

Abiotic and biotic predictors of macroecological patterns in bird and butterfly coloration

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Abstract. Animal color phenotypes are invariably influenced by both their biotic community and the abiotic environments. A host of hypotheses have been proposed for how variables such as solar radiation, habitat shadiness, primary productivity, temperature, rainfall, and community diversity might affect animal color traits. However, while individual factors have been linked to coloration in specific contexts, little is known about which factors are most important across broad taxonomic and geographic scales. Using data collected from 570 species of birds and 424 species of butterflies from Australia, which inhabit an area spanning a latitudinal range of 35° and covering deserts, tropical and temperate forests, savannas, and heathlands, we test multiple hypotheses from the coloration literature and assess their relative importance. We show that bird and butterfly species exhibit more reflective and less saturated colors in better-lit environments, a pattern that is robust across an array of variables expected to influence the intensity or quality of ambient light in an environment. Both taxa display more diverse colors in regions with greater net primary production and longer growing seasons. Models that included variables related to energy inputs and resources in ecosystems have better explanatory power for bird and butterfly coloration overall than do models that included community diversity metrics. However, the diversity of the bird community in an environment was the single most powerful predictor of color pattern variation in both birds and butterflies. We observed strong similarities across taxa in the covariance between color and environmental factors, suggesting the presence of fundamental macroecological drivers of visual appearance across disparate taxa.

Key words: abiotic environment; bird; butterfly; color; community diversity; ecological gradients; traits.

INTRODUCTION

The evolution of animal color phenotypes is expected to achieve a balance across a range of often-competing demands, including attracting mates, deterring or intimidating rivals, evading and/or being successful predators, and regulating body temperature. This balance is intrinsically linked to abiotic features of scene and setting, such as the amount/spectral quality of habitat light, the visual background and the availability of critical nutrients. While the importance of these influences has been demonstrated (Grether et al. 1999, Heindl and Winkler 2003, Gomez and Théry 2004, Clusella Trullas et al.

2007, Hancox et al. 2013, Morales et al. 2017), most research into the evolution of coloration has either focused on one aspect of the abiotic or biotic environment, or on the trade-off between the effects of two selection pressures (Endler 1983, McNaught and Owens 2002, Smith et al. 2016a). What is lacking is the simultaneous consideration of the wealth of functions that biological coloration can serve.

The relative importance of the abiotic and biotic environment in shaping coloration remains unresolved over broad spatial and taxonomic scales. Millar et al. (2006) quantified the role of different predators, canopy shading, and stream conditions in affecting the color of male guppies, demonstrating that sympatric predator communities explained the most variation. Likewise, Smith et al. (2016a) determined that as thermoregulation and camouflage are competing functions of color change in a bearded dragon, the greater potential cost of failed

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camouflage means that there is more effect of background color in eliciting color change than temperature. In an analysis of rump coloration of an Australian robin species, Morales et al. (2017) determined that variation is most strongly influenced by population history and geography at a continental scale, but that their species' color trait is more influenced by local environmental conditions such as climate and visual environment at a regional scale. Hovanitz (1941) found consistent changes in colors of the Californian butterfly community across a number of broad environmental gradients, but resolving the relative importance of the multiple habitat variables included was beyond the reach of the qualitative data employed. A more integrative understanding of color evolution will require pluralistic approaches that simultaneously address the potential role of multiple abiotic and biotic factors at community scales. We provide the first large-scale quantitative attempt at doing so, by exploring the effect of multiple habitat variables on the coloration of resident birds and butterflies. The literature has identified a range of predictions concerning selection on coloration, which broadly fall into three main categories: energy and resources, habitat, and diversity, which are outlined in the following subsections (and in Table 1).

Energy and resources

Organisms require energy, not only to sustain short-term metabolic processes but for the development of phenotypes optimal for survival and/or reproduction

TABLE 1. Overview of hypotheses tested in our exploration of the drivers of bird and butterfly color across broad spatial scales.

Category and hypothesis
Energy and resources
1. Solar radiation will be negatively correlated with the saturation of bird and butterfly colors
2. There will be a positive correlation between temperature and the luminance of bird and butterfly colors
3. Rainfall will be negatively correlated with luminance of bird and butterfly colors
4. Species in higher NPP conditions and in areas with longer growing season length will have higher saturation and higher diversity of colors
Habitat
5. There will be a positive correlation between color luminance and both plant height and LAI.
6. LAI and saturation of colors will be positively correlated
7. Plant height and LAI will be positively correlated with color contrast and color diversity.
8. Cloud cover will be positively correlated with hue disparity
Community diversity
9. There will be positive correlations between community diversity and color diversity.

(Uetz et al. 2002). The production of some animal colors is known to be dependent on the acquisition of resources (McGraw 2003, 2006a, Hill 2006, Kemp 2008, Guindre-Parker and Love 2014). However, there has not been a spatially and taxonomically broad quantification of how energy budgets at the ecosystem scale affect color pattern variation in resident animals. We address this knowledge gap by investigating the importance of solar radiation, rainfall, net primary production, temperature, and growing season length to the coloration of many species of birds and butterflies across a broad geographic and ecological gradient.

The ultimate source of global energy (including light and heat) is the sun. Variation in the amount of radiant energy experienced over a geographic range is predicted to influence the color of resident animal species. Regions that experience higher solar radiation have greater amounts of ultraviolet (UV) light (International Agency for Research on Cancer 2012). Melanin-based coloration may offer protection against damaging UV radiation (Burt 1986, Jablonski and Chaplin 2000). Melanic pigments generally result in less chromatic markings, such as black, gray, brown, and earthy or rufous tones (McGraw 2006b). This predicts that low saturation colors would be more prevalent in habitats with higher overall solar radiation. Temperature also may be a crucial selection pressure on coloration in animals, not only for ectothermic groups such as butterflies and lizards (Guppy 1986, Clusella Trullas et al. 2007, Smith et al. 2016a) but also for endotherms, due to the reflection and absorption properties of skin, pelage, or plumage of different colors (Walsberg et al. 1978, Hochscheid et al. 2002, Geen and Johnston 2014). In some groups, darker color patches or schemes may have adverse effects by increasing the rate of solar absorption and hence contributing to heat stress (Hamilton and Heppner 1967, Hochscheid et al. 2002, Hetem et al. 2009, Smith et al. 2016a, b). In temperate ectotherms (such as many well-studied butterflies), however, darker markings are adaptive in allowing faster rates of warming or higher operational body temperatures (e.g., Kingsolver 1995). Very generally, both effects predict more reflective color schemes should be more likely in warmer climates. Whereas solar irradiation and ambient temperature would generally covary across a geographic range and/or habitats within that range, we include both in our analyses in order to disentangle the potential role of solar irradiance in affecting thermal vs. visual selection on coloration.

Diet, nutritional condition, and resource availability are well known to influence the ability to express both pigmentary and structural coloration (McGraw 2003, Hill 2006, Kemp 2008, Guindre-Parker and Love 2014). Net primary production (henceforth NPP) is a measure of the energy stored as plant biomass annually, and may indicate the abundance of crucial plant- or algal-based resources on which higher trophic levels depend. Growing season length, indicating the length of time during which growth and primary resource production accrue,

is also important for understanding resource dynamics and the rate at which ecological processes and biological activity can proceed (Huston and Wolverton 2009, Michaletz et al. 2014). Growing season length may be associated with color variation in Californian butterflies (Hovanitz 1941). In addition, areas with high NPP may have a greater diversity of light environments and visual background colors, which could favor a higher diversity of colors. Environments with greater NPP and longer growing seasons may provide better resource conditions for the expression of vibrant coloration.

We will explore the importance of rainfall to bird and butterfly coloration. Gloger's rule describes the phenomenon whereby animal species tend to be more heavily pigmented in more humid climates; that is, in wetter conditions species tend to have darker, less luminant colors. Support for Gloger's rule has been found in birds, mammals, and butterflies (Hovanitz 1941, Zink and Remsen 1986, Kamilar and Bradley 2011, Vanderwerf 2012, Zheng et al. 2014, Delhey 2017), as well as in plants (Koski and Ashman 2015). These results suggest that the amount of rainfall in a habitat is also a key aspect of resource availability that will affect the coloration of birds and butterflies, but the relative importance of rainfall remains unknown. There has long been debate about what drives the pattern observed as Gloger's rule. Hypothesized mechanisms include the change in the amount and nature of ambient UV and visual light when it rains, a prevalence of parasites in humid conditions, or camouflage against darkened visual background colors when a habitat is wet (Burt and Ichida 2004, Vanderwerf 2012). We will establish the correlations between coloration and precipitation itself, and the effects of ambient light and habitat conditions are considered separately using other variables.

We test four predictions on how energy and resources may affect the coloration of birds and butterflies, considering the effects of solar radiation, temperature, NPP, length of growing season, and rainfall:

1. *Solar radiation will be negatively correlated with the saturation of bird and butterfly colors.* Putative mechanism: greater amounts of UV light under increased solar radiation will select for the greater incidence of colors of low saturation that result from melanin pigments (Jablonski and Chaplin 2000, McGraw 2006b).
2. *There will be a positive correlation between temperature and the luminance of bird and butterfly colors.* Putative mechanism: under lower temperatures, darker, more absorptive coloration will aid thermoregulation by the absorption of radiant energy; under hotter conditions, highly reflective coloration should aid in reducing heat stress through reflection (Clusella Trullas et al. 2007, Geen and Johnston 2014, Smith et al. 2016b).
3. *Rainfall will be negatively correlated with luminance of bird and butterfly colors.* Putative mechanism: following Gloger's rule, animals should be more heavily pigmented in wetter conditions (Zink and Remsen 1986, Kamilar and Bradley 2011).
4. *Species in higher NPP conditions and in areas with longer growing season length will have higher saturation and higher diversity of colors.* Putative mechanism: greater resource availability may mean a wider variety of nutrients are available, and may provide better resource conditions for the expression of vibrant coloration (Grether et al. 1999, Hill 2006).

Habitat

The theory of sensory drive predicts that animal coloration will be shaped in part by habitat structure, because different ambient light conditions favor the use of different colors (Endler 1992, 1993, Marchetti 1993, Endler and Thery 1996, McNaught and Owens 2002, Gomez and Théry 2004, White and Kemp 2016). Properties of habitat including vertical arrangement, density of canopy or cloud cover may change the light environment directly by altering amount and color of ambient light (Hovanitz 1941, Endler 1993). For example, a tall forest with a thick closed canopy has an inherently different light conditions from other, more open, habitat types such as an open woodland or a grassland (Endler 1993). As signaling environments may impose selection or constraint on color signals, the predictions for visual signal design differ between habitats of different structure and light conditions (Endler 1992, 1993, Endler and Thery 1996, Zahavi and Zahavi 1997, Heindl and Winkler 2003, Gomez and Théry 2004, Hancox et al. 2013). The shady, low-light conditions in a forest may select for colors used in communication or attraction to be brighter (Zahavi and Zahavi 1997) or richer and more saturated in color (Endler 1993, Zahavi and Zahavi 1997). Shady or dense vegetation may also select for the use of a greater diversity of colors (Marchetti 1993) or the use of more contrasting colors that can enhance conspicuousness (Endler 1993). For example, although the greenish color of ambient illumination under a forest canopy would elevate the luminance of green signals, this would have little contrast against the green vegetation background. Displaying multiple, heavily saturated or strongly contrasting colors would increase conspicuousness (Endler 1993, Gomez and Théry 2007). The distance over which visual communication occurs alters predictions for color signal design (Zahavi and Zahavi 1997, Heindl and Winkler 2003) and structural complexity and vegetation layers in forests such as tree trunks, branches, and shrub layers can obscure long-distance visual communication. It is expected that species in more open habitat, environments with lower plant height and lower leaf area index (LAI), will display less within-pattern color contrast so as to not obscure shape and visibility or object detection over long distances (Zahavi and Zahavi 1997, Heindl and Winkler 2003).

The amount and quality of the light shining over a habitat is affected by cloud cover. Clouds act as light

diffusers, and may thus increase the light entering a habitat, change the color of light in an environment, and reduce heterogeneity of ambient light color between habitats (Endler 1992, 1993). As light environments of different habitats are more homogenized under cloudy skies (Endler 1993), and a diffuse, white-light environment does not favor any particular color combination, selection for habitat-tailored color signals may be reduced in regions with frequent cloud bank (Endler 1992, 1993); hence, the incidence of high cloud cover affects predictions for species' phenotypes.

We will test four predictions on how habitat may affect the coloration of birds and butterflies, considering the effects of plant height, LAI, and cloud cover.

5. *There will be a positive correlation between color luminance and both plant height and LAI.* Putative mechanism: an increase in plant height and leaf area index reduces light in an environment by creating shade, and darker habitats are expected to house species with more luminant visual signals (Marchetti 1993).
6. *LAI and saturation of colors will be positively correlated.* Putative mechanism: in shadier conditions, more heavily saturated colors are more conspicuous and more constant, and there may be greater use of saturated green for crypsis in environments with large leaf mass and green light (Endler 1992, 1993).
7. *Plant height and LAI will be positively correlated with color contrast and color diversity.* Putative mechanism: conspicuousness in short-distance communication in shaded forest habitats can be enhanced by increasing within-pattern color contrast (Heindl and Winkler 2003).
8. *Cloud cover will be positively correlated with hue disparity.* Putative mechanism: a diffuse, white-light environment does not favor any particular color combination, and so any selection for certain color combinations by the light environment of a habitat will be relaxed; thus, there will be an increase in differences between hues (i.e., an increase in color complementarity) under higher cloud cover (Endler 1993).

Community diversity

Coloration has been shown to be important in evolution and speciation (Iwasa and Pomiankowski 1995, Moller and Cuervo 1998, Albert et al. 2007, Anderson and Grether 2010), and is thus expected to be correlated with the diversity of a community. Essentially, high species diversity means more species are sympatric, and character displacement theory predicts that lineages with a higher degree of sympatry will experience accelerated rates of trait evolution involved in pre-mating barriers to gene flow (Coyne and Orr 2004). For instance, sympatry has been shown to have a direct role in the divergence and accelerated evolution of color pattern in high-latitude birds (Martin et al. 2010). The

prevalence of plumage ornamentation is correlated with lineage diversity (Moller and Cuervo 1998) due to sexual selection for diversified and distinct species signals, which is expected to drive divergence in coloration even in allopatric populations (Iwasa and Pomiankowski 1995). Additionally, sexual selection is likely to favor signals indicating a low parasite load and honest indicators of mate quality, and as such conditions of greater parasite diversity may drive the evolution of sexually enhanced ornamental colors and greater sexual ornamentation in resident species (Hamilton and Zuk 1982, Moller 1998).

Due to the importance of color in interspecific interactions, it is expected that diversity of other, ecologically important taxonomic groups will be correlated with coloration traits. Coloration is recognized as an important trait in predator avoidance. Under risk of predation from a diversity of predators with different tendencies (who may vary in frequency across space), prey species may become more cryptically colored, or there may be selection for startling aposematic warning coloration or seemingly conspicuous but visually disruptive coloration (Endler and Greenwood 1988, Mappes et al. 2005). Coloration of species in the presence of a greater diversity of predators (and/or more predator guilds) may therefore be significantly different from those in an environment of lower predation risk.

We will test one prediction on how diversity may affect the coloration of birds and butterflies.

9. *There will be positive correlations between community diversity and color diversity.* Putative mechanism: due to a need to identify themselves visually in interactions with closely related species and/or ecologically important interacting taxa, there will be higher diversity of colors on any one species (who may better identify themselves using increasingly complex color arrangements with more visually identifiable aspects; Coyne and Orr 2004, Martin et al. 2010, Maan and Sefc 2013).

Establishing the relative importance of variables at broad spatial scales

Here, we test predictions for how 11 variables related to energy and resources, habitat conditions, and community diversity affect the color of birds and butterflies (see Table 1). Of course, these factors are rarely likely to act in isolation. Therefore, we also determine the relative importance of the variables, and the total amount of variation in different color traits that can be explained by models that incorporate multiple variables simultaneously.

Dalrymple et al. (2015) showed that, contrary to popular belief, birds and butterflies are not more colorful in the tropics, and in fact species further away from the equator have a greater diversity of more saturated and contrasting colors. Here, we also extend that

work by asking whether the biotic and abiotic variables considered in the present study are sufficient to explain the latitudinal gradients in bird and butterfly color, or whether other, unmeasured factors may play an important role.

In summary, this paper seeks to establish the generality of a range of current predictions regarding the selection of color in animals by testing them on broad spatial and taxonomic scales, and to provide the first determination of the relative importance of multiple biotic and abiotic community variables in shaping the coloration of resident animal species.

APPROACH AND METHODOLOGY

We collated a database including a total of 812 species of birds and butterflies native to the eastern states of Australia (Dalrymple et al. 2015), spanning 34.5° of latitude from 9.25° S to 43.75° S, a geographic range that includes deserts, savannas, heathlands, temperate woodlands, and tropical rainforests. Colors of adult males of 570 species/subspecies of bird were measured by reflectance spectrometry of three specimens in the Australian National Wildlife Collection, CSIRO, Canberra, Australian Capital Territory, Australia. The Australian National Insect Collection was used to measure the colors of three adult males of 424 species/subspecies of butterfly using waveband-limited photography (Dalrymple et al. 2015). Both of these techniques allowed measurement of human visual and ultraviolet coloration. Hybrids, introduced species and rare vagrants were excluded. The full list of species can be found in Appendix S1; further details of sampling provided in Appendix S2, see Dalrymple et al. (2015) for complete details.

For each species, we calculated five visual-system-independent indices of coloration (that is, data are not adjusted for visual acuity or spectral sensitivity of any one organism), derived from summary values of 100-nm segments of the 300–700 nm spectral range (Endler 1990), adjusted as per the Michaelis-Menten equation (approximately log-normal; Endler and Mielke 2005). The relative reflectances in these four equal-length spectral bands were used to calculate our colorfulness indices, allowing us to undertake a visual system-independent appraisal based on the “segment analysis” technique (Endler 1990). We chose a non-sensory approach because color traits function in contexts other than signaling relevant to our hypotheses (e.g., thermoregulation), and are viewed by multiple different sensory systems simultaneously. The indices consisted of the (1) luminance and (2) saturation (or chroma) of all color patches, and (3) the diversity of colors, (4) average hue disparity, and (5) maximum contrast between colors displayed (as per Dalrymple et al. 2015). Luminance, or overall brightness, is calculated as the total sum of the reflectance values for the 300–700 nm spectral range. Color saturation is the richness or intensity of the color (as per Endler and Mielke 2005). Color diversity is the

diversity of colors displayed by a species; it is calculated as volume in tetrahedral space for each bird species, and as the count of dominant colors for each butterfly species. Average hue disparity indicates the mean difference between all patch hues on a species, independent of the saturation of the colors (hue is the “color,” e.g., yellow or red). Hue disparity is a measure of overall angular differences between two hues, with complementary colors being maximally disparate and having a value equal to π . Hue disparity can be understood in terms of color similarity or complementarity as $\frac{\text{hue disparity}}{\pi}$ places values on a proportional scale from 1, where colors are complementary, to 0, which indicates that colors are identical (Stoddard and Prum 2008). We calculated the average hue as the average disparity between hues of all patches on a species’ plumage. Maximum contrast is the greatest Euclidian distance achieved between patch colors on a species, and thus considered the greatest difference between patches both in terms of hue and saturation. Average hue disparity, maximum contrast, and the diversity of bird colors were calculated using TETRACOLORSPACE (Stoddard and Prum 2008).

Geographic range data for all species were derived from the Atlas of Living Australia database (ALA [*available online*]; as per Dalrymple et al. [2015]).⁸ All bird species included were represented by >10 spatially explicit, geo-referenced range records from the ALA. For the 38 butterfly species that had fewer than 10 spatial range records available, we produced presences in spatial grid cells following the geographic range data in Braby (2000). Range records for bird and butterfly subspecies were edited from full species occurrence records (following Schodde and Mason 1999, Braby 2000, Simpson and Day 2010) where necessary, and were checked for obvious errors using ArcGIS10.1 (ESRI, Redlands, California, USA). The color metrics for all species were mapped onto the species’ geographic ranges, and gridded into 0.5° latitude cells using Biodiverse (Laffan et al. 2010). The mean value of the color metrics for all of the species present in each grid cell was exported for analysis; that is, we produce the average trait value for the community in each of the grid cells for the analyses described here. In our analyses, we have excluded grid cells for which five or fewer butterfly sample species or five or fewer bird sample species were present.

We have three categories of explanatory variables that relate to predictions about the evolution and ecology of color: energy and resources, habitat, and diversity. For each category we have multiple variables, allowing us to explore the relative importance of different facets of each. We mapped all of the habitat variables into 0.5° latitude (~55.5 km) spatial grid cells in Biodiverse (Laffan et al. 2010), using the longitude and latitude of the data points. The mean value of the habitat variable in each grid cell was exported for analysis.

⁸ <http://www.ala.org.au>

Energy and resources

We included five indices that reflect energy and resources in the environment: solar radiation, net primary production (NPP), mean annual rainfall, length of growing season, and mean annual temperature.

Solar radiation data were extracted from the Bureau of Meteorology (BOM) “daily global solar exposure” model, which calculates downward irradiance (radiative fluxes) as well as cloud albedos hourly, and derives the daily insolation totals in megajoules per square meter (MJ/m^2 ; Australian Government Bureau of Meteorology [BOM] 2014b). From this data set, we calculated the average daily solar exposure experienced by each weather station for the period October 2003 until October 2013; referred to hereafter as “solar radiation.” We used station longitude and latitude to map the solar radiation experienced by the weather stations into the 0.5° latitude grid cells spatial grid cells (as described for species trait data).

Net primary production data were obtained from Haverd et al. (2013), which was modeled using remotely sensed vegetation cover and constrained by multiple observation data sets. We extracted point data of grams of carbon per square meter per day ($\text{g C}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$) at a 5.5-km grid (0.05°) resolution.

We calculated length of growing season in months using mean minimum temperature, mean temperature, and mean precipitation for each calendar month between 2003 and 2013, from a 0.5° resolution gridded data set (Harris et al. 2014). Using these data, we calculated the potential evapotranspiration for each of our grid cells using the Thornthwaite equation in the SPEI package in R (Beguería and Vicente-Serrano 2013). We also calculated a moisture index (MI), which is the ratio between rainfall and potential evapotranspiration (Kerckhoff et al. 2005). Using an MI above 0.05 and temperatures above 0°C (following Kerckhoff et al. 2005) we calculated the number of growing season months for every year between 2003 and 2013.

Temperature and rainfall data were derived for the years 2003–2013 from a 0.5° resolution gridded data set (Harris et al. 2014). Mean annual rainfall was calculated from averaging the sum of monthly mean rainfall data, and mean annual temperature was derived from averaging the sum of monthly mean temperature data over all years.

Habitat

We have included three indices of habitat structure and complexity: plant height, LAI, and cloud cover.

Plant height data were extracted from a global canopy height map (Simard et al. 2011), based on the 2005 LiDAR (light detection and ranging) data from the Geoscience Laser Altimeter System (GLAS) aboard ICESat (Ice, Cloud, and land Elevation Satellite). These data were extracted in meters (m) at a 5.5-km grid resolution

(0.05°) using ArcGIS 10.1 (ESRI) and gridded into the 0.5° latitude spatial grid cells.

Leaf area index is the amount of leaf area per ground area (m^2/m^2). Australia-wide eight-day composite LAI maps of 1-km resolution (Paget and King 2008) derived from the Moderate Resolution Imaging Spectroradiometer (MODIS) satellite by NASA LP DAAC, were obtained through AusCover (the remote sensing data products facility of the Terrestrial Ecosystem Research Network TERN, *available online*).⁹ All complete LAI maps for the years 2010, 2011, and 2012 were averaged in ArcGIS 10.1 (ESRI) and exported at 5 km resolution for mapping into the spatial grid cells.

Data for cloud cover were obtained from the Bureau of Meteorology, Australia (BOM). Cloud cover data consists of daily 09:00 visual estimations of the fractions of the dome of sky covered by cloud; it is measured in eighths or oktas, where clear sky is zero oktas and a completely overcast sky is 8 oktas. Using data from every weather station in the Australian states of Queensland, New South Wales, Victoria, Australian Capital Territory, and Tasmania, we averaged all daily readings from the period October 2003 until October 2013 for each individual station (Australian Government Bureau of Meteorology [BOM] 2014a), which was mapped into the grid cells using longitude and latitude of the weather stations.

Diversity

The community diversity of birds and butterflies was taken from the count of species in each grid cell as per the ALA database, as our sampling for these groups was near exhaustive of all species native to the study range (Appendix S1). We use species richness throughout as our measure of community diversity; while there are established diversity indices that account also for the relative abundance of species in the community, this data is not available for all of the bird and butterfly communities in the eastern states of Australia. The diversity (also species richness) of plants was derived from the Atlas of Living Australia (see footnote 8) geographic range records of all species in the Flora of Australia Online, for which there were >10 records (*available online*)¹⁰. This data set was mapped into 0.5° latitudinal spatial grid cells in Biodiverse (Laffan et al. 2010), and plant species richness per cell was derived.

Statistical analysis.—Analyses are performed on the data of each grid cell, derived from the averages of the trait values of all species present or the environmental variable data within. All multivariate regression analyses and the bivariate models testing hypotheses 1–9 were performed in a resampling-based inference framework using the mvabund package 3.12.3 (Wang et al. 2012,

⁹ <http://data.auscover.org.au>

¹⁰ <http://www.environment.gov.au/biodiversity/abrs/online-resources/flora/main/>

2017) in R 3.1.0 (R Core Team 2014). We have used this technique because (1) color data violate the assumptions of parametric statistics (Endler and Mielke 2005) and by using resampling-based inference methods that rely on random permutation of model residuals in order to relax the normality assumption of the linear model, we improve the precision of our outputs (Winkler et al. 2014) and (2) this resampling technique has the additional benefit of remaining robust to any spatial autocorrelation in the data set.

Sample sizes for tests vary as the availability of data for the explanatory variables differs. Data for rainfall, LAI, plant height, and butterfly and plant diversity were normalized using the \log_{10} transformation. The variance explained by simple linear models is taken from Hooper's R^2 statistic, a multivariate derivation from the average of all univariate R^2 values (Wang et al. 2017). For the multivariate multiple regression models we calculated the variance explained for individual predictors (analogous to partial R^2 values) in a model as $(\eta^2 \text{ statistic/number of response variables})/(\text{Hooper's } R^2)$. We investigated a principal component analysis (PCA) for condensing the dimensions of trait color trait variation across fewer response variables, however, this approach did not reduce our trait dimensions enough to justify the loss of clear interpretability in the results and was thus deemed inappropriate.

Given our focus on intraspecific variation, we considered the need to account for evolutionary history (i.e., the potential strength of a phylogenetic signal among color trait data). This was impeded for butterflies because a sufficiently resolved phylogeny does not presently exist for the Australian butterfly fauna, at least at

the species level. For birds, there was no evidence of a significant phylogenetic signal in our color traits (see Appendix S3 for full description and results). For these reasons, and the difficulty in applying phylogenetic methods to the summary community data used in our analyses, we refrained from incorporating phylogenetic analyses in the current paper.

We began by establishing the generality of current predictions (1–9 in *Introduction*) on the selection of coloration traits by environmental or community variables. To achieve this we ran simple bivariate linear models where the independent variable (x) was an environmental or community variable at a grid cell, and dependent variable (y) was the average value of one color trait for all species of birds or all species of butterflies in a grid cell (variables outlined in Fig. 1). We tested predictions (as outlined in the introduction) using the slopes and statistical significance of covariances among relevant variables. This approach allowed us to identify differences in the direction and strength of correlations between predictor variables and the coloration in each taxon and hence to assess whether predictions are supported across broad spatial and community scales.

Next, we conducted a multivariate multiple regression analysis to define the relative explanatory power of individual habitat variables. This model included all 10 response variables (all five color traits of both taxa), and all environmental variables as explanatory variables (see Fig. 1). We hereafter refer to this as the “full model”.

While the mvabund resampling methodology used has significant benefits over regular linear modeling that improve the precision and validity of our results (outlined above), collinearity of the environmental variables within

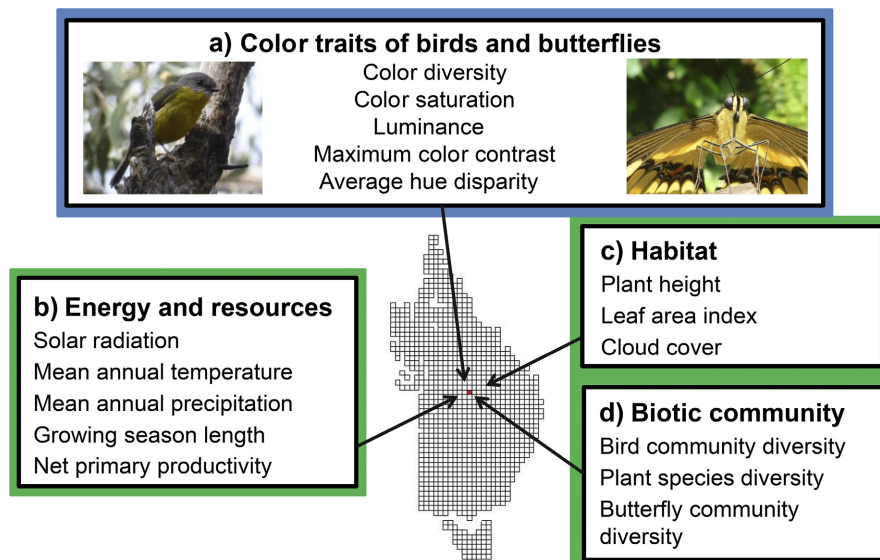


FIG. 1. Explanatory and response variables used in analyses. (a) The five color traits that were measured for birds and butterflies form the response variables (in the blue box). The explanatory variables (in green boxes) are grouped into three broad categories: (b) energy and resources, (c) habitat, and (d) diversity. The gridded map depicts the study range, the eastern states of Australia: Queensland, New South Wales, Australian Capital Territory, Victoria, and Tasmania.

models has the potential to skew results. In light of this, and in order to corroborate the importance of our environmental variables in determining the coloration of birds and butterflies, we performed a principal component analyses (PCA) outside of the mvabund framework. This PCA collapsed the environmental variables into fewer unrelated axes using the Kaiser-Guttman criterion (Legendre and Legendre 2012), and resulted in two PC axes as explanatory variables that explained 68% of the variation in environmental variables (see Fig S1 and Table S5–S6 Appendix S4: Section 2). PC Axis 1 showed a positive relationship between the amount of shading in the environment (LAI), plant height, and productivity (NPP). Rainfall, growing season length, plant diversity, and lepidopteran diversity marginally contributed to this PC axis. PC axis 2 showed a positive relationship between solar radiation and temperature. Bird diversity marginally contributed to this axis and was positively associated with temperature and solar radiation. We then ran two multiple regression analyses, one for PC axis 1 and one for PC axis 2.

Next, to establish if the five color traits are differently affected by habitat variables, we ran multivariate multiple regression models for each of the five types of color trait (brightness, saturation, color contrast, hue disparity, and color diversity). These models had the color trait of all taxa as the response variable (for example, the saturation of colors in birds and in butterflies), and all environmental variables as the explanatory variables. This allowed us to identify the importance of each variable in determining the variation in each color trait across both taxa, relative to other environmental and community variables. We compare the importance of each variable to the color trait across birds and butterflies using *P* values and variance explained. We also performed multiple regression analyses using PC axis 1 and PC axis 2 of our environmental variables for each of the five color traits.

Next, we wished to determine which category of variable best explains variation in bird and butterfly coloration on a broad scale. We constructed multivariate multiple regression models, each of which have all color traits of both animal groups as a multiple response variable, and the predictor variables from one category at a time (e.g., color ~ habitat, when habitat = plant height + LAI + cloud cover). Recognizing that the energy and resources category has five variables while the other categories have three, we have compared the total R^2 explained by the diversity and habitat categories to (1) a model with all five energy and resources variables, (2) a model with the three energy and resources variables that performed best in the full model, and (3) a

model with the three energy and resources variables with the least explanatory power in the full model.

We do not assess Akaike information criterion (AIC) values of the models because (1) the technique cannot be used for cases of multivariate response variables and (2) we are not concerned with comparing model adequacy as much as we are with identifying the importance of each variable.

Then, we sought to establish how much of the variation we could explain in each of the color traits in birds and butterflies using variables from all categories of variables. We used AIC values of bivariate linear regression models to identify the predictor variable from each category with the best fit for explaining variation in a color trait for each taxon separately. These three predictors (one from each category) were then used to build a linear model for the dependent variable; we refer to these models as “selected models.” As the goodness of fit of models needs to be compared across data sets of the same size with no missing values, these analyses were performed on a reduced subset of the data (256 grid cells, instead of the full set of 874 grid cells).

Finally, we wished to determine the extent to which latitude may still explain variation in the color traits after accounting for a variable from each category. This was achieved by running each of the selected models with an additional term for latitude. The change in explanatory power with and without this latitude term was assessed using a log-likelihood ratio test (with a significance level of $\alpha = 0.05$; Crawley 2013).

RESULTS

Energy and resources

Our first prediction was that solar radiation would be negatively correlated with the saturation of bird and butterfly colors. Our data support this prediction. Solar radiation was negatively correlated with color saturation in both birds ($P \leq 0.001$, $R^2 = 0.15$) and butterflies ($P \leq 0.001$, $R^2 = 0.28$; Fig. 2a, b, Table 2). On average, butterfly species that live in regions with solar radiation of 20 MJ/m² or greater (much of the area above the tropic of Capricorn) have colors that are 25.7% less chromatic (color-saturated) than do butterfly species in regions where solar radiation is 15 MJ/m² or less (much of Tasmania). The same gradient in solar radiation only relates to a 2.6% difference in bird color saturation.

The luminance of bird colors was positively correlated with temperature ($P \leq 0.001$; Fig. 2d), and negatively correlated with rainfall ($P \leq 0.001$; Fig. 2f). These

FIG. 2. Energy and resources in the environment are strongly related to the color of butterflies (left column) and birds (right column). Significant relationships are denoted with red regression lines. All predictions for how coloration would relate to energy and resources in the environment were supported by data for birds, but two butterfly color traits showed no correlation. There are a number of consistencies in how bird and butterfly colors relate to the environment, including that saturation is negatively correlated with solar radiation (a, b) and positively correlated with NPP (i, j), and the diversity of colors is higher in regions with longer growing season.

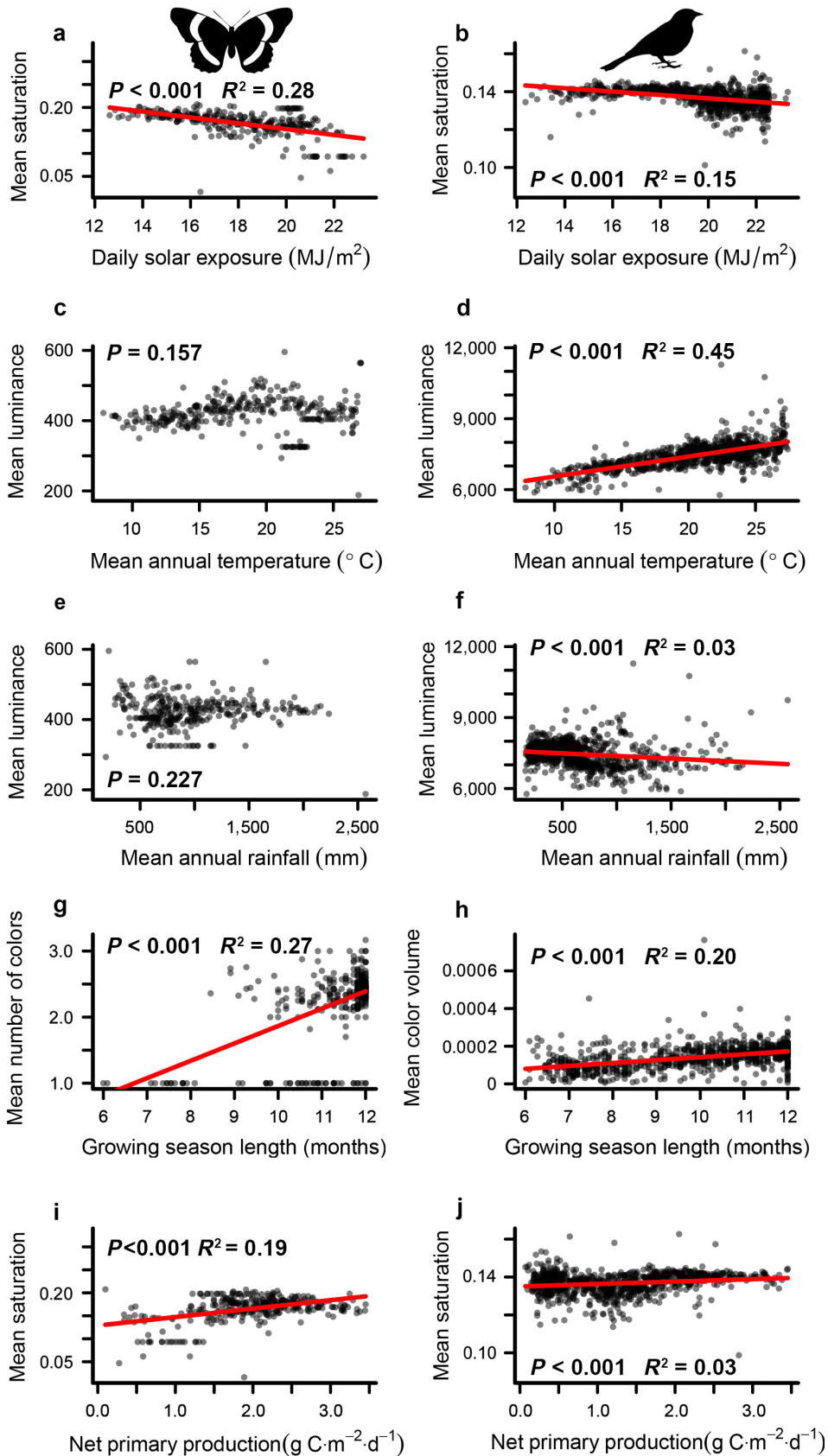


TABLE 2. Results of simple linear models of habitat variables vs. color traits.

Variable	Bird				Butterfly					
	Color diversity	Color saturation	Average hue disparity	Maximum contrast	Luminance	Color diversity	Color saturation	Average hue disparity	Maximum contrast	Luminance
Energy and resources										
Solar radiation										
<i>P</i>	≤0.001	≤0.001	0.026	≤0.001	≤0.001	≤0.001	≤0.001	≤0.001	≤0.001	<i>P</i> = 0.04
<i>R</i> ²	0.154	0.145	0.007	0.327	0.579	0.270	0.277	0.245	0.080	<i>R</i> ² = 0.015
Direction	—	—	—	—	+	—	—	+	—	+
Net primary production										
<i>P</i>	≤0.001	≤0.001	≤0.001	≤0.001	≤0.001	≤0.001	≤0.001	0.007	0.834	<i>P</i> = 0.674
<i>R</i> ²	0.098	0.031	0.017	0.145	0.193	0.177	0.188	0.029	0.002	<i>R</i> ² = 0.001
Direction	+	+	+	+	—	+	+	—	+	—
Growing season length										
<i>P</i>	≤0.001	≤0.001	≤0.001	≤0.001	≤0.001	≤0.001	≤0.001	0.077	0.028	<i>P</i> = 0.79
<i>R</i> ²	0.199	0.028	0.022	0.218	0.228	0.271	0.249	0.012	0.019	<i>R</i> ² = 0.001
Direction	+	+	+	+	—	+	+	—	+	—
Mean annual rainfall										
<i>P</i>	≤0.001	0.004	≤0.001	≤0.001	≤0.001	≤0.001	≤0.001	0.025	0.412	<i>P</i> = 0.227
<i>R</i> ²	0.033	0.010	0.049	0.047	0.032	0.032	0.056	0.018	0.002	<i>R</i> ² = 0.004
Direction	+	—	+	+	—	+	+	—	—	—
Mean annual temperature										
<i>P</i>	≤0.001	≤0.001	0.138	≤0.001	≤0.001	≤0.001	≤0.001	≤0.001	≤0.001	<i>P</i> = 0.157
<i>R</i> ²	0.175	0.111	0.003	0.261	0.449	0.188	0.146	0.136	0.054	<i>R</i> ² = 0.006
Direction	—	—	—	—	+	—	—	+	—	+
Habitat										
Plant height										
<i>P</i>	≤0.001	≤0.001	≤0.001	≤0.001	≤0.001	≤0.001	≤0.001	≤0.001	≤0.001	<i>P</i> = 0.079
<i>R</i> ²	0.088	0.098	0.015	0.217	0.395	0.206	0.265	0.201	0.064	<i>R</i> ² = 0.010
Direction	+	+	+	+	—	+	+	—	+	—
Leaf Area Index										
<i>P</i>	≤0.001	≤0.001	≤0.001	≤0.001	≤0.001	≤0.001	≤0.001	≤0.001	0.003	<i>P</i> = 0.084
<i>R</i> ²	0.132	0.023	0.041	0.198	0.262	0.253	0.285	0.197	0.036	<i>R</i> ² = 0.010
Direction	+	+	+	+	—	+	+	—	+	—
Cloud cover										
<i>P</i>	1	0.098	0.006	≤0.001	≤0.001	0.033	≤0.001	0.002	0.057	<i>P</i> ≤ 0.001
<i>R</i> ²	0.005	0.016	0.039	0.133	0.285	0.029	0.092	0.078	0.026	<i>R</i> ² = 0.154
Direction	+	+	+	+	—	+	+	—	+	—

TABLE 2. (Continued)

Variable	Bird					Butterfly				
	Color diversity	Color saturation	Average hue disparity	Maximum contrast	Luminance	Color diversity	Color saturation	Average hue disparity	Maximum contrast	Luminance
Diversity										
Bird diversity										
<i>P</i>	≤ 0.001	≤ 0.001	≤ 0.001	≤ 0.001	≤ 0.001	≤ 0.001	0.183	≤ 0.001	0.79	$P \leq 0.001$
<i>R</i> ²	0.120	0.204	0.013	0.206	0.175	0.171	0.006	0.053	0.001	$R^2 = 0.081$
Direction	+	+	-	+	-	+	+	+	+	+
Plant diversity										
<i>P</i>	≤ 0.001	≤ 0.001	0.025	≤ 0.001	≤ 0.001	≤ 0.001	≤ 0.001	0.551	0.09	$P = 0.077$
<i>R</i> ²	0.122	0.091	0.006	0.232	0.238	0.256	0.088	$R^2 > 0.001$	0.012	$R^2 = 0.009$
Direction	+	+	+	+	-	+	+	-	+	+
Butterfly diversity										
<i>P</i>	1	0.006	0.143	0.127	0.14	0.519	0.32	0.108	0.075	$P = 0.921$
<i>R</i> ²	0.008	0.031	0.008	0.009	0.009	0.002	0.004	0.009	0.012	$R^2 > 0.001$
Direction	-	+	-	+	-	+	+	-	+	-

Notes: Significance, variance explained, and direction of relationships are reported (*P*, *R*², and +/−, respectively). Number of replicates per test (*n*) can be found in Appendix S4; Table S1.

results support our second and third predictions, respectively. Temperature explained 44.9% of the variation in bird color luminance. Birds in regions that have a mean annual temperature of 25°C or more display colors that are on average 17.8% more luminant than those in regions where mean annual temperature is 15°C or less. Rainfall explained a small amount of the variation in bird color luminance (3.2%) across the study range and, in areas with more than 1,000 mm mean annual rainfall, bird colors are on average only 3.4% less luminant than those where mean annual rainfall is less than 500 mm. However, contrary to expectations, there was no effect of either mean annual rainfall ($P = 0.23$; Fig. 2e) or temperature ($P = 0.16$; Fig. 2c) on butterfly color luminance on a broad scale (Table 2).

Our fourth prediction was that there would be positive correlations between NPP and the length of growing season, and the saturation and diversity of colors displayed by birds and butterflies. Our data support this prediction. That is, color saturation of both animal groups is positively related to NPP (bird, $P \leq 0.001$, $R^2 = 0.03$; butterfly, $P \leq 0.001$, $R^2 = 0.19$) and to growing season length (bird, $P \leq 0.001$, $R^2 = 0.03$; butterfly, $P \leq 0.001$, $R^2 = 0.25$), and diversity of colors is also positively related to NPP (bird, $P \leq 0.001$, $R^2 = 0.10$; butterfly, $P \leq 0.001$, $R^2 = 0.18$) and growing season length in both groups (bird, $P \leq 0.001$, $R^2 = 0.20$; butterfly, $P \leq 0.001$, $R^2 = 0.27$; Fig. 2g–j). Butterflies and birds in regions that have NPP of $1 \text{ g C} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$ or less (much of the inland area of the study range, and where mean annual rainfall is less than 500 mm/yr) on average display fewer dominant colors than those where NPP is $3 \text{ g C} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$ or more (forests on the coastal fringes of New South Wales and Queensland; Table 2).

Habitat

Our fifth prediction, that color patch luminance would increase with LAI and plant height, was not supported by the data. Birds display duller (less reflective) color schemes when associated with taller overhead vegetation and under canopies with greater LAI ($P \leq 0.001$, $R^2 = 0.26$; plant height, $P \leq 0.001$, $R^2 = 0.40$; Fig. 3a). For example, bird communities of habitats with LAI of $2 \text{ m}^2/\text{m}^2$ or lower (generally savanna or temperate shrubland; Asner et al. 2003) exhibit colors that are 12.1% more luminant on average than species in regions with $6 \text{ m}^2/\text{m}^2$ or greater LAI (generally forests or wetlands; Asner et al. 2003; Table 2). Adding a quadratic term for LAI to the model for bird luminance improved the AIC value (see Appendix S4: Section 3). Butterflies show a marginally non-significant relationship, but the sign of covariance is opposite to the prediction (plant height, $P = 0.08$; Fig. 3b). That is, our findings do not generally support the prediction that shady habitats select for organisms with brighter colors.

The data support our sixth prediction. Leaf area index is positively correlated with average color patch

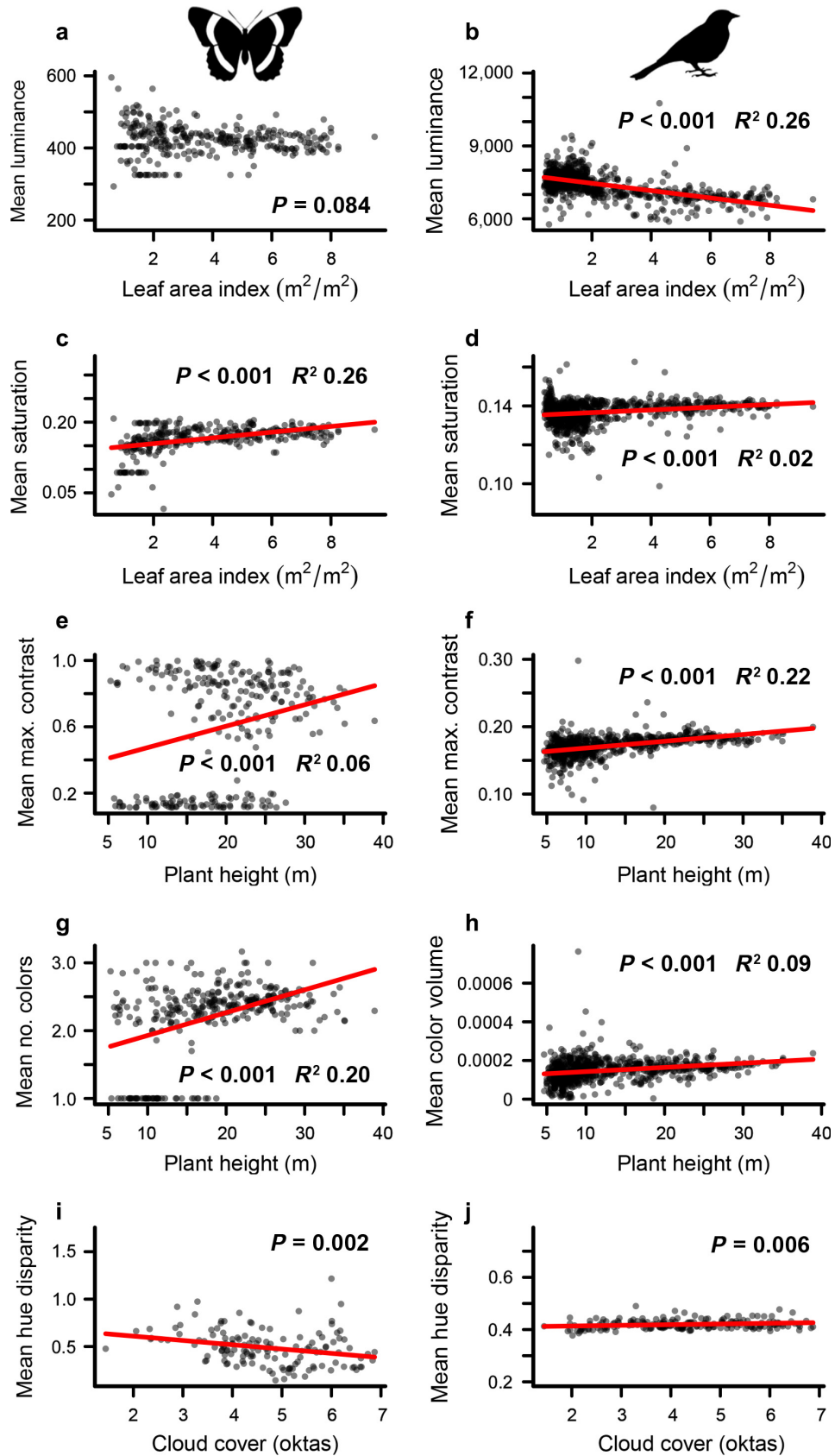


FIG. 3. The colors of butterflies (left column) and birds (right column) are related to the structure and complexity of the habitat. Significant relationships are denoted with red regression lines. Contrary to expectation, the luminance of bird colors is negatively related to leaf area index (b), and there is no significant correlation for butterfly colors (a). Both birds and butterflies have colors that are more saturated under higher LAI, and more contrasting and diverse colors in taller habitats (c–h). However, the hue disparity of bird and butterfly colors show different relationships to cloud cover (i and j).

saturation in birds ($P \leq 0.001$, though the relationship is very weak; $R^2 = 0.02$) and butterflies ($P \leq 0.001$, $R^2 = 0.29$; Fig. 3c, d). Compared to those in regions where LAI is $2 \text{ m}^2/\text{m}^2$ or less, butterflies resident in habitats with $6 \text{ m}^2/\text{m}^2$ or greater exhibit colors that are 25.7% more chromatically intense; bird colors are only 3.2% more chromatic (Table 2). Adding a quadratic term to these models improved the fit based on AIC values (see Appendix S4: Section 3).

We also predicted positive correlations between both color contrast and diversity of each taxon with plant height and LAI of their habitat. Our data support this prediction. Open habitats (those with lower plant height and LAI) are associated with the display of fewer different color patches (plant height:bird $R^2 = 0.09$, butterfly $R^2 = 0.21$; LAI:bird $R^2 = 0.13$, butterfly $R^2 = 0.25$; all $P \leq 0.001$) and lower maximum within-pattern contrast (plant height:bird $P \leq 0.001$, $R^2 = 0.22$, butterfly $P \leq 0.001$, $R^2 = 0.06$; LAI:bird $P \leq 0.001$, $R^2 = 0.20$, butterfly $P = 0.003$, $R^2 = 0.04$; Fig. 3e–h). For example, in a region where average canopy height is $\geq 25 \text{ m}$ the average number of dominant colors displayed by resident butterflies is 2.4, whereas butterflies under canopies of $\leq 10 \text{ m}$ display an average of 1.7 different color patches. Within-pattern contrast of butterflies in the taller vegetative habitat is also 72.1% greater.

Our eighth prediction was that cloud cover would be positively correlated with hue disparity of bird and butterfly colors. Support for this prediction varied across groups. Whereas cloud cover was positively associated with hue disparity in birds ($P = 0.006$, $R^2 = 0.04$; Fig. 3j), butterflies demonstrated the opposite pattern, displaying colors of more similar hue under cloudy conditions ($P = 0.002$, $R^2 = 0.08$; Fig. 3i, j; Table 2).

Community diversity

Our final prediction was that there would be positive correlations between community diversity and color diversity. There was no effect of butterfly community species richness on color diversity in either butterflies ($P = 0.52$) or birds ($P = 1.00$; Fig. 4c, d). However, the color diversity in each group was positively correlated with the avian community diversity (bird, $P \leq 0.001$, $R^2 = 0.12$; butterfly, $P \leq 0.001$, $R^2 = 0.17$; Fig. 4a, b) and the diversity of plants in the community (bird, $P \leq 0.001$, $R^2 = 0.12$; butterfly, $P \leq 0.001$, $R^2 = 0.26$; Fig. 4e, f). Birds in regions with 200 or more resident plant species on average display 81.8% greater diversity in their coloration than those in communities with 50 or fewer plant species. In communities where there are 200 or more bird species, the diversity

of colors displayed by butterfly species is 45.2% greater than in communities where there are 50 or fewer bird species (butterfly species display on average 2.4 dominant colors rather than 1.7; Table 2).

Which are the most influential variables in shaping coloration?

The multivariate multiple regression analysis of all variables accounted for 48.9% of the total variation in color traits of birds and butterflies on a broad scale. Bird diversity, rainfall, solar radiation, and temperature were the most influential individual environmental variables. Bird diversity explains 12.9% of the variation in color across the two groups. Rainfall contributes a further 9.5%, solar radiation 6.3%, and temperature 5.8%. Interestingly, while the diversity of birds in the community emerged as the best single variable overall, the variables with the second, third, and fourth most influence are all related to energy and resources. Growing season length and leaf area index explained the least variation overall, and in this all-encompassing model, they do not have an effect on coloration (Table 3).

The first two axes of the principal component analyses explained 28.2% of the variation in coloration of birds and butterflies. PC axis 1 explained 7.75% of the variation in bird and butterfly coloration ($P = 0.002$), and was negatively correlated with plant height, LAI, and NPP. PC axis 2 explained 20.5% of variation in animal coloration ($P = 0.002$), and was negatively correlated with solar radiation and temperature (see Fig. S1 and Tables S5–S6 in Appendix S4: Section 2).

When color traits (brightness, color diversity, color saturation, average disparity between hues, maximum contrast) were analyzed separately, solar radiation had an effect on all traits. Solar radiation was also the best predictor of color diversity (explaining 7.4% of the variation in this trait across birds and butterflies; both negative correlations; Fig. 5). Rainfall was the best predictor of luminance (explaining 26.7% of the cross-taxa variation in this trait), NPP was the best predictor of maximum contrast (partial $R^2 = 0.10$), and bird diversity was the best predictor of chroma and hue disparity (explaining 28.6% and 36.3% of the variation across taxa in these traits, respectively; Appendix S4: Table S3). Corroborating the importance of solar radiation, the PC analyses showed that PC2, which incorporated solar radiation and temperature, explained more variation in each of the color traits (variance explained ranged between 14.4% and 38.9%) than did PC1 (variance explained ranged from 3.37% to 18.77%; full results Appendix S4: Section 2).

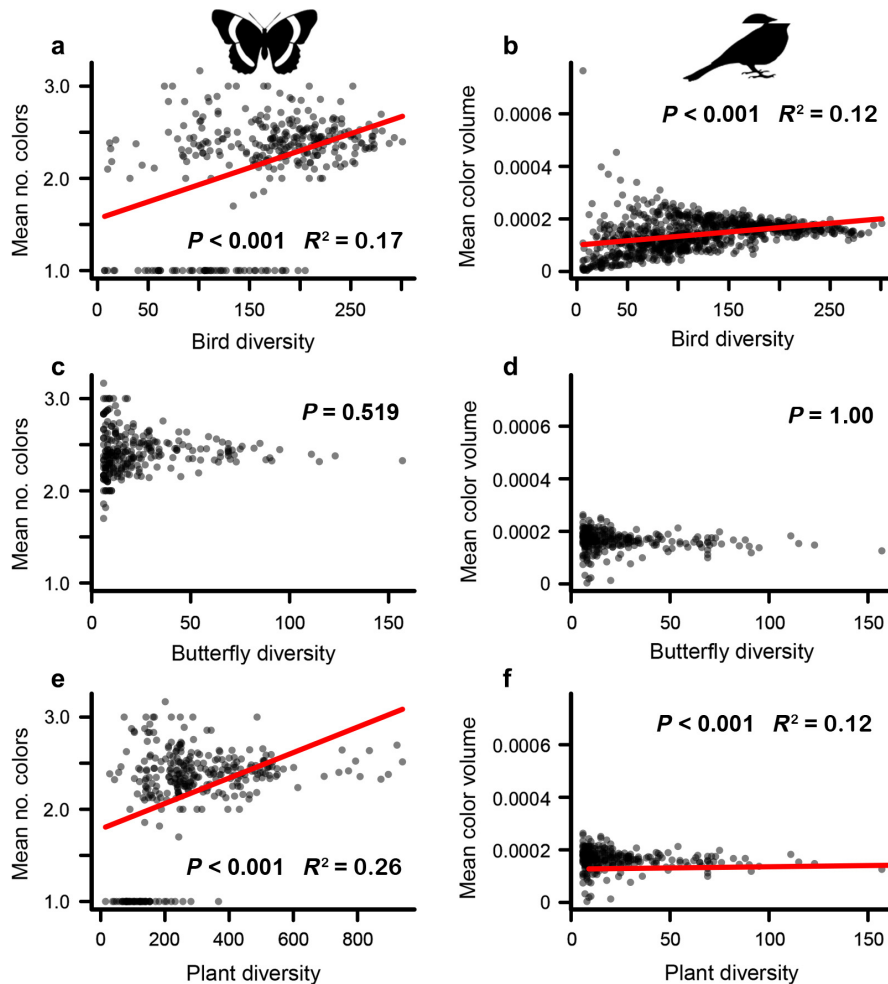


FIG. 4. The color diversity of butterflies (left column) and birds (right column) is significantly positively correlated with the bird community diversity (a, b) and the plant community diversity (e, f), as predicted. Significant relationships are denoted with red regression lines. There is no significant effect of butterfly community diversity on the colors of butterflies or birds.

Comparison of the variance explained by the three categories indicated that the combined energy and resources variables in the environment have the highest predictive power for bird and butterfly coloration. The energy and resources model explained 32.4% of the total variation in coloration across taxa, followed by habitat (which explained 18.2%), with diversity explaining the least (9.9%). This ranking of the predictive power of categories remained the same whether the full set of five energy and resources variables were considered whether we included only the top three (solar radiation, temperature, and rainfall: $R^2 = 0.28$), or the bottom three (NPP, length of growing season, and temperature: $R^2 = 0.21$) variables from this category (Appendix S4: Table S2).

When separate models were selected for each trait of birds and butterflies with one variable from each category, the best performing model selected for the bird

color traits was that for bird color luminance. This model incorporated solar radiation, cloud cover, and plant diversity and explained 64.2% of the variation in bird color luminance across the study range. The best performing model selected for butterflies was that for butterfly color saturation; that model incorporated solar radiation, LAI, and plant diversity and explained 36.5% of the total variation across the range (Appendix S4: Table S4).

Does a term for latitude improve variation explained by the selected models?

Including a term for latitude improved the selected model for four out of 10 traits: three of five bird color traits and one of five butterfly color traits. However, the addition of the term for latitude only explained an additional 0.7–7.0% of variance (Appendix S4: Table S4).

TABLE 3. Multivariate multiple regression of all five color traits of birds and of butterflies revealed that of bird diversity is the single most influential of all the environmental variables considered: full model; Rainfall, solar radiation, and temperature then follow; growing season length and LAI were non-significant overall. A multiple R^2 value for this model (0.489) indicates that it explains a total of 48.9% of the variation in bird and butterfly colors on a broad scale. Variance explained for the individual predictors in this model is similar to partial R^2 , derived as (η^2 statistic/number of response variables) /Hooper's R^2 .

Variable	Residual df	<i>F</i>	<i>P</i>	Variance explained
Bird diversity	126	140.637	0.001	0.632
Rainfall	135	134.423	0.001	0.466
Solar radiation	136	566.832	0.001	0.306
Temperature	130	22.524	0.03	0.286
Plant height	133	51.702	0.001	0.161
Butterfly diversity	128	60.371	0.001	0.159
Net primary production	131	34.558	0.002	0.145
Cloud cover	134	13.662	0.154	0.136
Plant diversity	127	39.947	0.001	0.134
Growing season length	129	35.092	0.003	0.118
Leaf area index	132	18.273	0.06	0.055

DISCUSSION

Birds and butterflies are more colorful in areas with high diversity

Bird diversity in the community ranked as the variable with greatest individual influence on bird and butterfly colors overall, and was the best predictor of variance in color saturation and hue disparity across species. Bird colorfulness was positively correlated with the species richness of the bird community, consistent with the hypothesis that diversity can drive character divergence or displacement in traits used for communication or species identification (Iwasa and Pomiankowski 1995, Albert et al. 2007, Anderson and Grether 2010). An alternative explanation may be that factors that promote diversity (i.e., promoting speciation and sympatry among new species) do so by promoting the evolution of color. For example, strong sexual selection could favor the evolution of color signals, increasing speciation rates and diversity. In the presence of higher bird species richness, butterflies also tended to display a higher diversity of colors that are more dissimilar in hue. These results may indicate an increase in the use of disruptive coloration or aposematism (rather than crypsis), and may reflect an associated change in predation risk (either in overall rate, number of predator guilds, or change in relative frequency of predation strategies/tendencies). We acknowledge that we were not able to quantify every aspect of the environments in which these animal species occur (for example, no data on foliage height diversity were available for this region), so it is possible that the strong

correlations with avian community diversity may actually result from a shared correlation between bird diversity, variation in color traits and a third, unmeasured environmental variable.

Plant species richness was a strong correlate of color traits in both birds and butterflies. This might reflect the importance of plants as resources in ecosystems. More diverse plant communities may provide a wider range of resources for animals as food (adding a range of nutrients, including carotenoids that plants synthesize *de novo* while most animals cannot; McGraw 2006a). A species-rich plant community may also serve as host plants and nesting sites for more animal species, and there may be higher structural complexity in the habitat provided by a greater diversity of plant forms present. Our results indicate that, while environmental filtering by abiotic conditions is an important influence on bird and butterfly colors overall, the diversity of ecologically important taxa forms a vital component of environmental effects on coloration.

Bird and butterfly colors are affected by the climate

Rainfall explained a considerable proportion of all variation in color traits of birds and butterflies. That rainfall was negatively associated with brightness in birds is consistent with Gloger's rule, an eco-geographical hypothesis that suggests that humid areas are home to animals with darker coloration than those in more temperate climates. Ordinarily this pattern has been explored within species, however, support for this pattern has been found across species in primates (Kamilar and Bradley 2011), in two families of Australian birds (Friedman and Remeš 2016), across 551 species of Australian land birds (Delhey 2017), and it may exist in lagomorphs, carnivores, and artiodactyls (Caro 2005). There was no effect of rainfall on butterfly color brightness, and we therefore find no evidence of Gloger's rule in butterflies.

A major focus of the effects of solar radiation on animal color has centered on the protective role that melanic coloration can play. While the significance of solar radiation for all color traits was unexpected, the pattern of color changes (brighter, less saturated, and less diverse color patterns; Table 2) with increasing solar exposure may be consistent with an overall increase in melanin-based colors. It may be that species tend to converge on melanic coloration in harmful light conditions, thereby reducing the range of hues displayed and overall variety, diversity, and contrast of colors. Additionally, that less solar radiation and cooler conditions are correlated with less reflective and more saturated colors is likely indicative of the thermal capture benefits that darker colors can provide, particularly in ectotherms such as butterflies (Kingsolver 1995, Zeuss et al. 2014).

The observed gradients in bird colors support the notion that reflective pelage and plumage can alter thermal resistance and aid in reducing radiative heat stress in warm environments (Hamilton and Heppner 1967, Walsberg et al. 1978, Guppy 1986, Hochscheid et al. 2002,

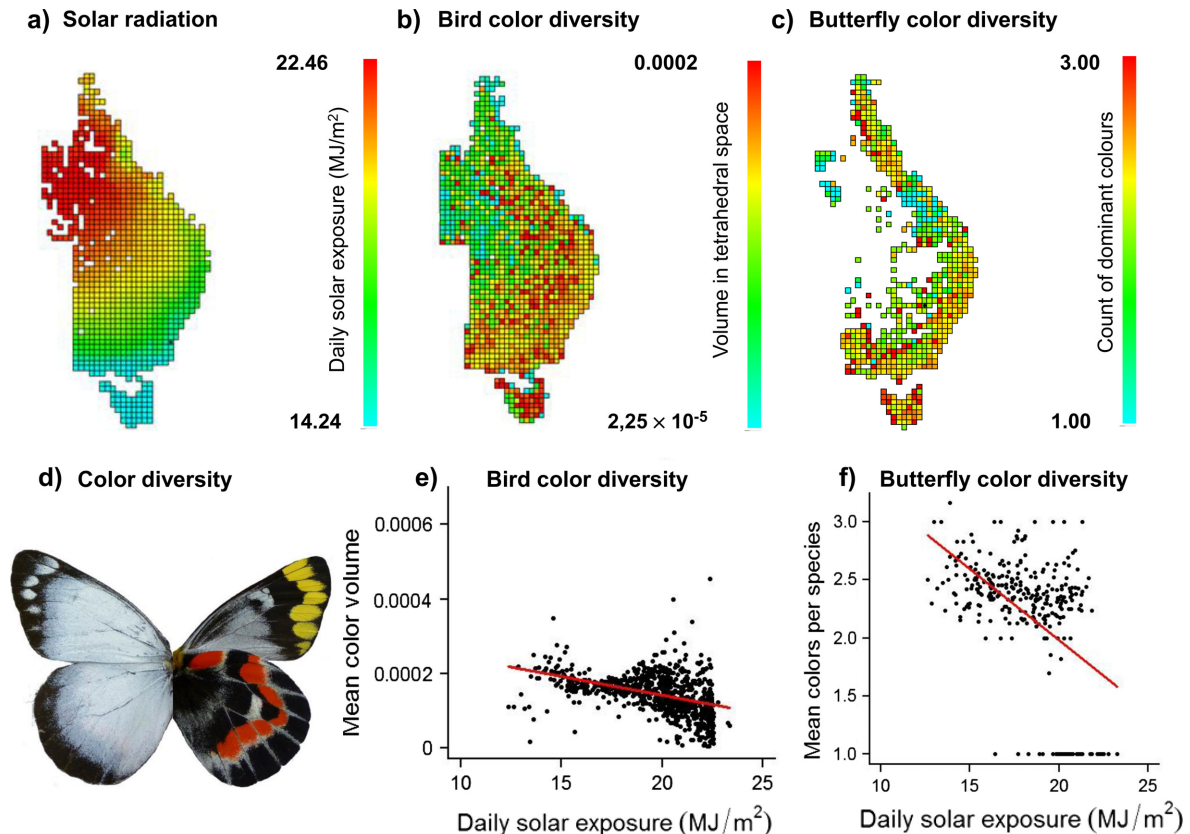


FIG. 5. Solar radiation is strongly correlated with the colors of birds and butterflies. For example, solar radiation correlates with the diversity of colors displayed by bird and butterfly species, with species displaying reduced color diversity in environments that experience greater solar radiation. (a) Solar radiation across the eastern states of Australia (MJ/m^2). (b) Mean of color diversity of bird species in 0.5° latitude grid cells (volume in tetrahedral color space). (c) Mean of color diversity of butterfly species in 0.5° latitude grid cells (count of dominant colors). (d) Graphical representation of color diversity: in butterflies, this is the number of dominant colors. The color diversity on the left wing is lower than that of the right wing, displaying three (black, gray-blue, and white) and four (black, gray-blue, yellow, and red) dominant colors, respectively. (e) Bird color diversity is negatively correlated with solar radiation ($P < 0.001$, $R^2 = 0.15$). (f) Butterfly color diversity is negatively correlated with solar radiation ($P < 0.001$, $R^2 = 0.27$).

Hetem et al. 2009). There was no effect of temperature on the luminance of butterflies, which appears at first to be counter to observations that insects tend to be darker in color in colder latitudes (Rapoport 1969). However, butterfly colors were strongly related to solar radiation in our data set. Regions with low solar exposure tend to have butterflies with darker, low luminant colors, which are needed for the absorption of the available radiative solar heat energy (Hamilton and Heppner 1967, Clusella Trullas et al. 2007, Hetem et al. 2009). Solar radiation may be more crucial than ambient temperature in thermoregulation of ectothermic insects, as they use solar basking to decouple themselves from the environment and achieve warmer body temperatures than the ambient conditions (Clench 1966, May 1979, Clusella Trullas et al. 2007).

Butterfly and bird species have less luminant colors in shady environments

Since the theory of sensory drive was first outlined, there has been great focus on testing predictions about

how habitat-specific ambient light shapes the colors of resident species (Endler 1992). This concept has formed a major topic of research in the color ecology literature, and a multitude of ways have been demonstrated for how signaling environment (often within forests) can affect the nature of visual signals (Endler 1993, Marchetti 1993, Endler and Thery 1996, McNaught and Owens 2002, Heindl and Winkler 2003, Gomez and Théry 2004, Hancox et al. 2013, Shultz and Burns 2013, Friedman and Remeš 2016). One debate in this literature is whether dark habitats tend to house brighter species of animals (Marchetti 1993, McNaught and Owens 2002). Compellingly, the positive correlation between brighter, more luminant colors with better-lit environments in our data holds across all variables that might influence the amount or quality of light in an environment. Species display less luminant colors in shadier habitat conditions under taller or thicker canopies, but also where cloud cover is thicker, where rainfall is higher or in areas that experience fewer sunlight hours annually. Our results were consistent in showing that species in conditions of

higher ambient light will tend to have more reflective colors overall, and like that of McNaught and Owens (2002), our data do not support the assertion that dark habitats are home to brighter species of animals (Marchetti 1993). While Friedman and Remeš (2016) found greater color span and saturation in more open habitats across 137 species of two Australian bird families, these patterns are not supported in our data for 570 species of birds from 76 families and 424 species of butterflies across 7 families. Rather, our results conform to predictions that species in open habitats would use fewer colors, that are more luminant, less saturated, and less contrasting, in order to aid communication across longer distances, and that species in more closed, structured environments such as forests would use more heavily saturated colors (Zahavi and Zahavi 1997).

Plant height was an important predictor of color contrast across birds and butterflies, with greater tree height correlating with more contrasting colors. Of the habitat category variables, plant height was the better predictor of bird and butterfly coloration overall, which may indicate that vertical structure and complexity of habitat are more important predictors than shading. Leaf area index and cloud cover both affect the color and amount of ambient light, which are central components of sensory drive theory, but neither variable had an effect on coloration in the all-encompassing model. The fact that these two variables performed poorly may be considered surprising in light of the prevalence of research on this aspect of forest habitat and its impact on coloration. We suggest that the focus on the effects of forest shade should be widened to better incorporate more of the multitude of light-affecting variables that can influence bird and butterfly colors, and that there is need to further disentangle the effects of the diversity of vertical structure and physical complexity of a habitat from the effects that such complexity might have on the light environments within that habitat. Given that non-linear models performed better than linear models for relationships between LAI and animal color saturation and luminance in almost all cases, it may be that when the amount and density of leaves are at intermediate levels, the variation and diversity of light microhabitats within the vegetation column peaks, affecting selection for color traits.

An important line of future research would be to delve into the complexities of why open habitat conditions are correlated with the color patterns we have shown. Across species of birds and butterflies we saw the same trends in coloration in the gradient from tall, dense canopy habitat to shorter, more open habitat as seen in the gradient from regions of low to high solar radiation (decreases in the diversity, saturation and maximum contrast of colors in birds and butterflies). There were also some consistencies in how solar radiation and temperature affect coloration. Teasing out the relative importance of longer distance communication and identification expected of species in more open habitat vs. the effect of the greater

solar radiation species are subject to in open habitat, and vs. the greater heat stress organisms may experience without much shade, is a challenging but fundamental next step. Research into these overlapping and probably interacting effects would require incorporation of visual modeling and background colors, as well as exploration of the mechanisms of color production and how the prevalence of melanin-, carotenoid- and structural-based colors might change across environmental gradients.

Key differences in the broad patterns in the coloration of birds and butterflies

There were a number of notable differences between how the colors of birds and butterflies related to their environments that might reflect the disparate ecological roles and life-history traits of the two groups. For instance, butterfly community diversity did not influence the diversity of butterfly colors displayed. Butterfly species richness also did not influence the diversity of bird colors, although we had no reason to expect that it would (as opposed to the predicted and observed effect of birds on butterflies). Next, while all bird color traits were affected by rainfall, two butterfly color traits displayed no correlation with rainfall, and there was no evidence of Gloger's rule in butterflies. This may relate to physical differences between feathers and butterfly wings. It has been hypothesized that darker feather colors might be important for drying out in humid environments (Burt and Ichida 2004), but the hydrophobic nature of butterfly wings (Wagner et al. 1996) likely negates this selection pressure on butterfly colors. It may also be that birds and butterflies interact differently with their environment and use different parts of habitat and/or canopy, and could thus be impacted differently by the weather. Furthermore, butterflies did not show the predicted decrease in color brightness in cooler conditions and instead their colors were much more strongly related to solar radiation. This likely reflects the advantage of darker colors for solar basking in ectothermic species (Clench 1966, May 1979, Clusella Trullas et al. 2007). It may be that in endothermic animals such as birds, reflective colors are more useful in resisting heat stress in regions that are warmer, but that capture of solar radiation is of considerable importance for maintaining internal temperatures in ectothermic insects at higher latitudes.

How do these results help us to understand the latitudinal gradient in color?

Contrary to long-held belief, evidence suggests that species in the tropics are less colorful than those in temperate regions, displaying colors that are on average less saturated, less diverse, and less contrasting (Dalrymple et al. 2015). In part, the current paper sought to provide some insight into these unexpected patterns. Latitude is used in macroecological studies as a proxy for many

ecological variables that vary across broad latitudinal space, and this study has included most of the common ones. Solar radiation and temperature have stronger correlations with latitude than do any of the other variables (Appendix S5), and both have emerged as important influences on bird and butterfly colors. Under higher solar radiation and higher temperatures both birds and butterflies display fewer colors, that are less saturated, and less contrasting overall (Table 2, Fig. 2a, b). As tropical latitudes experience higher solar exposure and higher mean annual temperature, it is easy to conclude that these are major contributors to the gradients in coloration demonstrated by Dalrymple et al. (2015). Interpreting the impact of bird species richness in driving the patterns in animal coloration can at first seem more convoluted; the more diverse the bird community, the richer and more complex the color patterns of birds and butterflies. In resolving this, it is crucial to note that our data do not show greater bird diversity in the tropical limits of the study range, and instead demonstrate the inverse of the classic biological diversity gradient (this is neither the first time that an inverse diversity gradient has been shown, nor is it the first time it has been demonstrated in birds (Kindlmann et al. 2007)). Productivity is negatively correlated with latitude in our study range, and bird species richness is highest in more productive ecosystems (Hurlbert and Haskell 2003; Appendix S5). Birds and butterflies are more colorful in more productive regions, where the bird community is diverse, and where solar radiation and temperature are lower, and all of these conditions are met in the temperate region of the study range, likely driving much of the latitudinal gradient in color (Dalrymple et al. 2015). In the future, it will be interesting to determine the extent to which these findings can be extrapolated to regions outside Australia, and to taxa other than birds and butterflies. Additionally, it may be worth exploring the differences in color pattern variation of the resident animal communities of mainlands vs. islands, given that the southern end of our latitudinal range is an island.

Much of northern Australia is open grassland, savanna or shrubland habitat (as are large parts of tropical Africa and parts of tropical South America; (ESA: CCI LC 2017)). In the spatial range we examined, lower latitude areas tended to have shorter, more open habitat. Tropical savanna ecotypes could play a more important role in latitudinal and macroecological color patterns than previously appreciated, and the importance of closed-canopy rainforest (covering only 7% of land area worldwide; Freeman 2005) may have been overstated. Finally, much of the theoretical footing for the colorful-tropics hypothesis rested on arguments of higher diversity in tropical ecosystems selecting for more flamboyant and conspicuous color signals (Adams et al. 2014). However, we have here shown that many components of the abiotic environment are as important (or more important) than the diversity of the wider biotic community in affecting bird and butterfly

coloration overall. While the inclusion of a term for latitude significantly improved the fit of the models more often than not, for most traits, it improved the R^2 values of the models by less than 1%. This additional variation may be the result of another, unmeasured factor that significantly covaries with latitude and has an effect on coloration across taxa across broad spatial scales (cf. Martin et al. 2010).

By exploring multiple dimensions of ecological variation we have gained insights into their relative importance to the coloration of birds and butterflies, two of the most famously colorful animal groups. Overall, variables related to energy and resources in the environment have consistently emerged as the most powerful predictors of bird and butterfly coloration. While diversity of the bird community is a powerful driver of the coloration of both taxonomic groups, emerging as the greatest single predictor in the full model, we have shown that biotic conditions do not result in as pervasive or consistent changes in coloration as abiotic conditions do across such broad spatial and taxonomic scales. Our results have also indicated that researchers examining the effects of habitat shade on coloration may benefit from extending their focus to include other aspects of the environment that can affect the evolution of signals used in visual communication. By providing spatially and taxonomically broad tests of a number of predictions central to the field of color ecology, we have gone a long way toward resolving why tropical species are less colorful than those at higher latitudes. There are several consistencies in how the colors of birds and butterflies relate to environmental conditions. Both birds and butterflies are more colorful in productive environments, and where the bird and plant community is diverse. Birds and butterflies also demonstrated the same direction of relationships with solar radiation for all five color traits measured. Both groups tend to display a greater diversity of more contrasting and more saturated colors in tall, dense canopy habitats. These similarities, which often conform to predictions established in the color ecology literature, imply that fundamental macroecological principles may drive patterns in animal colors across different taxa.

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SUPPORTING INFORMATION

Additional supporting information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/ecm.1286/full>

DATA AVAILABILITY

Data are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.30h0n>