</sup>Department of Ecology and Evolutionary Biology, Yale University, New Haven, Connecticut

<sup>2</sup>Department of Integrative Ecology, Estación Biológica de Doñana (EBD-CSIC), Sevilla, Spain

## Correspondence

Miranda A. Sinnott-Armstrong, Department of Ecology and Evolutionary Biology, Yale University, P.O. Box 208106, New Haven, CT 06520.  
Email: miranda.sinnott-armstrong@yale.edu

## Present Address

Alexander E. Downie, Laboratory of Parasitic Diseases, National Institute of Allergy and Infectious Diseases, National Institutes of Health, Bethesda, MD

Alfredo Valido, Island Ecology and Evolution Research Group, Instituto de Productos Naturales y Agrobiología (IPNA-CSIC), La Laguna, Tenerife (Canary Islands), Spain

## Funding information

National Science Foundation, Grant/Award Number: DGE-1122492; Ministerio de Economía y Competitividad, Grant/Award Number: CGL2013-47429-P; Severo Ochoa Excellence Award, Grant/Award Number: SEV-2012-0262; Ramón y Cajal research program, Grant/Award Number: RYC-2007-00620

## Abstract

**Aim:** Fruit colours attract animal seed dispersers, yet the causes of fruit colour diversity remain controversial. The lack of knowledge of large-scale spatial patterns in fruit colours has limited our ability to formulate and test alternative hypotheses to explain fruit colour, fruit size and fruit colour diversity. We describe spatial (especially latitudinal) variation in fruit colour, colour diversity and length, and test for correlations between fruit colour, length and plant habit.

**Location:** Global.

**Time period:** Present day.

**Major taxa studied:** Seed plants.

**Methods:** We assembled a database of fruit traits for 13,178 fleshy fruited plant species spanning 136 sites around the world. To assess whether fruit colour categories correspond with spectral reflectances, we tested for clustering of hue, chroma and saturation for 236 species for which we had reflectance data. We then quantified latitudinal gradients in fruit colour, fruit length and fruit colour diversity while controlling for the effects of plant habit and whether colour categories varied with respect to average fruit size.

**Results:** Colour categories corresponded well with reflectance data. The tropics show high colour diversity, while red fruits progressively constitute a higher proportion of the fleshy-fruited plant community towards high latitudes. All mammal-associated colours (green, orange, brown and yellow) are more common in the tropics than at high latitudes. Fruit length also increases towards the tropics.

**Main conclusions:** Tropical communities tend to have diverse fruit colours, including many mammal-associated fruit colours, while high latitude communities contain a higher percentage of red-fruited species. The correlation between colour and size is strong, and some latitudinal patterns may be partly driven by changes in fruit size. Differences in geography and in the history of plant lineages in the Southern versus the Northern Hemisphere may help to explain some biogeographic patterns, but alternative hypotheses related to fruit defence, development and metabolic costs are plausible.

## KEYWORDS

animal seed dispersal, dispersal syndrome hypothesis, fruit colour, latitudinal gradients, plant traits, seed dispersal syndromes

## 1 | INTRODUCTION

Colour is a key trait influencing how organisms interact with the environment. Animals frequently avoid predation by displaying warning or cryptic colours, and males of many vertebrate species attract females with bright, colourful displays (Caro, 2005; Hill & McGraw, 2006). In plants, the colours of flowers (Schaefer & Ruxton, 2011) and fleshy fruits (van der Pijl, 1969) attract pollinators and seed dispersers, respectively. Many plants rely on a mutualistic interaction with animals to disperse their seeds (Willson, Irvine, & Walsh, 1989): plants provide a reward to their animal dispersers in the form of a nutritive, fleshy pulp, in exchange for the animal carrying seeds to a new location (van der Pijl, 1969). Fruits display a diverse array of colours to attract seed dispersers (Schaefer & Ruxton, 2011; Turček, 1963), and this tremendous diversity has long fascinated biologists (Darwin, 1872; Ridley, 1930; van der Pijl, 1969). But, despite decades of research, large-scale spatial variation in fruit colours and other fruit traits has not been properly quantified.

The traditional hypothesis to explain fruit colour diversity – the disperser syndrome hypothesis (DSH) – suggests that different guilds of dispersers select for different fruit colours and, more broadly, for suites of traits corresponding to the preferences and perceptual abilities of those seed dispersers (van der Pijl, 1969). Typically, fleshy fruits are divided into a ‘bird’ syndrome of small fruits with bright or contrastive colours such as red, black and blue, and a ‘mammal’ syndrome of larger fruits with dull colours such as green, brown or yellow, often with an odour and/or protective husk (Janson, 1983; van der Pijl, 1969). A variety of complexities in these syndromes have been noted (e.g., Fadzly & Burns, 2010; Lord & Marshall, 2001), and doubt has been cast on the extent to which seed dispersers actually select for fruit traits. Many animals consume a broad range of fruit colours, including fruits displaying traits belonging to all syndromes (Fischer & Chapman, 1993; Kitamura et al., 2002; Poulsen, Clark, Connor, & Smith, 2002; van der Pijl, 1969), and preferences can vary even among individual animals and over time (Willson, 1994). In light of such observations, alternatives have been proposed: that fruit colours directly signal nutritional content (Cazetta, Galetti, Rezende, & Schaefer, 2012; Valido, Schaefer, & Jordano, 2011; Willson & Whelan, 1990), that fruits may compete for dispersers by displaying distinctive colours or mimicking more nutritious fruits in the same habitat (Stournaras, Prum, & Schaefer, 2015), or that pigments may play a functional role in defending fruits against UV radiation or fungal pathogens (Cipollini & Levey, 1997; Schaefer, Rentzsch, & Breuer, 2008; Willson & Whelan, 1990). Yet, most of these hypotheses implicitly assume that distinct combinations of fruit traits have evolved in relation to the preferences of different groups of frugivores.

An important challenge in the study of fruiting syndromes arises from the diffuse nature of plant–seed disperser interaction networks. Unlike flowers, where specialized interactions between flowers and their pollinators are possible and are common in some

groups (e.g., yuccas and their moths, Powell & Mackie, 1966; orchids and euglossine bees, Dressler, 1968), fruits generally do not form such specialized interaction networks with frugivores (Jordano, 1987; Wheelwright & Orians, 1982). Instead, each plant species is usually dispersed by many frugivore species and each frugivore typically consumes the fruits of many plant species (e.g., Kitamura et al., 2002; Wheelwright et al., 1984). The complexity of plant–seed disperser interaction networks does not preclude their study, but does highlight the need for new perspectives to help us understand the relative importance of seed disperser perceptual abilities and alternative selective factors (e.g., high UV radiation).

Both the DSH and the existing alternatives imply predictable spatial variation, yet the lack of global-scale data on fruit colours and other fruit traits has made it difficult to identify general patterns. The prevalence of red and black fruits in most plant communities has been described repeatedly (Fischer & Chapman, 1993; Nakanishi, 1996; Schmidt, Schaefer, & Winkler, 2004; Wheelwright & Janson, 1985; but see Camargo, Cazetta, Schaefer, & Morellato, 2013). Armesto, Rozzi, Miranda, and Sabag (1987) noted that black-fruited species are more common in the Neotropics than they are in Europe, and, more recently, Lo et al. (2011) tentatively reported that dark-coloured fruits may be more common at lower latitudes and red fruits more common at high latitudes. Although tropical organisms are frequently thought to be more colourful (and to exhibit higher colour diversity) than their temperate relatives, this has not been found for fruits (Burns, Cazetta, Galetti, Valido, & Schaefer, 2009). Additionally, although only a few sites have been compared, a spatial correlation between disperser assemblage and fruit colours (as predicted by the DSH) has not been found (Brodie, 2017; Fischer & Chapman, 1993; but see Dominy, Svenning, & Li, 2003). The limited spatial scope of these studies – typically comparing only a handful of sites, usually from the Neotropics and/or temperate Europe – renders the generality of these findings uncertain. Nonetheless, these studies offer tantalizing hints that spatial variation in fruit colours may exist, and that understanding these spatial patterns would help to test the various hypotheses that have been proposed to explain fruit colour diversity.

Here we describe a large database of fruit colours, fruit sizes and related traits, which we have assembled in order to provide an initial description of global variation in fruit traits. Given our emphasis on broad spatial patterns, we have endeavoured to span the range of latitudes, continents and biomes where fleshy-fruited plants occur. We focus here on fruit colour, fruit size and plant habit, as hypotheses on the selective forces driving the evolution of these traits provide clear spatial predictions, for example, that mammal-associated fruit colours will only occur where mammalian dispersers are extant or recently extinct. Specifically, we investigate global patterns in fruit colour and fruit size, and test whether latitudinal gradients persist even when potentially correlated explanatory variables – fruit length and plant habit – are included.

## 2 | METHODS

### 2.1 | Data collection

#### 2.1.1 | Species lists and sites

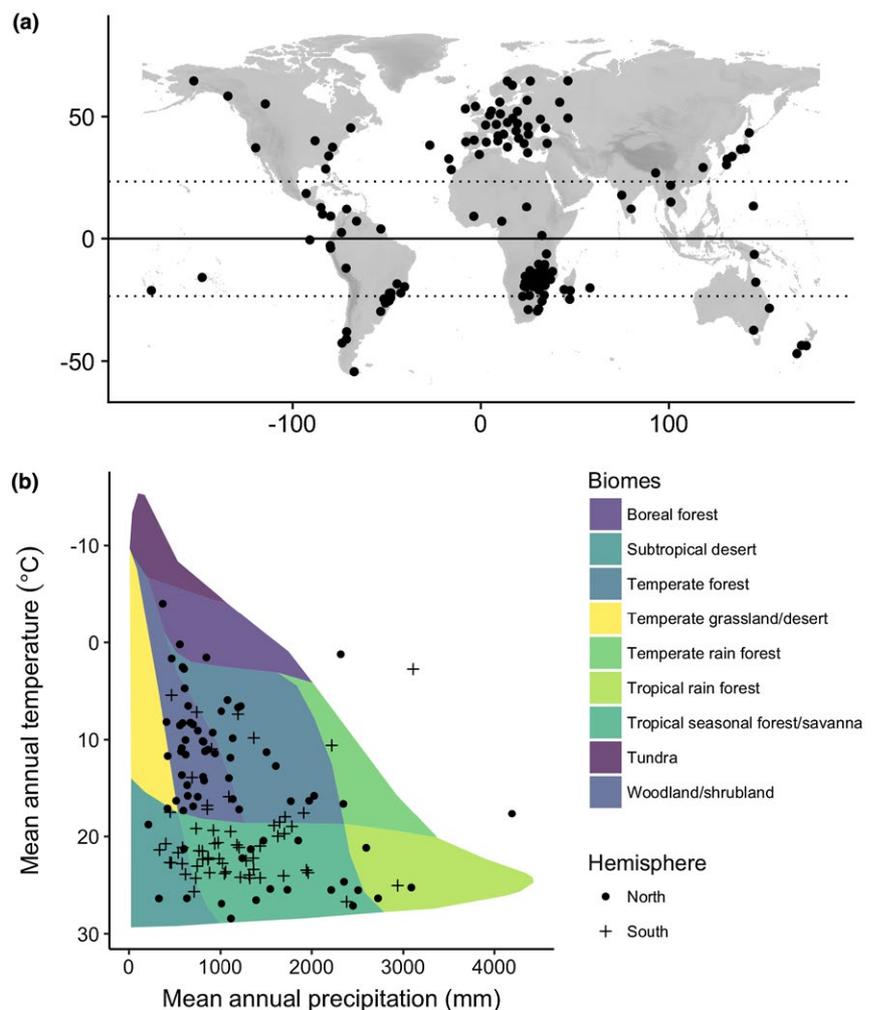
We compiled data on fruit colour, fruit length and plant habit from published studies, regional floras and local field guides, as well as from the ATLANTIC-FRUGIVORY database (Bello et al., 2017). We also incorporated eight additional sites from published studies that listed the number of species of each colour without identifying those species. Any species producing fleshy propagules was counted, including those that provide a reward via a secondary structure such as an arillate seed. We limited our data collection to sources that describe fruit traits for whole plant communities (or a sampling thereof) rather than those describing the diet of particular seed dispersers. Although studies focusing on the diets of specific dispersers provide valuable information about fruit colour, they also contain inherent, non-random missing data (i.e., the species that are present but not consumed by the disperser of interest) that could bias our results. Each study or flora served both as a species list for the sites described therein, and also as a source for trait data with

which to investigate global patterns. The complete list of sources can be found in Supporting Information Table S1. Species names were checked against The Plant List (The Plant List, 2013).

To determine the geographic location of each site, we relied on publicly available shapefiles (for geopolitical units, e.g., countries, provinces or states; Global Administrative Areas, 2012) and protectedplanet.net (for national parks and other protected areas; UNEP-WCMC and IUCN, 2018). For sites not falling into either of these categories, we georeferenced maps and descriptions from each source in order to create polygons in ArcMAP (v. 10.5.1). We then used the latitudinal and longitudinal centroid of each polygon in our analyses. The resulting dataset consists of 19,886 species by site combinations in total, of which there are 13,178 unique fleshy-fruited species spanning 134 globally distributed sites (Figure 1a).

#### 2.1.2 | Biomes

We sought to include sites from a wide range of latitudes and biomes in order to span as much of the breadth of habitat diversity as possible. To quantify the diversity of biomes for which we have data, we extracted mean annual temperature and precipitation from CHELSA climate layers at 30 arc-second resolution (Karger et



**FIGURE 1** (a) Map of studied locations. The sites are represented as dots at the centroid of the polygon for each site, the equator is indicated by a solid horizontal line and the Tropics of Cancer and Capricorn are indicated by dashed lines. (b) The Whittaker biome (mean annual temperature and mean annual precipitation) of each site is plotted. Point shape indicates Northern Hemisphere sites (dots) and Southern Hemisphere sites (crosses) [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

al., 2017) and took the median environmental variable per polygon (Park & Davis, 2017) to represent each site's climatic niche. Our sampled sites include localities from all of the major biomes (except tundra) described by Whittaker (1975), although temperate grasslands and rain forests are poorly represented (Figure 1b). In the Northern Hemisphere our sites come from all major biomes except tundra; in the Southern Hemisphere, despite the smaller number of sites, we have sites in all biomes except boreal forest and temperate grasslands/deserts (tundra does not occur in the Southern Hemisphere).

### 2.1.3 | Fruit colours

To quantify colour in our dataset, we used two different approaches: a traditional, eight category scheme derived from human vision, and a three-category scheme derived from an analysis of fruit colour reflectance spectra in relation to their human colour category. Recently, quantitative colour spectra have become more common as a method of analysing fruit colour (Cazetta et al., 2012; Stournaras et al., 2015; Valido et al., 2011). Spectra provide many advantages as they are independent of the human visual system (Endler, 1990), which differs from that of other frugivorous mammals and birds (some of which can see into the UV; Chen, Collins, & Goldsmith, 1984). However, the paucity of spectral measurements greatly limits our ability to assess large-scale spatial patterns in fruit colours using these measurements. As our goal was to provide a preliminary description of global patterns, qualitative colour descriptions permitted much more extensive data collection across a wider geographic range. To assess latitudinal gradients in fruit colours, we first classified fruit colour descriptions into the eight-category colour scheme (black/dark, blue, brown, red, green, yellow, orange and white/light) of Wheelwright and Janson (1985), which has been widely used in studies of fruit colour. Dark colours (e.g., dark red, dark brown, dark blue) were classified as 'black' and light colours (e.g., light yellow, light green) as 'white'. Fruits described as, for example, green-yellow, were lumped with 'green' fruits, while fruits described as, for example, greenish-yellow, were classified as 'yellow'. Pink and scarlet fruits fell into the 'red' category, while violet fruits were lumped with 'blue'. Finally, to assess variation in fruit colour diversity across latitude, we calculated Simpson's diversity index for each site, treating each colour category as 'species' and the number of species per colour category as 'abundance'.

We sought to validate our results using this qualitative colour scheme by comparing the qualitative variables to quantitative variables derived from fruit reflectance data. We gathered previously published data for hue, lightness and saturation (Cazetta et al., 2012) or calculated those variables from reflectance spectra (Regan et al., 1998, 2001; Valido et al., 2011) for 236 species by colour combinations (including some immature fruits and some fruits that display multiple colours when ripe). Spectra from Regan et al. (1998, 2001) were obtained from the Cambridge database of

natural spectra (<http://vision.psychol.cam.ac.uk/spectra/spectra.html>), which also included images for most species. We used those images to categorize fruit colours where possible, and otherwise extracted the qualitative colour category from our database. We calculated hue, lightness and saturation (HLS) according to Valido et al. (2011) and performed a linear discriminant (LD) analysis on the HLS variables. We then clustered the species on these LD axes with a Gaussian mixture model and compared our results using the traditional eight-colour classification scheme with the results of the clustering.

### 2.1.4 | Fruit length and plant habit

One hundred and twelve sites in our database reported fruit size, in most cases only fruit length; thus, our analyses are based on fruit length alone. We averaged the fruit lengths per species in cases where multiple sources described the same species. For plant habit, we classified all plant habit descriptions into four categories: herb, shrub, climber (including both lianas and vines) and tree using a similar methodology as for fruit colours. The 'climber' category included any plant described as climbing or scrambling. Descriptions with multiple categories, such as 'shrub or tree', were classified as the first category, except in cases where one category was clearly a modifier (e.g., 'shrubby tree' fell into the 'tree' category).

## 2.2 | Statistical analyses

We investigated correlations between fruit colour category and fruit length with ANOVA and post hoc Tukey's tests to identify differences between groups. Then, we tested whether latitude, fruit length and plant habit can differentiate between fruit colour categories using a multinomial logistic regression. A multinomial logistic regression is most appropriate because our response variable, fruit colour, consisted of eight or three unordered categories (see below). We chose green (for the eight-category models) and green-orange-brown-yellow (for the three-category models) as the reference levels because most fruits pass through a green stage when developing, and the frequency of green fruits across our dataset is roughly the median of all fruit colours.

Latitudinal patterns were assessed for both the eight-colour classification scheme and the three-colour classification scheme that resulted from the analysis of fruit reflectance data. Our dataset consists of some sites with data from woody plants only (typically tropical sites where only trees and shrubs were described) and some sites with both woody and herbaceous plants included. We repeated all latitudinal analyses with a subset of the data that included woody species only, and all results were qualitatively similar (see Supporting Information Figure S1). We therefore report results from the full dataset only.

All statistical analyses were performed in R v. 3.2.0 (R Core Team, 2016), and code and trait data are available on DataDryad (<https://doi.org/10.5061/dryad.bh84vs3>).

### 3 | RESULTS

#### 3.1 | Fruit reflectance and colour categories

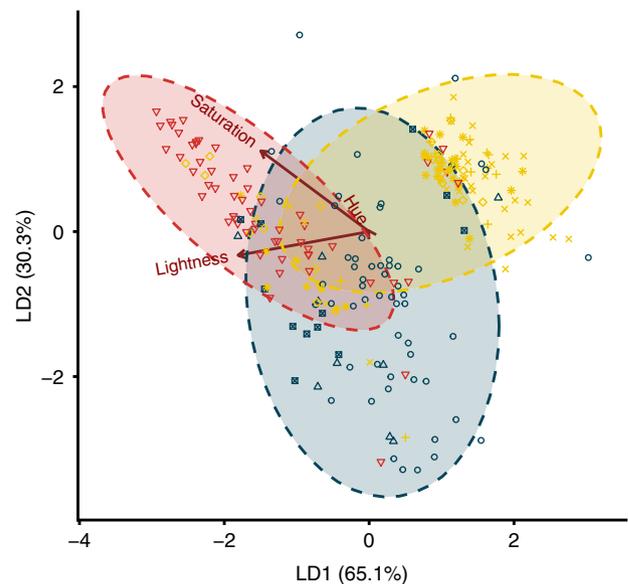
Clustering of fruit colours in LD space corresponded well with human colour categorizations. Gaussian mixture models revealed eight clusters, but three of those clusters contained mostly mammal-associated colours (green, yellow, brown and orange), two consisted largely of black, blue and white and two were almost entirely occupied by red-fruited species. As such, we collapsed these eight clusters down into three that correspond with green/yellow/brown/orange, black/blue/white and red. Although it may seem odd that black and white would cluster together, they in fact have similar spectral properties: they both have low saturation and differ primarily in the total amount of light reflected. Species were correctly classified into these categories 73, 78 and 81% of the time, respectively (Figure 2). As such, we reran our analyses using these three categories in addition to using the traditional eight-colour classification scheme.

#### 3.2 | Correlations between fruit colour, fruit length and plant habit

A one-way ANOVA revealed significant differences in fruit length between colour categories [ $F(7, 7,511) = 148.6; p < .0001$ ; Figure 3]. Tukey's post hoc honestly significant difference (HSD) test showed that the mean length of fruits with bird-associated colours ( $\bar{x}_{\text{black}} = 10.4$  mm,  $\bar{x}_{\text{blue}} = 9.1$  mm,  $\bar{x}_{\text{white}} = 10.9$  mm,  $\bar{x}_{\text{red}} = 11.8$  mm) were smaller than those with mammal-associated colours ( $p < .05$ ;  $\bar{x}_{\text{orange}} = 16.9$  mm,  $\bar{x}_{\text{yellow}} = 20.8$  mm,  $\bar{x}_{\text{brown}} = 21.8$  mm,  $\bar{x}_{\text{green}} = 22.7$  mm). Within the bird category, blue fruits were smaller than white and red ( $p < .05$ ) but not black ( $p > .05$ ), and white was not distinguishable from black or red ( $p > .05$ ) although red was larger than black ( $p < .05$ ). Among mammal-associated colours, orange was statistically different from the remaining colours ( $p < .05$ ).

#### 3.3 | Latitudinal patterns in fruit traits

We find strong, global latitudinal gradients in most fruit colours (Table 1; Figure 4). When modelled with latitude as the sole predictor, red increases dramatically from 17% of fruits at  $0^\circ$  to 54% of fruits at  $65^\circ$ , and black shows a similar but weaker pattern (increasing from 23% at  $0^\circ$  to 37% at  $65^\circ$ ). The mammal-associated colours show the opposite pattern, with increased frequency towards the tropics; the strongest patterns occur in yellow (constituting 20% of fruits at  $0^\circ$  and only 2% of fruits at  $65^\circ$ ) and orange (15% at  $0^\circ$  declining to 2% at  $65^\circ$ ). The bird-associated colours all show statistically different patterns than our reference level, green ( $p < .0001$ ), while the mammal-associated colours are not statistically different ( $p > .05$ , except in brown, where  $p < .0001$ ). Using the three-colour classification scheme (lumping black, blue and white, and also green, brown, yellow and orange), we find weaker patterns in black + blue + white (increasing from 31% at  $0^\circ$  to 39% at  $65^\circ$ ) than when we analyse those colours separately, but stronger patterns in the lumped green + brown + yellow + orange category (decreasing from 51% of fruits at  $0^\circ$  to 7% at  $65^\circ$ ).

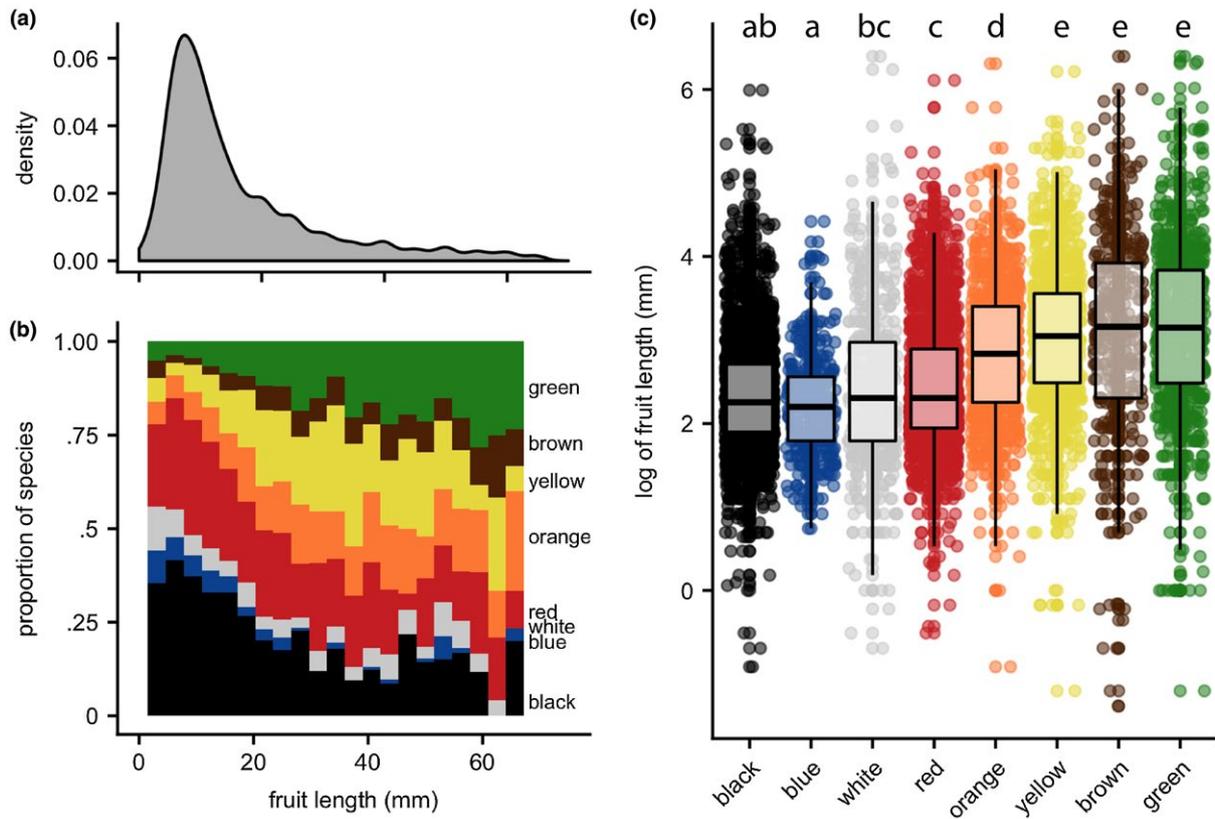


**FIGURE 2** Linear discriminant (LD) analysis of hue, saturation and lightness for 236 species by colour combinations. Using Gaussian mixture models, eight clusters were detected, but all of these eight corresponded with one of black/blue/white (BBW), green/orange/yellow/brown (GOBY), or red. We thus take three clusters as the best number and plot here the correspondence between the eight-category colour scheme (derived from verbal descriptions) and the three-category colour scheme (derived from clustering analyses of spectra). Point shape indicates the fruit colour category according to the eight-category colour scheme (○ = black, △ = blue, + = brown, × = green, ◇ = orange, ▽ = red, □ = white, \* = yellow). The ellipses indicate the 95% confidence interval around the three new, clustered categories. Fruits are correctly classified into the three-category scheme 78% of the time for black/blue/white, 73% for green/brown/orange/yellow and 81% for red [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

The best model for differentiating between fruit colours included all three predictor variables (latitude, fruit length and plant habit) as well as their interaction terms (Supporting Information Table S2). Although fruit colour was found to be an important predictor, fruit colour varied little between habit categories (Supporting Information Figure S2). Even when including fruit size and plant habit, latitude remains a significant predictor for black, blue, brown and red (and marginally yellow) in the eight-category colour scheme ( $p < .0001$ ), and for both black/blue/white (BBW) and red in the three-category colour scheme (Table 1).

Average fruit length varies across latitude ( $R^2 = .59, p < .0001$ ), such that the average length of fleshy fruits in tropical communities is more than twice as long as the average length of high latitude fruits (25.1 mm at  $0^\circ$ , vs. 9.1 mm at  $65^\circ$ ). Variance in fruit length was also higher in the tropics than at high latitudes ( $R^2 = .42, p < .0001$ ). This latitudinal gradient in length is found within all colour categories ( $p < .05$ ; marginally in blue,  $p = .08$ ; Supporting Information Figure S3).

Colour diversity increased towards the tropics (Figure 5;  $R^2 = .75, p < .001$ ), and this pattern was stronger in the Northern Hemisphere than the Southern Hemisphere ( $p < .001$ ).



**FIGURE 3** Fruit length correlates strongly with fruit colour. Fruits larger than 60 mm in length have been excluded due to very few fruits above this threshold (95% of fruits were  $\leq 60$  mm in length). (a) Density of fruit sizes (mean = 21.5 mm, median = 12.0 mm, max. = 600 mm). Most (69%) fruits are smaller than 20 mm in length. (b) Proportion of fruits of each colour category across fruit sizes. Smaller fruits tend to be black, blue, red or white, while large fruits and extremely small fruits tend to be brown, green, orange or yellow. (c) Brown, green, orange and yellow fruits are larger on average than black, blue, red and white fruits. Colour categories were statistically different according to a one-way ANOVA [ $F(7, 5,881) = 135.1; p < .0001$ ], and Tukey's post hoc honestly significant difference (HSD) test showed that fruits of all four bird-associated colours were statistically smaller than the mammal-associated colours ( $p < .05$ ), and that black, blue and white were statistically indistinguishable, as were yellow, brown and green. Statistically significant groups are indicated with letters (a-e) [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

## 4 | DISCUSSION

Despite considerable attention, the puzzle of the drivers of fruit colour diversity has persisted for decades. Underlying this discussion has been the assumption that colours primarily serve to attract animal seed dispersers, usually by targeting a specific disperser group. Because plant and seed-disperser interaction networks tend to be complex and diffuse (Wheelwright & Orrians, 1982), it is difficult in most cases to attribute different fruit colours to selection by a single dispersal agent or even particular guilds of dispersers. Alternative roles for pigments in fruits, such as protection against fungal pathogens and UV radiation, have also been proposed and variously supported (Cipollini & Levey, 1997; Schaefer, 2011; Schaefer & Braun, 2009; Willson & Whelan, 1990). In order to better elucidate the global landscape of fruit colour variation, we here describe global-scale spatial patterns in fruit traits for the first time. Red-fruited species are much more common at high latitudes, while the classic mammal-associated fruit colours (green,

yellow, brown and orange) are much more common in the tropics. Fruit length (both mean and variance) increases towards the tropics, as does fruit colour diversity. In all, these patterns suggest a global pattern in which fruits tend to be more similar both in colour (mostly red) and size (small) at high latitudes, while tropical communities show a higher diversity of colours and fruit sizes. There is a strong correlation between fruit length and fruit colour, which has frequently been noted (e.g., Janson, 1983; Link & Stevenson, 2004) but never quantified on a global scale. Despite the strong correlation between fruit length and fruit colour, latitude remains an important covariate, suggesting that understanding spatial patterns in fruit colours requires understanding the relationship between fruit colour and environmental variables that correlate with latitude.

The traditional explanation for fruit colour diversity, the DSH, is founded on differences in the visual abilities of seed dispersers. Fruit colours typically are classified into a 'bird syndrome' (small fruits with bright colours such as red, black or blue) or a 'mammal syndrome' (larger fruits with dull colours such as green, brown, yellow

**TABLE 1** Model results of multinomial logistic regression, where the full interaction model (using latitude, fruit length and plant habit as predictors) had the lowest Akaike's information criterion (AIC)

Colour category	$\beta$ -coef. of latitude (SE)	Predicted proportion (0°)	Predicted proportion (65°)	p-value of latitude
<i>Eight-category colour scheme</i>				
Green	n.a.	.102	.014	n.a.
Black	.120 (.018)	.228	.374	< .0001
Blue	.094 (.032)	.035	.008	.0034
Brown	.177 (.021)	.049	.020	< .0001
Orange	-.018 (.023)	.152	.020	.4416
Red	.129 (.018)	.173	.536	< .0001
White	.032 (.031)	.066	.010	.3065
Yellow	.039 (.020)	.195	.019	.0512
<i>Three-category colour scheme</i>				
GOBY	n.a.	.512	.072	n.a.
BBW	.029 (.005)	.314	.386	< .0001
Red	.028 (.005)	.174	.542	< .0001

Note. n.a. = not applicable. Each model is divided into both the eight-category traditional colour scheme and the three-category colour scheme derived from clustering of fruit reflectances (GOBY = green + orange + brown + yellow, BBW = black + blue + white). We report the predicted proportion of each fruit colour category at 0° latitude and 65° latitude in order to show the latitudinal variation in these colour categories.

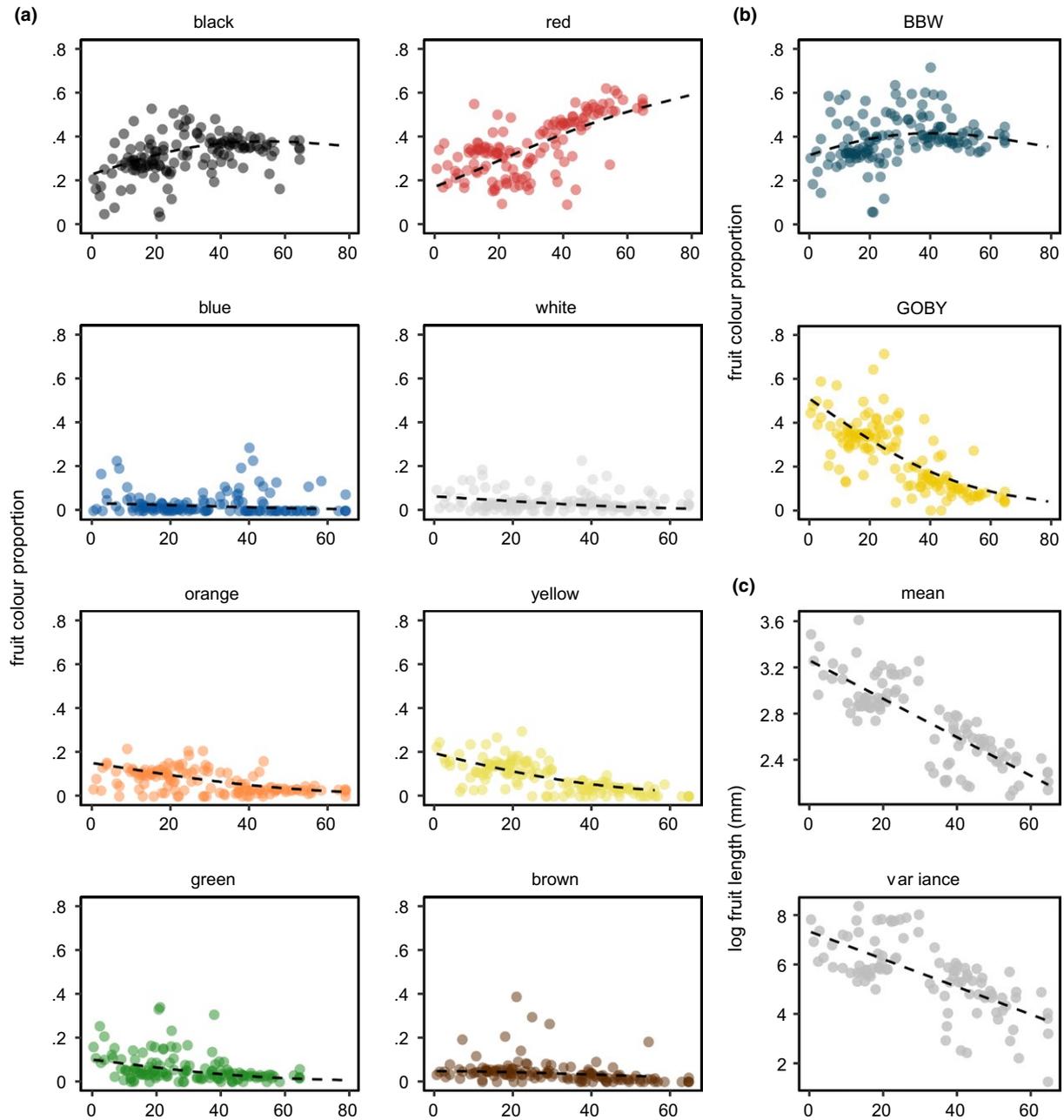
or orange) (van der Pijl, 1969). Our findings are broadly consistent with this hypothesis: bird-associated fruit colours tend to be smaller on average and are much more common at high latitudes (especially red), while mammal-associated fruit colours tend to be larger and are more frequent at low latitudes. Primates and frugivorous bats are both mostly restricted to the tropics and subtropics, and they provide the majority of seed dispersal services by mammals (Fleming, Breitwisch, & Whitesides, 1987). Mammalian dispersers tend to be larger than frugivorous birds (van der Pijl, 1969), so the presence of large-fruited species in the tropics corresponds with the presence of large-bodied seed dispersers. We also find greater colour diversity in the tropics, in contrast to recent work (Burns et al., 2009). Greater tropical diversity is also consistent with the DSH, as the greater diversity of frugivores may select for a larger variety of traits (Fleming et al., 1987; Stournaras et al., 2015). These broad patterns persist whether we use the eight-colour classification scheme of Wheelwright and Janson (1985) or the three-colour classification scheme derived here from the clustering of fruit reflectance data.

It is important to consider carefully the actual perceptual abilities of the relevant dispersers when addressing the question of whether these spatial patterns in fruit colours support the DSH. In Madagascar, the fruit colours partly match the expectations of the DSH and partly do not. Madagascar's disperser community consists largely of mammals, especially lemurs, rather than birds (Fleming et al., 1987; Razafindratsima, 2014; Voigt et al., 2004), and as a consequence the DSH predicts that Madagascar's flora should be dominated by mammal-associated colours. Our three Malagasy sites (Ranomafana, Kirindy and Ste. Luce) display considerable variation: Ranomafana has relatively few black-fruited species, but the remainder of its fruit colours are quite typical of its latitude. The prevalence

of red (rather than black) may be related to the fact that many lemurs are dichromatic and cannot differentiate red from green (Veilleux & Bolnick, 2009). In contrast, Kirindy displays a very unusual fruit colour distribution, with mostly green and brown fruits (c. 72% of fruits), which strongly supports the DSH. The differences between sites in Madagascar may reflect differences in the perceptual abilities of dispersers at each site, phylogenetic history of the plants present in each region, or differences in abundance of disperser species that our data are unable to capture.

As another example, New Zealand's disperser community mainly consists of birds, with a prevalence of lizard dispersers relative to most other locations (Whitaker, 1987). The enrichment of blue fruits in New Zealand has been attributed to lizard dispersal (Lord & Marshall, 2001; Lord, Markey, & Marshall, 2002). In our dataset, blue fruits are quite common in New Zealand, but also in eastern Australia, Papua New Guinea, Chiloé Island in Chile, and temperate and boreal North America. It thus appears that blue fruits in some places may correlate with certain types of dispersers, but in other regions may reflect selection by an entirely different set of factors. Overall, having a nuanced understanding of the dispersers in a particular area, as well as alternative selective forces, is essential to a deep understanding of the drivers of fruit colour diversity.

Despite the general congruence of our data with the DSH, questions remain. Perhaps most importantly, differing patterns *within* syndromes are difficult for the DSH to explain. Red fruits increase much more dramatically towards high latitudes than do black fruits, and yellow and orange show much stronger latitudinal gradients than do green and brown. In theory, differences between high and low latitude dispersers could account for some of these spatial patterns. Frugivorous birds at high latitudes are less diverse than in the

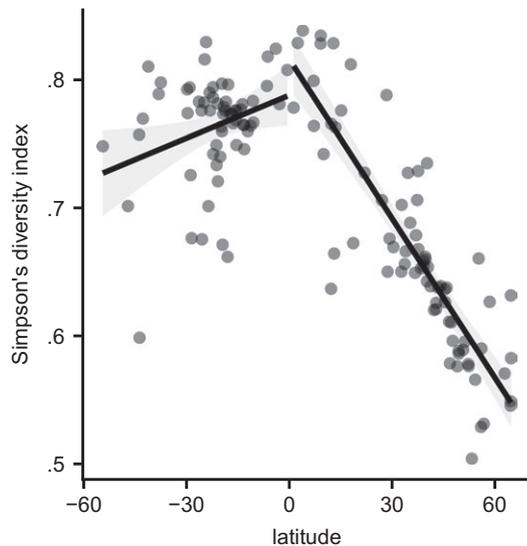


**FIGURE 4** Latitudinal gradients in: (a) fruit colours using the eight-colour classification scheme; (b) fruit colours in the two new lumped categories (GOBY = green + orange + brown + yellow; BBW = black + blue + white), with red the same as in the eight-colour scheme; and (c) mean and variance in fruit length. The lines represent multinomial regressions of the frequencies of each colour at each site as a function of latitude [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

tropics, and tend toward more general diets (Belmaker, Sekercioglu, & Jetz, 2012; Kissling, Böhning-Gaese, & Jetz, 2009). Consequently, they may preferentially consume fruits that are easy to find, for example, that contrast the most with background foliage (such as many red fruits; Cazetta, Schaefer, & Galetti, 2009; Schmidt et al., 2004).

At the same time, selection on fruit colours independent of dispersers may also influence the set of successful fruiting syndrome strategies. For example, short growing seasons at high latitudes could potentially constrain the set of possible fruit colours in a community. Many fruits start out green early in development and then progressively turn yellow, red and finally black. In areas

with shorter growing seasons, fruits may not have enough time to complete a lengthy developmental sequence, and may be selected to mature their seeds at a developmentally 'earlier' colour in their colour sequence. In this case, red fruits may have been derived through pedomorphosis (Box & Glover, 2010) as plants adapted to more seasonal high latitude habitats (Lo et al., 2011). Alternatively, the prevalence of black at low latitudes relative to red may indicate that high(er) pigmentation itself may be important in certain environments. As has been emphasized before, pigments provide protection against fungal pathogens and UV radiation (Cipollini & Levey, 1997; Schaefer et al., 2008; Willson & Whelan, 1990), and black fruits tend



**FIGURE 5** Simpson's diversity index shows that the tropics are more diverse in their fruit colours, especially relative to the high latitudes in the Northern Hemisphere ( $R^2 = .77$ ,  $p < .001$ ), and this pattern was stronger in the Northern Hemisphere than the Southern Hemisphere ( $p < .001$ )

to have greater concentrations of anthocyanin pigments than red fruits (Lancaster, Lister, Reay, & Triggs, 1997). Greater pigmentation may be advantageous in environments with more pathogens and UV radiation, such as in the tropics (and especially on tropical mountains; Beckmann et al., 2014).

Another factor that may influence fruit colour irrespective of putative dispersers is fruit size (measured here as fruit length). Colour and size are so interrelated in fruits that it is difficult to distinguish between selection on colour and size together (as might be predicted by the DSH) versus selection on fruit size alone with corresponding shifts in colouration. We find strong evidence that larger fruits tend to be green, yellow, brown and orange, and that fruits with these colours are typically larger than those with bird-associated colours. Fruits may be larger in the tropics than at high latitudes because dispersers in the tropics tend to be larger, but there are other possible explanations. For example, seeds tend to be larger in the tropics, possibly to enable the greater provisioning of embryos in low-light environments (Moles et al., 2007; Salisbury, 1942). Larger seeds necessitate larger fruits. Large fruits may incur greater metabolic costs in producing pigments to colour their larger surface area (Willson & Whelan, 1990), and, as a result, large-fruited plants may produce less concentrated pigments than their smaller fruited relatives. Mammals may not select for duller colours directly so much as for larger fruits, with duller coloration evolving as fruit size increases. Remaining green or dull-coloured also prolongs photosynthesis in fruit development, which might itself support fruit growth (Bazzaz, Carlson, & Harper, 1979; Cipollini & Levey, 1991). In any case, the correlation documented here between large fruit size and dull colours makes it difficult to precisely identify the selective force(s) driving the evolution of mammal-associated colours.

Latitudinal patterns in colour and size within disperser categories will also need to be explained, and we have offered several alternative hypotheses here that relate to particular fruit categories (paedomorphy, defence against UV, metabolic constraints in large fruits). But, as attention shifts to testing such hypotheses, it seems especially important to focus further attention on the relationship between the colours that humans commonly distinguish and the reflectance properties that may influence the functioning of fruits in nature. To this end, we analysed fruit reflectance data and tested for the number of clusters that emerge in those data. We recovered three clusters and these fell into two major groups: the mammal-associated colours (which we treated as a single category in our three-category scheme) and the bird-associated colours (which are arrayed along an axis between black and red; Figure 2). This provides support for the traditional notion that these two syndromes are in fact distinct and separable, and, even more generally, that at least some human-derived fruit colour categories do cluster into different regions of reflectance space. Similar findings have recently been reported using a very different methodology (Bergeron & Fuller, 2018), suggesting that, despite the potential problems with relying on human vision, broad patterns such as those identified here are based on real biological differences.

#### 4.1 | Hemispheric differences

The Northern and Southern Hemispheres differ in the diversity of fruit colours across latitude, with the Southern Hemisphere having higher colour diversity, similar to the tropics. The differing histories of the two hemispheres may help to explain the observed patterns in fruit colour diversity. Many of the major tropical clades with fleshy fruits (e.g., Rubiaceae, Myrtaceae, Solanaceae, Arecaceae) are better represented in southern temperate than in northern temperate floras (Dominy et al., 2003; Svenning, Borchsenius, & Bjorholm, 2008), and the greater tropical diversity of fruit colours may carry over to these southern temperate plants with tropical relatives. In the north, many fleshy fruits are found in clades that have radiated extensively in temperate areas, including maloid Rosaceae, vaccinioid Ericaceae, Dipsacales and Liliaceae, among others. There are some biogeographic connections between the temperate latitudes, and some mainly northern temperate fleshy-fruited lineages have moved south and are well represented in southern temperate areas (e.g., *Ribes*, *Ilex*; Manen, Barriera, Loizeau, & Naciri, 2010; Schultheis & Donoghue, 2004), while others exhibit amphitropical distributions (e.g., *Empetrum*; Popp, Mirr , & Brochmann, 2011). Such movements may have contributed to higher colour diversity, adding northern fruit colours to the southern temperate flora.

Geological factors differ between the hemispheres as well. Geographic connections around the Northern Hemisphere, in contrast to the widely separated continents of the Southern Hemisphere, have facilitated the spread of many fleshy-fruited clades throughout temperate Asia, Europe and North America (e.g., *Viburnum*, *Cornus*, *Prunus*, etc.; Chin, Shaw, Haberle, Wen, & Potter, 2014; Winkworth & Donoghue, 2005; Xiang, Thomas, Zhang, Manchester, & Murrell,

2006). This sharing of clades may help to explain the lower diversity of fruit colours in the Northern Hemisphere. Furthermore, as a consequence of extensive glaciation in some northern temperate areas, some high latitude plant communities in the Northern Hemisphere have been assembled *de novo* over the last 12,000 years (Kropf, Comes, & Kadereit, 2006; Svenning & Skov, 2007). Traits that facilitate plant dispersal, potentially including certain fruit colours, may therefore be enriched in northern temperate and boreal forests. Red fruits tend to be preferred by birds over other colours (Camargo et al., 2013; Duan, Goodale, & Quan, 2014; Schaefer & Schmidt, 2004; Schmidt et al., 2004), which might result in more rapid range expansion in red-fruited species.

## 4.2 | Evolutionary mechanisms

Evolutionary processes are integral to generating latitudinal gradients. Patterns in species richness reflect a combination of species origination, extinction and migration or range expansion (e.g., Jablonski et al., 1983; Wiens & Donoghue, 2004). Analogous processes may generate spatial patterns in traits as well. As an example, the correlation that we document here between red fruits and higher latitudes is some function of the following: (a) origination bias (e.g., red fruits may have evolved multiple times as lineages moved into to colder climates), (b) extinction bias (e.g., green and yellow fruits may have been selected against in colder climates), (c) migration bias (e.g., species with red fruits may have been better able to move into high latitudes) or (d) diversification bias (e.g., clades with red fruits radiated more extensively in colder climates). Regional floras around the Northern Hemisphere clearly document that red fruits are common in many successful and distantly related fleshy-fruited clades at higher latitudes in the north (e.g., Rosaceae, Dipsacales, Liliaceae). This implies that there have, indeed, been multiple origins of red fruits at higher latitudes. However, it is also the case that some of these northern red-fruited lineages have diversified rapidly, possibly for reasons unrelated to fruit colour (e.g., the *Succotinus* clade within *Viburnum*, Spriggs et al., 2015). In any case, studies need to be designed to test the relative importance of these evolutionary processes at various phylogenetic and spatial scales.

## 5 | CONCLUSIONS

For the first time, we report global-scale spatial patterns in the traits of fleshy fruits, in particular that red fruits are much more common at high latitudes, while yellow and orange are much more common in the tropics. Our results are broadly consistent with the DSH: mammal-associated fruit colours are more common in the tropics where mammalian dispersers are more common (although we did not directly test for an association between frugivore diversity and fruit colour distributions). However, much variation remains to be

explained, especially within the disperser categories, and the role of fruit size is clearly strong and poorly understood. The prevalence of red-fruited species at high latitudes is particularly striking. Plausible alternative hypotheses driving global patterns in fruit colour and size, relating to defence, development and metabolic costs, should be investigated, as well as the relative importance of the various evolutionary mechanisms that underlie these patterns.

## ACKNOWLEDGMENTS

We are grateful to Caroline Schlutius, Zoe Makoul, Ellie Handler and Eric Ringen for their assistance in data collection, and to Thomas Hovestadt for sharing his data with us. Beth Spriggs and two anonymous referees provided comments that greatly improved the manuscript, and we are indebted to Walter Jetz, Colin Chapman, Kim Valenta, Nicholas Sinnott-Armstrong and Caroline Pannell for their advice. We especially wish to thank Eugenia Lo for her early work on this problem in comparing fruit colours from several sites in eastern North America and Japan. This research was supported by National Science Foundation Graduate Research Fellowships to M. Sinnott-Armstrong (DGE-1122492) and S. Federman (DGE-1122492). A. Valido and P. Jordano were supported by the Ministerio de Economía y Competitividad (CGL2013-47429-P) and a Severo Ochoa Excellence Award (SEV-2012-0262) and A. Valido was additionally supported by a Ramón y Cajal research program (RYC-2007-00620).

## DATA ACCESSIBILITY

All fruit trait data, locality information, as well as GIS polygons and analysis code, are publicly available on DataDryad: <https://doi.org/10.5061/dryad.bh84vs3>.

## ORCID

Miranda A. Sinnott-Armstrong  <http://orcid.org/0000-0002-1806-565X>

## REFERENCES

- Armesto, J. J., Rozzi, R., Miranda, P., & Sabag, C. (1987). Plant/frugivore interactions in South American temperate forests. *Revista Chilena De Historia Natural*, 60, 321–336.
- Bazzaz, F. A., Carlson, R. W., & Harper, J. L. (1979). Contribution to reproductive effort by photosynthesis of flowers and fruits. *Nature*, 279, 554–555. <https://doi.org/10.1038/279554a0>
- Beckmann, M., Václavík, T., Manceur, A. M., Šprtová, L., von Wehrden, H., Welk, E., & Cord, A. F. (2014). gIUV: A global UV-B radiation data set for macroecological studies. *Methods in Ecology and Evolution*, 5, 372–383. <https://doi.org/10.1111/2041-210X.12168>
- Bello, C., Galetti, M., Montan, D., Pizo, M. A., Mariguela, T. C., Culot, L., ... Jordano, P. (2017). Atlantic-frugivory: A plant-frugivore interaction dataset for the Atlantic forest. *Ecology*, 98, 1–49. <https://doi.org/10.1002/ecy.1818>

- Belmaker, J., Sekercioglu, C. H., & Jetz, W. (2012). Global patterns of specialization and coexistence in bird assemblages. *Journal of Biogeography*, *39*, 193–203. <https://doi.org/10.1111/j.1365-2699.2011.02591.x>
- Bergeron, Z. T., & Fuller, R. C. (2018). Using human vision to detect variation in avian coloration: How bad is it? *The American Naturalist*, *191*, 269–276.
- Box, M. S., & Glover, B. J. (2010). A plant developmentalist's guide to paedomorphosis: Reintroducing a classic concept to a new generation. *Trends in Plant Science*, *15*, 241–246. <https://doi.org/10.1016/j.tplants.2010.02.004>
- Brodie, J. F. (2017). Evolutionary cascades induced by large frugivores. *Proceedings of the National Academy of Sciences USA*, *114*, 11998–12002. <https://doi.org/10.1073/pnas.1710172114>
- Burns, K. C., Cazetta, E., Galetti, M., Valido, A., & Schaefer, H. M. (2009). Geographic patterns in fruit colour diversity: Do leaves constrain the colour of fleshy fruits? *Oecologia*, *159*, 337–343. <https://doi.org/10.1007/s00442-008-1227-3>
- 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. <https://doi.org/10.1111/j.1600-0706.2013.00328.x>
- Caro, T. (2005). The adaptive significance of coloration in mammals. *BioScience*, *55*, 125–136. [https://doi.org/10.1641/0006-3568\(2005\)055\[0125:TASOC\]2.0.CO;2](https://doi.org/10.1641/0006-3568(2005)055[0125:TASOC]2.0.CO;2)
- Cazetta, E., Galetti, M., Rezende, E. L., & Schaefer, H. M. (2012). On the reliability of visual communication in vertebrate-dispersed fruits. *Journal of Ecology*, *100*, 277–286. <https://doi.org/10.1111/j.1365-2745.2011.01901.x>
- Cazetta, E., Schaefer, H. M., & Galetti, M. (2009). Why are fruits colorful? The relative importance of achromatic and chromatic contrasts for detection by birds. *Evolutionary Ecology*, *23*, 233–244. <https://doi.org/10.1007/s10682-007-9217-1>
- Chen, D.-M., Collins, J. S., & Goldsmith, T. H. (1984). The ultraviolet receptor of bird retinas. *Science*, *225*, 337–340. <https://doi.org/10.1126/science.6740315>
- Chin, S. W., Shaw, J., Haberle, R., Wen, J., & Potter, D. (2014). Diversification of almonds, peaches, plums and cherries—Molecular systematics and biogeographic history of *Prunus* (Rosaceae). *Molecular Phylogenetics and Evolution*, *76*, 34–48. <https://doi.org/10.1016/j.ympev.2014.02.024>
- 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. <https://doi.org/10.1007/BF00317581>
- Cipollini, M. L., & Levey, D. J. (1997). Secondary metabolites of fleshy vertebrate-dispersed fruits: Adaptive hypotheses and implications for seed dispersal. *The American Naturalist*, *150*, 346–372. <https://doi.org/10.1086/286069>
- Darwin, C. (1872) *The origin of species by means of natural selection* (6th ed.). London: John Murray.
- 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. [https://doi.org/10.1016/S0047-2484\(02\)00167-7](https://doi.org/10.1016/S0047-2484(02)00167-7)
- Dressler, R. L. (1968). Observations on orchids and euglossine bees in Panama and Costa Rica. *Revista De Biología Tropical*, *15*, 143–183.
- Duan, Q., Goodale, E., & Quan, R. (2014). Bird fruit preferences match the frequency of fruit colours in tropical Asia. *Scientific Reports*, *4*, 5627. <https://doi.org/10.1038/srep05627>
- Endler, J. A. (1990). On the measurement and classification of color in studies of animal color patterns. *Biological Journal of the Linnean Society*, *41*, 315–352.
- Fadzly, N., & Burns, K. C. (2010). What weta want: Colour preferences of a frugivorous insect. *Arthropod-Plant Interactions*, *4*, 267–276. <https://doi.org/10.1007/s11829-010-9109-0>
- Fischer, K. E., & Chapman, C. A. (1993). Frugivores and fruit syndromes: Differences in patterns at the genus and species level. *Oikos*, *66*, 472–482. <https://doi.org/10.2307/3544942>
- Fleming, T. H., Breitwisch, R., & Whitesides, G. H. (1987). Patterns of tropical vertebrate frugivore diversity. *Annual Review of Ecology and Systematics*, *18*, 91–109. <https://doi.org/10.1146/annurev.es.18.110187.000515>
- Global Administrative Areas. (2012). *GADM database of global administrative areas*, version 2.0. <http://gadm.org/>. Accessed December 2017.
- Hill, G. E., & McGraw, K. J. (2006). *Bird coloration: function and evolution*. Cambridge, MA: Harvard University Press.
- Jablonski, D., Roy, K., & Valentine, J. W. (2006). Out of the tropics: evolutionary dynamics of the latitudinal diversity gradient. *Science*, *314*, 102–106.
- Janson, C. H. (1983). Adaptation of fruit morphology to dispersal agents in a Neotropical forest. *Science*, *219*, 187–189. <https://doi.org/10.1126/science.219.4581.187>
- Jordano, P. (1987). Patterns of mutualistic interactions in pollination and seed dispersal: Connectance, dependence asymmetries, and coevolution. *The American Naturalist*, *129*, 657–677. <https://doi.org/10.1086/284665>
- Karger, D. N., Conrad, O., Böhner, J., Kawohl, T., Kreft, H., Soria-Auza, R. W., ... Kessler, M. (2017). Data from: Climatologies at high resolution for the earth's land surface areas. Scientific Data. <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. <https://doi.org/10.1111/j.1466-8238.2008.00431.x>
- Kitamura, S., Yumoto, T., Poonswad, P., Chuailua, P., Plongmai, K., Maruhashi, T., & Noma, N. (2002). Interactions between fleshy fruits and frugivores in a tropical seasonal forest in Thailand. *Oecologia*, *133*, 559–572. <https://doi.org/10.1007/s00442-002-1073-7>
- Kropf, M., Comes, H. P., & Kadereit, J. W. (2006). Long-distance dispersal vs vicariance: The origin and genetic diversity of alpine plants in the Spanish Sierra Nevada. *New Phytologist*, *172*, 169–184. <https://doi.org/10.1111/j.1469-8137.2006.01795.x>
- Lancaster, J. E., Lister, C. E. E., Reay, P. F., & Triggs, C. M. (1997). Influence of pigment composition on skin color in a wide range of fruit and vegetables. *Journal of American Society of Horticultural Science*, *122*, 594–598.
- Link, A., & Stevenson, P. R. (2004). Fruit dispersal syndromes in animal disseminated plants at Tinigua National Park, Colombia. *Revista Chilena De Historia Natural*, *77*, 319–334. <https://doi.org/10.4067/S0716-078X2004000200010>
- Lo, E. Y. Y., Stournaras, K. E., Schaefer, H. M., Oliver, J., Edwards, E. J., Donoghue, M. J., ... Donoghue, M. J. (2011). *A possible global pattern in the distribution of fruit colors*. Contributed talk presented at the Evolution Conference in Norman, OK. June 17–21, 2011.
- Lord, J. M., Markey, A. S., & Marshall, J. (2002). Have frugivores influenced the evolution of fruit traits in New Zealand? In D. J. Levey, W. R. Silva, & M. Galetti (Eds.), *Seed dispersal and frugivory: ecology, evolution and conservation* (pp. 55–68). Wallingford, UK: CAB International.
- Lord, J. M., & Marshall, J. (2001). Correlations between growth form, habitat, and fruit colour in the New Zealand flora, with reference to frugivory by lizards. *New Zealand Journal of Botany*, *39*, 567–576. <https://doi.org/10.1080/0028825X.2001.9512760>
- Manen, J. F., Barrera, G., Loizeau, P. A., & Naciri, Y. (2010). The history of extant *Ilex* species (Aquifoliaceae): Evidence of hybridization within a Miocene radiation. *Molecular Phylogenetics and Evolution*, *57*, 961–977. <https://doi.org/10.1016/j.ympev.2010.09.006>
- Moles, A. T., Ackerly, D. D., Tweddle, J. C., Dickie, J. B., Smith, R., Leishman, M. R., ... Westoby, M. (2007). Global patterns in seed

- size. *Global Ecology and Biogeography*, 16, 109–116. <https://doi.org/10.1111/j.1466-8238.2006.00259.x>
- Nakanishi, H. (1996). Fruit color and fruit size of bird-disseminated plants in Japan. *Vegetatio*, 123, 207–218. <https://doi.org/10.1007/BF00118272>
- Park, D. S., & Davis, C. C. (2017). Implications and alternatives of assigning climate data to geographical centroids. *Journal of Biogeography*, 44, 2188–2198. <https://doi.org/10.1111/jbi.13029>
- Popp, M., Mirré, V., & Brochmann, C. (2011). A single Mid-Pleistocene long-distance dispersal by a bird can explain the extreme bipolar disjunction in crowberries (*Empetrum*). *Proceedings of the National Academy of Sciences USA*, 108, 6520–6525. <https://doi.org/10.1073/pnas.1012249108>
- Poulsen, J. R., Clark, C. J., Connor, E. F., & Smith, T. B. (2002). Differential resource use by primates and hornbills. *Ecology*, 83, 228–240.
- Powell, J. A., & Mackie, R. A. (1966). *Biological interrelationships of moths and Yucca whipplei (Lepidoptera: Gelechiidae, Blastobasidae, Prodoxidae)*. Berkeley, CA: University of California Publications in Entomology.
- R Core Team. (2016). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.
- Razafindratsima, O. H. (2014). Seed dispersal by vertebrates in Madagascar's forests: Review and future directions. *Madagascar Conservation and Development*, 9, 90–97. <https://doi.org/10.4314/mcd.v9i2.5>
- Regan, B. C., Julliot, C., Simmen, B., Viénot, F., Charles-Dominique, P., & Mollon, J. D. (1998). Frugivory and colour vision in *Alouatta seniculus*, a trichromatic platyrrhine monkey. *Vision Research*, 38, 3321–3327. [https://doi.org/10.1016/S0042-6989\(97\)00462-8](https://doi.org/10.1016/S0042-6989(97)00462-8)
- Regan, B. C., Julliot, C., Simmen, B., Vienot, F., Charles-Dominique, P., & Mollon, J. D. (2001). Fruits, foliage and the evolution of primate colour vision. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 356, 229–283. <https://doi.org/10.1098/rstb.2000.0773>
- Ridley, H. (1930). *The dispersal of plants throughout the world*. Kent, UK: Reeve and Ashford.
- Salisbury, E. J. (1942). *The reproductive capacity of plants. Studies in quantitative biology*. London, UK: G. Bell & Sons.
- Schaefer, H. M. (2011). Why fruits go to the dark side. *Acta Oecologica*, 37, 604–610. <https://doi.org/10.1016/j.actao.2011.04.008>
- Schaefer, H. M., & Braun, J. (2009). Reliable cues and signals of fruit quality are contingent on the habitat in black elder (*Sambucus nigra*). *Ecology*, 90, 1564–1573.
- Schaefer, H. M., Rentzsch, M., & Breuer, M. (2008). Anthocyanins reduce fungal growth in fruits. *Nature Product Communications*, 3, 1267–1272.
- Schaefer, H. M., & Ruxton, G. D. (2011). *Plant-animal communication*. New York, NY: Oxford University Press.
- Schaefer, H. M., & Schmidt, V. (2004). Detectability and content as opposing signal characteristics in fruits. *Proceedings of the Royal Society B: Biological Sciences*, 271 (Suppl. 5), S370–S373. <https://doi.org/10.1098/rsbl.2004.0191>
- Schmidt, V., Schaefer, H. M., & Winkler, H. (2004). Conspicuousness, not colour as foraging cue in plant-animal signalling. *Oikos*, 106, 551–557. <https://doi.org/10.1111/j.0030-1299.2004.12769.x>
- Schultheis, L. M., & Donoghue, M. J. (2004). Molecular phylogeny and biogeography of *Ribes* (Grossulariaceae), with an emphasis on gooseberries (subg. *Grossularia*). *Systematic Botany*, 29, 77–96.
- Spriggs, E. L., Clement, W. L., Sweeney, P. W., Madriñán, S., Edwards, E. J., & Donoghue, M. J. (2015). Temperate radiations and dying embers of a tropical past: The diversification of *Viburnum*. *New Phytologist*, 207, 340–354.
- 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. <https://doi.org/10.1007/s10682-015-9766-7>
- Svenning, J., Borchsenius, F., & Bjorholm, S. (2008). High tropical net diversification drives the new world latitudinal gradient in palm (Arecaceae) species richness. *Journal of Biogeography*, 35, 394–406. <https://doi.org/10.1111/j.1365-2699.2007.01841.x>
- Svenning, J.-C., & Skov, F. (2007). Ice age legacies in the geographical distribution of tree species richness in Europe. *Global Ecology and Biogeography*, 16, 234–245. <https://doi.org/10.1111/j.1466-8238.2006.00280.x>
- The Plant List. (2013). Version 1.1. Published on the Internet; <https://www.theplantlist.org/>. Accessed December 2017.
- Turček, F. J. (1963). Color preference in fruit- and seed-eating birds. *Proceedings XIII International Ornithological Congress*, 1, 285–292.
- UNEP-WCMC & IUCN. (2018). *Protected planet: The world database on protected areas*. <https://www.protectedplanet.net/>. Accessed December 2017.
- 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. <https://doi.org/10.1111/j.1420-9101.2010.02206.x>
- van der Pijl, L. (1969). *Principles of dispersal in higher plants*. Berlin, Germany: Springer.
- Veilleux, C. C., & Bolnick, D. A. (2009). Opsin gene polymorphism predicts trichromacy in a cathemeral lemur. *American Journal of Primatology*, 71, 86–90. <https://doi.org/10.1002/ajp.20621>
- Voigt, F. A., Bleher, B., Fietz, J., Ganzhorn, J. U., Schwab, D., & Böhning-Gaese, K. (2004). A comparison of morphological and chemical fruit traits between two sites with different frugivore assemblages. *Oecologia*, 141, 94–104. <https://doi.org/10.1007/s00442-004-1654-8>
- Wheelwright, N. T., Haber, W. A., Murray, K. G., Guindon, C., Rican, C., Montane, L., ... Rica, C. (1984). Tropical fruit-eating birds and their food plants: A survey of a Costa Rican lower montane forest. *Biotropica*, 16, 173–192.
- 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. <https://doi.org/10.1086/284453>
- Wheelwright, N. T., & Orians, G. H. (1982). Seed dispersal by animals: Contrasts with pollen dispersal, problems of terminology, and constraints on coevolution. *The American Naturalist*, 119, 402–413. <https://doi.org/10.1086/283918>
- Whittaker, A. H. (1987). The roles of lizards in New Zealand plant reproductive strategies. *New Zealand Journal of Botany*, 25, 315–328. <https://doi.org/10.1080/0028825X.1987.10410078>
- Whittaker, R. H. (1975). *Communities and ecosystems*. New York, NY: Macmillan Publishing Co., Inc.
- Wiens, J. J., & Donoghue, M. J. (2004). Historical biogeography, ecology and species richness. *Trends in Ecology and Evolution*, 19(12), 639–644.
- Willson, M. F. (1994). Fruit choices by captive American robins. *The Condor*, 96, 494–502. <https://doi.org/10.2307/1369331>
- 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. <https://doi.org/10.2307/2388704>
- Willson, M. F., & Whelan, C. J. (1990). The evolution of fruit color in fleshy-fruited plants. *The American Naturalist*, 136, 790–809. <https://doi.org/10.1086/285132>
- Winkworth, R. C., & Donoghue, M. J. (2005). *Viburnum* phylogeny based on combined molecular data: Implications for taxonomy and biogeography. *American Journal of Botany*, 92, 653–666. <https://doi.org/10.3732/ajb.92.4.653>

Xiang, Q.-Y.-J., Thomas, D. T., Zhang, W., Manchester, S. R., & Murrell, Z. (2006). Species level phylogeny of the genus *Cornus* (Cornaceae) based on molecular and morphological evidence—Implications for taxonomy and tertiary intercontinental migration. *Taxon*, 55, 9–30. <https://doi.org/10.2307/25065525>

#### BIOSKETCH

MIRANDA SINNOTT-ARMSTRONG is a Ph.D. candidate at Yale University. Her research examines plant-animal interactions, in particular describing large-scale spatial and evolutionary patterns driving variation in fruit color.

#### SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

**How to cite this article:** Sinnott-Armstrong MA, Downie AE, Federman S, Valido A, Jordano P, Donoghue MJ. Global geographic patterns in the colours and sizes of animal-dispersed fruits. *Global Ecol Biogeogr*. 2018;27:1339–1351. <https://doi.org/10.1111/geb.12801>