

Adaptive fruit colour variation along an elevational gradient in a colour-polymorphic plant

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Research Article

Keywords: Dispersal, Frugivore, Fruit colour, New Zealand, Plant-animal interactions, Polymorphism, Ultraviolet radiation

Posted Date: June 22nd, 2022

DOI: <https://doi.org/10.21203/rs.3.rs-1709462/v1>

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Abstract

Many plants produce colour polymorphic fruits. However, the processes responsible for the evolution and maintenance of fruit colour polymorphisms are poorly understood. We investigated the fruit colour polymorphism in *Gaultheria depressa* var. *novae-zealandiae* (Ericaceae), a predominantly bird-dispersed, alpine shrub from New Zealand, by testing whether colour morph frequencies vary geographically to maximise fruit-foliage colour contrasts. We also conducted a seed germination experiment to test whether fruit colour morphs vary in their susceptibility to UV damage. Results showed that 'red' fruits were more abundant at lower elevations, while 'white' fruits were predominant at higher elevations. Leaf colours shifted from 'green' in appearance at lower elevations to 'red' at higher elevations. Analyses of fruit-foliage colour contrasts showed that 'red' fruits were more conspicuous at lower elevations, and 'white' fruits being more conspicuous at higher elevations, which was consistent with the hypothesis that colour morph frequencies vary geographically to maximise their conspicuousness to dispersers. However, 'red' fruits were generally more conspicuous than 'white' fruits, regardless of elevation, indicating that the maintenance of the polymorphism could not be attributed to fruit-foliage colour contrasts alone. The seed germination experiment showed that 'white' fruits were more resistant to UV damage, suggesting the preponderance of 'white' fruited individuals in the landscape results from a greater degree of protection from UV damage. The fruit colour polymorphism in *Gaultheria depressa* var. *novae-zealandiae* therefore appears to be maintained by trade-offs between conspicuousness to dispersers and tolerance to UV damage, advocating a pluralistic approach to the problem in the future.

Introduction

Most animal dispersed plant species produce fruits that are monochromatic (see Schaefer et al. 2004; Schaefer and Ruxton 2011). However, a small but significant fraction of fleshy fruited plant species are colour polymorphic (Whitney 2005). Colour polymorphic species collectively produce several fruit colours, with individual plants producing just a single hue. Although fruit colour polymorphisms have been studied extensively (e.g. Gervais et al. 1999; Burns 2005; Bach & Kelly 2007; Amico et al. 2011; Bhatt et al. 2019; Chen et al. 2020; Sun et al. 2021), a thorough understanding of their origin and maintenance is still in its infancy (see Whitney & Stanton, 2004; Sinnott-Armstrong et al., 2021).

Different types of dispersers can select for different fruit hues (Willson and Whelan 1990; Lomáscolo et al. 2008; Cazzeta et al. 2009; Sinnott-Armstrong et al. 2018; 2020). For example, recent work has solidified links between frugivore behaviour and monomorphic fruit hues across broad spatial and taxonomic scales (Albrecht et al. 2018; Valenta et al. 2018). Mammal-dispersed fruits in the tropics are generally green, brown, orange, or yellow (Voigt et al. 2004), while bird-dispersed fruits are usually red or black (Duan et al. 2014). Differential attraction to different types of frugivores has frequently been hypothesised to explain fruit colour polymorphisms (Amico et al., 2011). However, evidence for this hypothesis is equivocal (see Whitney, 2005; Burns, 2015; Valenta & Nevo, 2020).

Abiotic drivers have also been hypothesised to explain fruit colour polymorphisms. For example, fruit colour morphs could result from habitat-specific adaptations to different soil types (Traveset and Willson, 1998) or edge effects (Bach and Kelly 2004). Fruit colour polymorphisms can also vary over broader, biogeographic gradients, suggesting they might be linked to broad-scale gradients in temperature and precipitation (Burns 2015; Valenta et al. 2018; Sinnott-Armstrong et al., 2020). Alternatively, ultraviolet radiation (UV) can damage seeds and seedlings (Valenta et al. 2020; Ozel et al. 2021) and is known to increase with elevation (Blumthaler et al. 1997; Ballaré et al. 2011). However, whether particular fruit hues can mediate ultraviolet damage to seeds and affect the maintenance of fruit colour polymorphisms has never been tested.

We investigated the fruit colour polymorphism in *Gaultheria depressa* var. *novae-zealandiae* (Ericaceae) on the South Island of New Zealand. We conducted field surveys, spectrographic analyses and seed germination experiments to test whether the fruit colour polymorphism might be maintained by a combination of biotic and abiotic mechanisms. We conducted field observations to determine whether the frequency of 'red' and 'white' fruited individuals vary along a steep elevation gradient. Next, we conducted spectrographic analyses to document changes in background leaf colours with elevation. These data were then analysed statistically to test whether the maintenance of the fruit colour polymorphism could be attributed by fruit-foliage colour contrasts. Lastly, we conducted a seed germination experiment to determine whether differences in UV tolerance between colour morphs could also contribute to the maintenance of the fruit colour polymorphism.

Methods

All field data were collected from March-April in 2019 in the St Arnaud Range, Nelson Lakes National Park, New Zealand (41°48'S, 172°49'E, Fig. 1). The St Arnaud Range lies at the northern end of a mountain range that stretches the length of the South Island (i.e. 'the Southern Alps') and experiences an average temperature of 7.9°C and average annual rainfall of 1518mm. The area is dominated by southern beech forest (Nothofagaceae), primarily *Fuscospora cliffortioides*, which gives way to subalpine shrubs and alpine herb fields at approximately 1400m (Simpson, 1978).

Gaultheria depressa var. *novae-zealandiae* (Ericaceae) is an endemic, low-growing shrub that grows from 700m to 1500m in elevation. It produces fruits that are consumed mainly by birds, and appear to be either 'red' or 'white' to human observers. Fruits of intermediate colour (i.e. 'orange') were not observed and all individuals produced either 'red' or 'white' fruits, never both.

To test for geographic variation in fruit colour frequencies, we located all plants growing within two meters of a narrow trail (the St Arnaud Range Track) between 1100m and 1450m and classified them as either 'red' or 'white'. Plants devoid of ripe fruits were excluded. We then conducted a simple linear model to determine whether fruit colour morph frequencies varied continuously across the elevation gradient. To calculate fruit colour frequencies, we first split our colour morph observations into 50m elevation categories (n = 8). We then calculated the frequency of 'white' fruits by dividing the total number of 'white'

fruited individuals by the sum total of both 'red' and 'white' fruit individuals within each elevational category. Then, we used fruit colour as the dependent variable and elevational category as a covariate. We also conducted a binomial test to determine whether one colour was more prevalent than the other across the entire gradient.

Next we conducted spectrographic analyses to test the hypothesis that fruit colour morph frequencies vary with elevation to maximise their conspicuousness to avian consumers. Across the gradient in elevation where reproductively active individuals were detected (1100m – 1500m), one fruit and leaf pair was removed from 20 randomly selected individuals of each colour morph, resulting in a maximum of 40 paired samples (20 'red' fruit-leaf pairs and 20 'white' fruit-leaf pairs).

Fruit and leaf reflectance spectra were then measured using a USB OceanOptics 2000 (Ocean Optics, Florida, USA) spectroradiometer and a Xenon Pulse X2 standardised light source (Ocean Optics, Florida, USA) following Fadzy et al. (2009). Reflectance was measured as the proportion of a white reflectance standard (Diffuse Reflectance Standard WS-1) with a fibreoptics probe set at an angle of 45° and analysed in the SpectraSuite software (Ocean Optics, Florida, USA).

To calculate fruit conspicuousness, fruit and leaf hues were quantified in avian tetrahedral colour space according to Goldsmith (1990) using the UVS visual system based on the Eurasian blue tit (*Cyanistes caeruleus*). Relative output values of each of the four avian cones (u, s, m and l) were calculated in MatLab (MatLab 2018) following Stoddard & Prum (2008) and transformed into three new variables representing their position in tetrahedral colour space following Endler and Mielke (2005). Finally, we calculated fruit conspicuousness as the Euclidean distance between the fruit and the background foliage in tetrahedral colour space (Burns et al. 2009).

To test whether elevational changes in fruit morph frequencies could be explained by changes in their conspicuousness to avian consumers, we conducted a second linear model. Fruit conspicuousness (Euclidian distances between fruits and leaf backgrounds in tetrahedral colour space) was used as a dependent variable. Elevation was included in the model as a covariate and fruit colour morph was included as a fixed factor with two levels (red and white).

Lastly, we conducted a glasshouse experiment to determine whether fruit hue protects seeds from UV damage. We collected two sets of five fruits each from ten, randomly selected individuals of each colour morph and exposed them to potentially damaging levels of UV radiation. The first set (n = 50) was treated with UV light with a compact UVB 10.0 26W light bulb (Reptile One, Australia) set at a distance of 15cm for 10 hours per day for five days. The second set (n = 50) was used as a control and expose to ambient levels of UV light for five days. After treatment, all the seeds were removed from the fruits and cleaned and subjected to cold stratification at a constant temperature of 4°C for two months in a domestic refrigerator following Moore and Bannister (2002). Five seeds from each fruit were then placed on moist sterile cotton pads in transparent plastic containers and kept in a glasshouse at 20 degrees Celsius (UV =

50 seeds, Control = 50 seeds). Seeds were checked for signs of germination once every five days for 60 days.

To test whether 'red' and 'white' fruits differed in their tolerance to UV damage, we conducted a third linear model. Total germination rate after 60 days (the fraction of seeds from each fruit that germinated) was used as the dependent variable. Fruit colour morph was included as a fixed factor with two levels ('red' and 'white'). Treatment was included as a second fixed factor with two levels (UV and control). All analyses were conducted using the standard linear model procedure in the R environment (R Core Team, 2018).

Results

Spectrographic analyses showed that 'red' and 'white' fruit morphs had markedly different reflectance properties (Fig. 1). The 'red' fruit colour morph absorbed greater total amounts of radiation than the 'white' morph, particularly at lower wavelengths (i.e. 300nm – 600nm). In contrast, the 'white' fruit colour morph reflected greater levels of electromagnetic radiation across a wider range of wavelengths, most notably in the ultra-violet spectrum (350nm – 400nm).

Leaf colours also varied across the elevation gradient (Fig. 1). The leaves at low elevations (1100m – 1200m) showed a peak in reflectance at 550nm, which is consistent with the absorption properties of chlorophyll a and b, making them appear 'green'. On the other hand, leaves at high elevations (1200m – 1300m) had a more uniform reflectance curve, making them appear 'reddish-brown'.

We recorded a total of 154 'red' fruited individuals and 209 'white' fruited individuals across the elevation gradient, which differed from a 50–50 ratio ($p = 0.002$). Forty-one individuals without ripe fruits were encountered and subsequently excluded from study. The linear model evaluating changes in fruit colour morph frequencies with elevation showed that the fraction of 'white' fruited individuals increased linearly with elevation (Fig. 2, $F = 28.27$, $p = 0.002$), while the fraction of 'red' fruited individuals in each elevation category declined.

Results from the second linear model were consistent with the hypothesis that fruit colour morph frequencies vary with elevation to maximise their conspicuousness relative to changes in leaf backgrounds. Spectral contrasts between each fruit colour morph and their leaf backgrounds varied with elevation ($F = 40.68$, $p < 0.001$). However, a significant interaction was observed between elevation and fruit colour ($F = 7.39$, $p = 0.010$), indicating that the conspicuousness of 'red' fruits decreased with elevation, while the conspicuousness of 'white' fruits increased (Fig. 3). A significant effect of fruit colour on conspicuousness was also observed ($F = 153.13$, $p < 0.001$), indicating that the 'red' morph was consistently more conspicuous than the 'white' morph across the gradient. Therefore, although changes in fruit conspicuousness can potentially explain elevational changes in the frequency of 'red' and 'white' fruit morphs, it cannot explain the persistence of the 'white' morph in the landscape, given they are consistently less conspicuous.

Results from the seed germination experiment showed that seeds within the 'white' fruits were better predicted from UV radiation than 'red' fruits (Fig. 4, Fig S1). The third linear model revealed a significant effect of colour morph on seed germination rates ($F = 71.88$, $p < 0.001$), with white fruits having higher overall levels of germination than the 'red' morph. A significant effect of UV treatment on seed germination ($F = 22.74$, $p < 0.016$) was also observed, indicating UV radiation decreased overall seed germination rates. However, a significant interaction between colour morph and UV treatment on germination success was observed as well ($F = 9.02$, $p = 0.005$), indicating UV radiation had a stronger effect on the successful germination of seeds in 'red' fruits.

Discussion

Field observations showed a clear gradient in the distribution of fruit colour morphs with elevation. 'Red' fruited individuals were more abundant at low elevations, while 'white' fruited individuals were more prevalent at high elevations. The observed gradient in colour morph frequencies was consistent with elevational changes in fruit conspicuousness. Due to changes in the colour of leaf backgrounds, 'red' fruits declined in conspicuousness with elevation, while 'white' fruits increased. However, 'red' fruits were consistently more conspicuous than 'white' fruits, and 'white' fruits were generally more abundant across the landscape, indicating elevational gradients in fruit conspicuousness could not account for the maintenance of the polymorphism. Results from the seed germination experiment reconciled this discrepancy. It showed that seeds in 'white' fruits, which reflected UV radiation, were less vulnerable to UV damage than seeds in 'red' fruits. Overall results from our study therefore suggest that a combination of biotic factors (fruit conspicuousness to avian dispersers) and abiotic factors (tolerance to UV damage) are jointly responsible for the maintenance of the fruit colour polymorphism in *Gaultheria depressa* var. *novae-zealandiae*.

Most previous work on the evolutionary ecology of fruit colour polymorphisms has investigated differential fruit choice by different types of dispersers. For example, Amico et al. (2011) found that the colour-polymorphic fruits of a South American mistletoe were consumed by two types of dispersers. In geographic locations where birds were the predominate frugivores, plant populations tended to produce 'yellow' fruits, which are attractive to avian consumers. On the other hand, in locations that were dominated by marsupial dispersers, fruits tended to be 'green' in colour, which better facilitate mammalian dispersal. However, examples like this are rare and most tests for a purely biotic explanation for fruit colour polymorphisms are equivocal (see Willson and Whelan 1990; Burns 2015).

In this study, clear geographic gradients in the conspicuousness of each colour morph were observed, with 'red' fruits being more conspicuous at lower elevations and 'white' fruits being more conspicuous at high elevations. However, the reflectance properties of each fruit colour morph were remarkably consistent and opposing geographic gradients in fruit conspicuousness were not generated by changes in fruit colour *per se*. Instead, they were generated by an elevational gradient in leaf colour. Changes in leaf colour with elevation is readily apparent to human observers; leaves at low elevation appear 'green', while leaves at higher elevation appear 'red', 'brown' or 'dark purple'. Changes in leaf colour likely result from the

synthesis of accessory pigments, most notably anthocyanins, which are known to protect plant tissues from radiation damage (Landi et al. 2015; Gould 2004) and enable them to survive under more demanding environmental conditions (Sinnott-Armstrong et al. 2021). Changes in leaf colour with elevation are not restricted to *G. depressa* var. *novae-zealandiae* and are readily observable in a wide variety of plants distributed at high elevations in the Southern Alps.

Spatial and temporal patterns in fruit-foliage colour contrasts have been observed previously (Caramgo et al. 2013). For example, in southern British Columbia, Canada 'red' fruits predominate in summer, while 'black' fruits are more abundant in autumn. Seasonal changes in fruit colours occur concomitantly with variation in the colour of background foliage, which changes from 'green' in summer to 'reddish-orange' in autumn (Burns and Dalen 2002). This temporal gradient in leaf colours, and the corresponding pattern in fruit colour variation, is conceptually similar to the spatial gradient in fruit colour frequencies observed here. When viewed jointly, these results suggest that fruit colours may often evolve as a by-product of selection for selection for foliage pigmentation to enhance physiological performance.

Many species in the genus *Gaultheria* are colour polymorphic and phylogenetic analyses have shown the fruit colours show biogeographic patterns that are consistent with bird dispersal (Lu et al. 2019; Fritsch et al. 2021). Birds are the predominant seeds dispersers across much of the globe and this study focused on birds as the primary seed dispersers of *G. depressa* var. *novae-zealandiae*. However, other frugivores are known to consume fleshy fruits in New Zealand, including some unusual seed dispersers such as reptiles (Wotton et al., 2016) and large orthopterans known as weta (Burns 2006; Duthie et al. 2006; King et al. 2011; Larsen and Burns 2012). Non-avian seed dispersers might disperse significant numbers of seeds across the elevation gradient. However, their potential affect the maintenance of the fruit colour polymorphism remains unknown.

Although results showed clear gradients in fruit conspicuousness, we did not investigate the relationship between fruit conspicuousness and their removal by birds. Previous work has documented clear relationships between conspicuousness and the behaviour of frugivores (Ordano et al. 2017). However, other fruit attributes, such as nutrient concentrations and secondary metabolites, can over-ride the importance fruit conspicuousness in determining the behaviour of frugivores (see Lim and Burns 2021).

Results suggest that frugivore mediated selection pressures play a key role in the maintenance of the fruit colour polymorphism in *G. depressa* var. *novae-zealandiae*. However, results also indicate that abiotic processes may be important. A growing body of evidence suggests that the colours of fleshy-fruits may help protect against harm from factors other than frugivore selection (Whitney and Stanton 2004). For example, detailed study of the fruit colour polymorphism in *Rubus spectabilis* (Rosaceae), a common shrub in western North America, found little evidence for frugivore-mediated selection (Traveset and Wilson 1998). However, particular colour morphs predominate in different precipitation and temperature regimes and may help protect fruits from desiccation damage (Burns 2015).

Ultraviolet radiation is well known to be harmful to plants (Wang et al. 2014). Furthermore, UV radiation increases with altitude across the globe (Blumthaler et al. 1997; Sommaruga 2011; Ballaré et al. 2011).

Spectrographic analyses showed that ‘red’ fruits absorb the majority of incoming photons between 300–400nm in wavelength. Conversely, ‘white’ fruits reflect UV wavelengths and glasshouse experiments indicate they are less prone to UV damage. Although UV reflectance in ‘white’ fruits may enhance their conspicuousness to frugivores such as birds, reptiles and insects, which possess visual systems that can detect UV wavelengths, results from this study indicate that UV reflectance might also protect seeds from damage.

Overall results from this study suggest that a combination of processes are responsible for the maintenance of the fruit colour polymorphism in *G. depressa* var. *novae-zealandiae*. Although the frequencies of each colour morph vary geographically in a way that enhances their conspicuousness to frugivores, ‘red’ fruits are consistently more conspicuous ‘white’ fruits. However, ‘white’ fruits reflect UV radiation and help protect seeds from damage. Combined with other recent work supporting a pluralistic explanation for the evolution of fruit colours (e.g. Valenta et al. 2018; Sinnott-Armstrong et al. 2021), results from this study suggest that fruit colour polymorphisms may often be maintained a combination of both ‘abiotic’ and ‘biotic’ selection pressures.

Declarations

Author contributions:

GL and KCB conceived the idea, designed the methods and wrote the manuscript together. GL collected and analysed the data.

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Figures

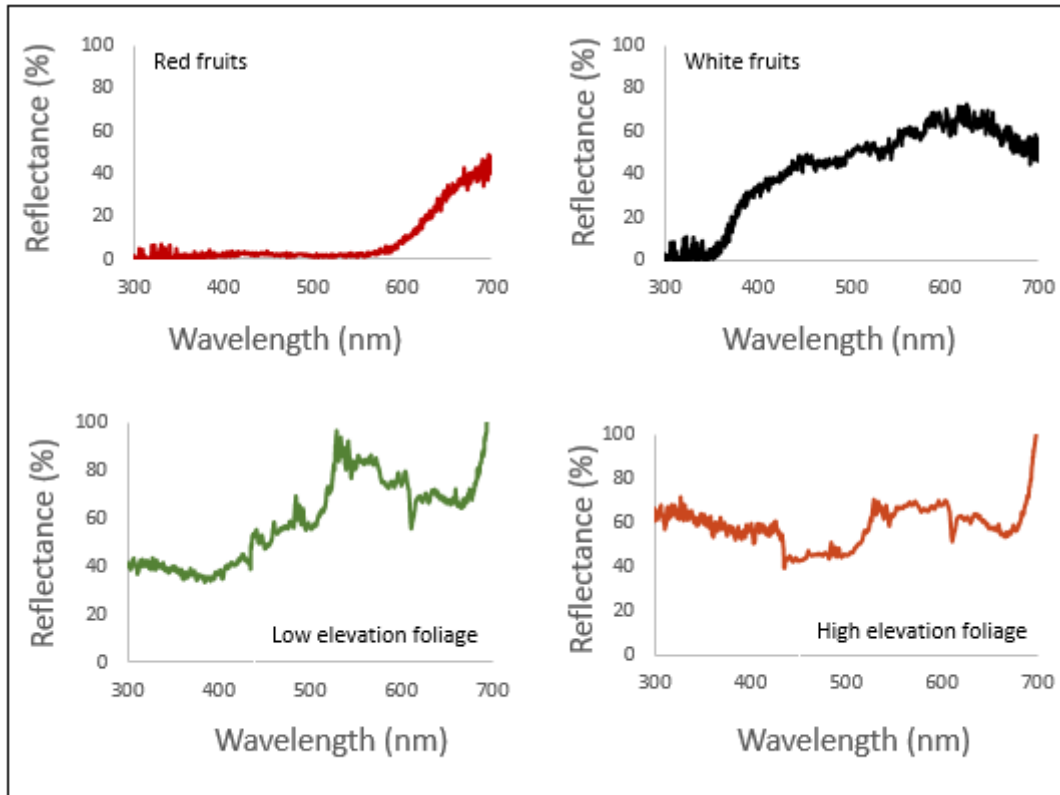


Figure 1

(top) Study site, Saint Arnaud Range, Nelson Lakes National Park, South Island New Zealand; (middle left) Average reflectance of 20 red fruits collected across the gradient; (middle right) Average reflectance of 20 white fruits; (bottom left) average reflectance properties at lower elevations (1100m – 1200m, n = 15); (bottom right) average reflectance properties at higher elevations (1200m – 1300m, n = 25).

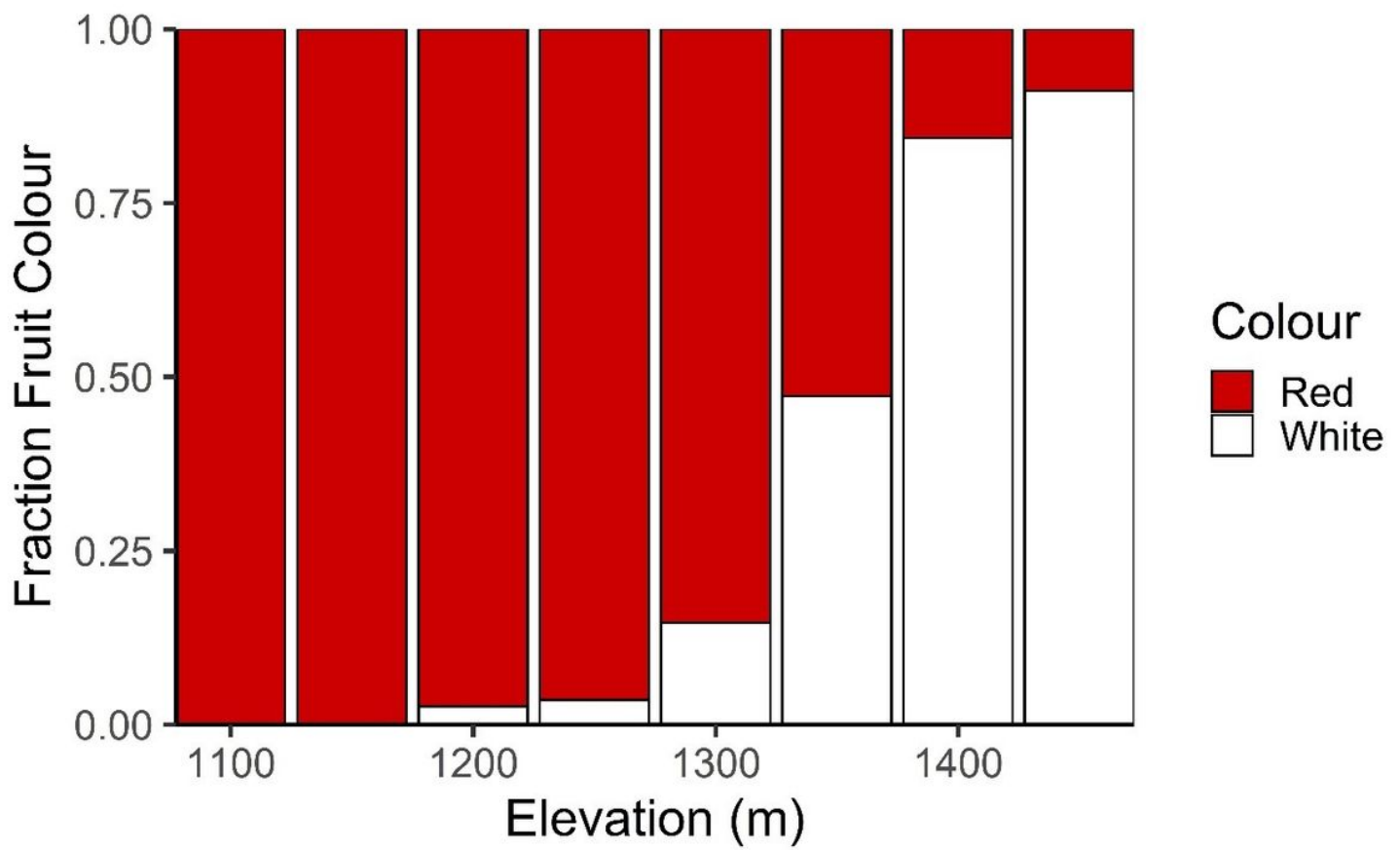


Figure 2

Relative frequencies of 'red' and 'white' fruit morphs across the gradient in elevation.

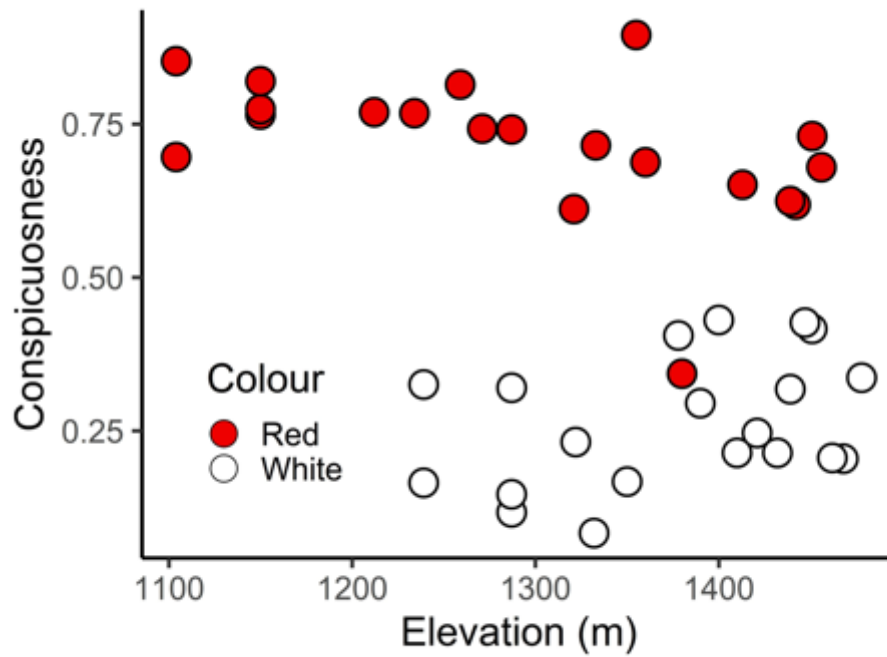


Figure 3

Patterns in fruit conspicuousness (i.e. spectral contrasts between fruits and their leaf backgrounds) along the elevation gradient.

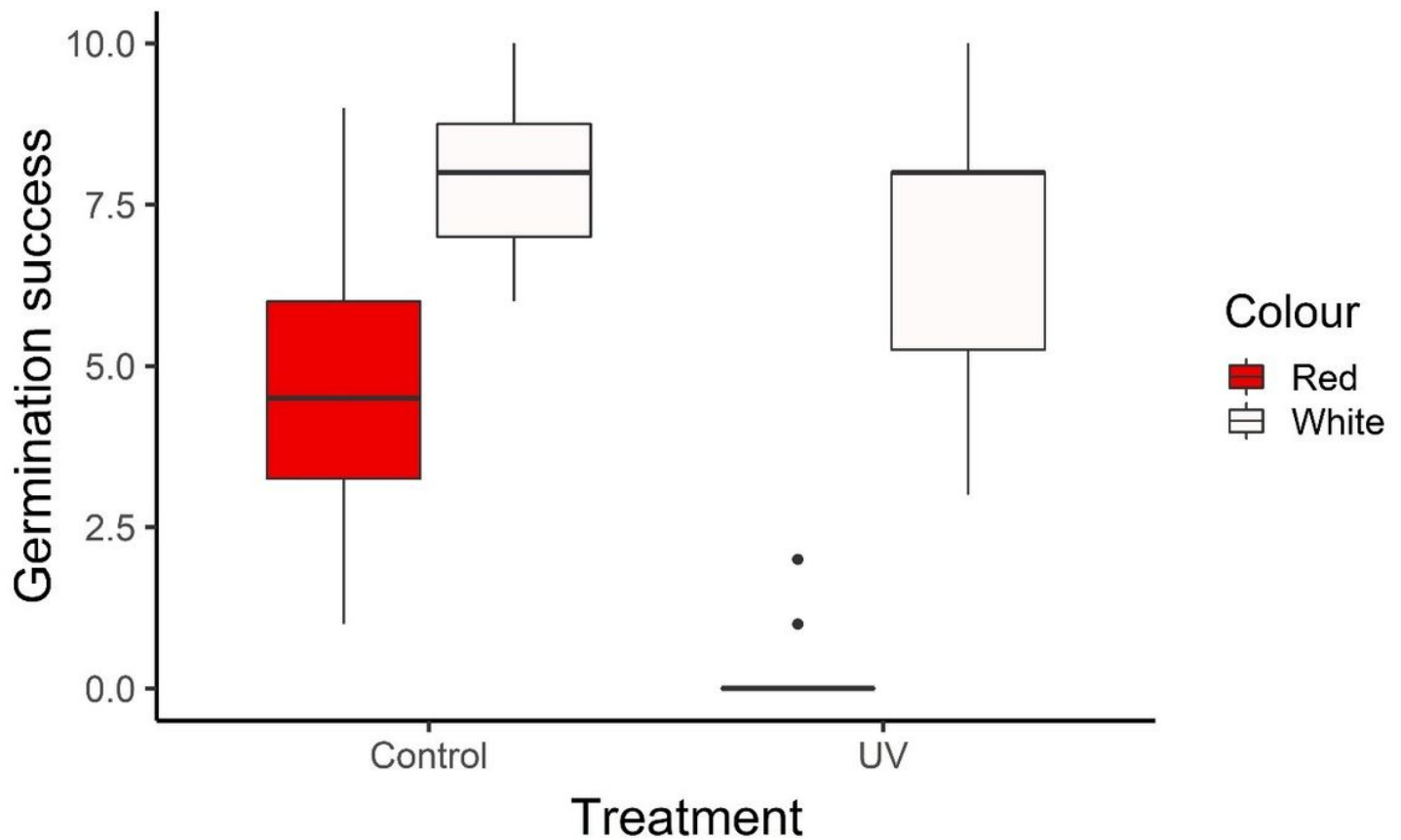


Figure 4

Results from a laboratory experiment investigating the effects of UV radiation on the germination rates of seeds within 'red' and 'white' fruits. Results showed that 'white' fruits had higher germination rates than 'red' under ambient UV conditions. However, when exposed to potentially hazardous UV levels, germination rates of seeds in 'red' fruits declined to zero, while germination in 'white' fruits were unchanged.

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