

Nowhere to Run, Nowhere to Hide: The Importance of Enemies and Apparency in Adaptation to Harsh Soil Environments

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ABSTRACT: Bare, simplified searching environments, often associated with sparsely vegetated harsh soils, may cause both plant and animal inhabitants to be apparent and conspicuous. “Apparency” has been a key concept to explain the diversity of plant defensive chemistry but has been difficult to test. In animals, there is extensive work on camouflage and crypsis, adaptations to apparency that reduce detection by predators. Here, we explore apparency as a challenge in bare soil habitats characterized by sparse vegetative cover for both plants and animals. Using experiment and observation, we show that attack rates from enemies on vulnerable plants and undefended caterpillar models are greater in barer serpentine habitats than in adjacent more vegetated ones. Palatable *Streptanthus* species (Brassicaceae) may have adapted to apparency with a crypsis defense, typically considered the purview of animals. In *Streptanthus breweri*, leaf color is locally matched to soil outcrop color, and experimental mismatching of leaf and substrate color increases damage to plants, suggesting adaptation to apparency per se. Herbivore coloration may, too, have been influenced by greater enemy pressure and apparency in these sites. Adaptation to increased enemy pressure and apparency, with concomitant trade-offs in competitive ability, may be an underappreciated aspect of specialization to harsh soils, especially in plants. Apparency may be a useful framework for understanding trade-offs driving soil specialization and global biodiversity patterns.

Keywords: apparency, enemies, plant defense, crypsis, soil specialization, Brassicaceae-Pieridae.

Introduction

Ecological specialization is a major driver of biodiversity, and in plants, soil specialists comprise a large proportion

of global plant biodiversity (Kruckeberg 1984; Cowling et al. 1994). Besides their unique biota, harsh soils, especially in drier climates, often have sparsely vegetated communities that may render plants and animals inhabiting them more conspicuous or apparent to enemies (Rausher 1981; Barbosa et al 2009; Stankowich et al. 2011). Apparency to enemies has long been proposed as an attribute that might explain the diversity of plant defensive compounds against herbivores (Feeny 1976; Rhoades and Cates 1976; Endara and Coley 2011). Apparent plants are defined as those that are predictably or easily found by herbivores (Courtney 1986; Parmesan 1991). In addition, apparency must necessarily depend on the perceptions of the searching organism (Parmesan 1991). Despite its long history, plant apparency has been difficult to assess, often as a result of confounding effects with plant size and life history (Feeny 1976; Endara and Coley 2011), and experimental tests of apparency per se remain few (but see Rausher 1981).

We suggest that apparency for both plants and animals may be high in sparsely vegetated communities and that, as a result, organisms that persist in these habitats must have traits that reflect adaptation to high enemy pressure. Selective pressures exerted by harsh soils on plants have been thought to be primarily through toxic elements or low nutrient availability (Rajakaruna et al. 2003; Bratteler et al. 2006; El Mehdawi and Pilon-Smits 2012). Less attention has been paid to enemies as a source of selection in harsh soil environments (but see Fine et al. 2004, 2006; Van Zandt 2007), and those few studies examining pressures resulting from herbivores have focused on relationships with resource availability, not on conspicuousness. In contrast, the adaptive value of coloration for animals in sparsely vegetated areas or other simplified environments such as sand dunes or the arctic tundra has been extensively explored (Rosenblum et al. 2009; Vignieri et al. 2010; Robertson et al. 2011), though to our knowledge

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only one group (Stankowich et al. 2009, 2011) has suggested that, globally, bare habitats are linked to increased enemy pressure and are major drivers of defensive coloration and syndromes in animals.

Plants may be more apparent in bare sites because (1) fewer neighbors result in fewer olfactory and visual signals to serve in associational resistance (Barbosa et al 2009), (2) clearer outlines tend to increase prey detection or recognition in both plants and animals (Schaefer and Stobbe 2006), and (3) more obvious leaf outlines generally increase host finding for at least some insects (Rausher 1978, 1981; Mackay and Jones 1989; Masumoto et al. 1993). Plants living in diverse and dense vegetation can gain protection from herbivores through “associational resistance” conferred when plant neighbors disrupt visual or olfactory cues used by herbivores to locate hosts (Tahvanainen and Root 1972; Rhoades and Cates 1976), among other mechanisms (reviewed in Barbosa et al 2009). Animals too gain protection from enemies in more vegetated areas where they can be less detectable (Butler and Gillings 2004) and less vulnerable (Cassini 1981; Dickman 1992) than in barer sites.

While apparency may be greater in bare areas, a number of non-mutually exclusive processes other than apparency might also result in greater attack rates in barer sites. For example, enemies might select bare habitats because they are warmer and subsequently encounter prey more often in these sites (Velde et al 2011). Or, behavior affected by vegetation density and identity (Kareiva 1982; Parker 1984) could alter relative encounter rates with prey (*sensu lato*) in barer sites. Herbivores engaging in “spreading-the-risk” behavior across oviposition sites have been found to overexploit more sparsely vegetated areas (Root and Kareiva 1984). Many of these mechanisms, including apparency, predict greater attack rates in barer sites.

If specialists on bare soil habitats experience, or have historically experienced, strong selection from enemies as a result of increased apparency or other mechanisms, then it follows that to persist in these environments, these species must be effectively defended. Defense could be in numerous forms, including inedibility through toxins or structural defenses. Edible organisms might have other kinds of adaptations including cryptic coloration, Batesian mimicry, phenological/circadian mismatching from enemies, or escape behaviors. Here, we focus on defensive coloration in vulnerable species as adaptations to enemy attack and specifically as defensive adaptations most closely linked to apparency.

Defensive coloration has received much attention in animals (see Merilaita and Stevens 2011 for review) but relatively little in plants (Schaefer and Ruxton 2011). Crypsis and camouflage allow vulnerable organisms to avoid detection and are often achieved through background match-

ing (Merilaita and Stevens 2011). Givnish (1990) proposed that leaf mottling served as camouflage to escape herbivores in forest understory plants. Some more recent studies have considered functions of leaf or plant coloration that might affect interactions with higher trophic levels (Schaefer and Ruxton 2011) by increasing the conspicuousness of leaf-feeding herbivores to their own enemies (Lev-Yadun et al. 2004), serving directly in defense (Lev-Yadun 2006), mimicking herbivore damage (Soltau et al. 2009) or dead leaves (Fadzly et al. 2009; Klooster et al. 2009), mimicking thorns, and cryptic background matching (Burns 2010; Lev-Yadun 2006; Givnish 1990). However, only a few of these studies have taken an experimental approach to understand the adaptive function of leaf coloration.

We use observation and experiment to ask (1) Is there increased enemy pressure on plants and animals inhabiting sparsely vegetated habitats, where we predict they are more apparent than in more vegetated habitats? and (2) Is there evidence for defensive coloration in plants and insect herbivores as an adaptation to apparency *per se*? Our goals are first to examine whether inhabitants of barer microsites and habitats experience greater rates of attack from enemies than inhabitants of more vegetated sites. We then explore whether coloration represents a defensive adaptation to apparency *per se* at our sites.

Material and Methods

The System

We explore these questions in sparsely vegetated northern California serpentine outcrops that are characterized by high nickel concentrations and low calcium : magnesium ratios (Kruckeberg 1984; Brooks 1987) and that thus represent stressful growing conditions to many plant species (Kruckeberg 1984; Brooks 1987). Jewelflowers, mustards in the Streptanthoid complex (Brassicaceae), often occur on sloped rocky outcrops, and about a third of the species are serpentine specialists (*Jepson Manual*; Baldwin 2012). Several species in this complex have leaves that are mottled brown or gray (brownish-leaved *Streptanthus barbiger*, *Streptanthus batrachopus*, *Streptanthus breweri*, *Streptanthus drepanoides*, and *Streptanthus hesperidis*, and gray-leaved scree-living *Caulanthus amplexicaulis* var. *amplexicaulis*; fig. 1) and live in sparsely vegetated habitats with soils that vary in color from brown to gray (fig. 1) to blue-green. To human omnivores, these plants are very difficult to find in their vegetative stages.

The most common herbivores of *Streptanthus* at our sites include two species of diurnally active pierid butterflies that are mustard specialists, *Pontia sisymbrii* (fairly common at our sites) and *Euchloe hyantis* (rarer)



Figure 1: A, *Caulanthus amplexicaulis amplexicaulis*; B, *Streptanthus breweri*; C, *Streptanthus barbiger* (three plants); D, *Streptanthus hesperidis*; E, Xrite Colorchecker Mini Card with *S. breweri* (left of card); F, *S. breweri* presand treatment; G, same *S. breweri* postsand treatment. Photographs copyright S. Y. Strauss.

(Courtney 1986; Shapiro 1981*b*); black-tailed deer and other small mammals; and grasshoppers. Occasional herbivores are chrysomelid specialist beetles and aphids. Herbivory by sparrows at the seedling stages and nocturnal herbivores may also be important.

Vertebrate herbivores browse shoots and leaves of *Streptanthus* spp. while females of *P. sisymbrii* and *E. hyantis* lay eggs on brown leaf rosettes (A. M. Shapiro, S. P. Harrison, and S. Y. Strauss, personal observations; see also Wiklund 1984), as well as on flowering stalks. The larvae eat leaves but also feed on flower and fruits at the top of the plant in daytime. Each larva can completely consume one medium-sized or several small hosts, a behavior that may have selected for both cannibalism in larvae and preoviposition visual inspection of rosettes and stalks by females (Shapiro 1981*a*, 1981*c*). The latter behavior is also found in other diverse cannibalistic lepidopterans (*Anthocharis cardamines*, *Pontia protodice* [Wiklund and Åhrberg 1978; Wiklund 1984]; *Battus philenor* [Rausher 1978]; *Heliconius cydno* [Williams and Gilbert 1981], and *Mechanitis lysimnia* [Vasconcelosneto and Monteiro 1993]) and reflects the acute visual capacities of butterflies. Herbivorous mammals have good color vision in the green spectrum (Yokoyama and Radlwimmer 1998; Dominy and Lucas 2001), and the importance of visual cues in host location by insects has been well documented (Wiklund 1978; Finch and Collier 2000; Reeves 2011). Even night-feeding orthopterans and lepidopterans have been found to discriminate among colors in dim starlight and moonlight (Fadzly and Burns Kelber et al. 2002; 2010). Thus, leaf-substrate matching may be an effective defense against a diverse assemblage of herbivores, and may be a trait under selection from apparency.

Experimental Methods

1. Do Vulnerable Organisms Living on Bare Substrates Experience High Rates of Enemy Attack?

We addressed this question using a combination of descriptive and experimental approaches assaying enemy attack rates on both palatable *Streptanthus* spp. and (undefended) polymer clay caterpillar models across more and less vegetated areas.

Observation 1: Damage Surveys. Starting November 2010 and throughout the growing season, we followed 160 randomly selected naturally occurring seedlings of *Streptanthus breweri* and *Streptanthus hesperidis* in transects along the center and edge of two outcrops at the University of California, Davis, McLaughlin Reserve in Napa/Lake Counties, California. We recorded percent bare ground in a 20-cm diameter circle centered on a plant as a measure

of apparency, visually estimated the amount of leaf damage to plants every 10–14 days, measured plant height, and counted fruit number produced by each plant. We measured height to use as a covariate in the analysis of damage because in some cases herbivores prefer larger, more vigorous plants to smaller ones (Price 1991), and we wanted to the separate effects of plant size on damage from those arising from amount of bare ground.

Experiment 1A: Transplant/Neighbor Removal. To partially control for potential bias in plant establishment sites and correlations with herbivory, as well as to test attack rates in more vegetated adjacent grassland sites, we also experimentally transplanted pairs of similar-sized seedlings along transects extending from the center of outcrops into the adjacent nonserpentine grasslands, which are heavily invaded by exotic grasses. We used experimental neighbor removal to increase apparency (see also Rausher 1981) at each position along transects and predicted that neighbor removal would increase damage from herbivores for reasons stated earlier.

At two outcrops with *S. breweri* and one with *S. hesperidis*, in fall 2010, we transplanted pairs of similar-sized seedlings in 3–7 transects per outcrop, one pair in each transect position. Each transect of ~20–30 m had five positions located at outcrop center (position 1), midway to the edge of outcrop (position 2), the edge of outcrop (position 3), into grassland with a few serpentine-associated species still present (position 4), and full grassland (position 5). Positions 1–3 were located on the outcrop, while 4 and 5 were off-outcrop and had tall exotic grasses (see fig. 3*b*). One member of each pair at each location was randomly selected to have neighbors removed within a 9-cm radius; as these were very young seedlings, this procedure caused minimal disturbance to the soil. Removed biomass was dried and weighed to provide a measure of associational resistance for that position/transect location. A total of 105 pairs of seedlings were planted and then censused for damage and height every ~14 d, as well as collected for biomass after 5 months. We again measured plant height to include as a covariate in our analyses to incorporate indirect effects of neighbor removal on damage via changes in plant size (as above).

Experiment 1B: Attack Rates on Caterpillar Models. We also tested the hypothesis that bare habitats result in increased enemy attack, using realistic polymer clay caterpillar models representing an “undefended” animal species colonizing serpentine outcrops (see Vignieri et al 2010 and references on the benefits of models). Predators leave clear beak or tooth marks in the clay, allowing us to identify predation events. In 2009, 3-cm-long models made of emerald and green apple Sculpey III polymer clay were su-

perglued at 0.4-cm height (a height where pierid and other caterpillars feed), to old flowering stalks of *Chlorogalum pomeridianum* and *Hemizonia congesta*, species that occur both on the outcrop and in the immediately adjacent grasslands. We individually placed 60 models per week—30 on stems on the outcrop and 30 on stems of the same plant species in adjacent grasslands within 20 m of the outcrop. Models were placed 3 m from each other along transects; those in the grassland ran parallel to the outcrop edge to keep proximity to outcrop constant. We recorded attack rates (from beak or tooth marks) on caterpillar models in both habitats every week for 3 weeks.

2. Does Leaf Coloration, a Trait That Likely Reflects Selection Via Apparency, Contribute to Defense in Bare Habitats?

Conventionally, crypsis is measured by how well an organism matches a random sample of the background where predation risk is highest (Endler 1984, 1990; Uy and Endler 2004). Because there are diverse herbivores of these plants with very different, often unknown, spectral perceptions, we do not attempt to simulate the perceptions of these herbivores. Mammalian herbivores have color vision in the wavelengths reflected by *Streptanthus* leaves and substrates (Yokoyama and Radlwimmer 1998; fig. S1; figs. S1, S2 are available online); butterflies also have the ability to distinguish green from brown paper models of leaves in the absence of olfactory cues (Finch and Collier 2000). We used both a spectrometer and digital images to compare similarities of leaf and substrate spectra and a leaf-substrate mismatching experiment to explore this question.

Observation 2A: Reflectance. To determine whether *S. breweri* plants more closely match their rocky substrate than green-leaved neighboring plants, we calculated the difference in the light reflected by *S. breweri* and its surrounding substrate and compared it to the difference between green-leaved species and their surrounding substrate (fig. S2). We expected a smaller difference in putatively cryptic *Streptanthus* compared to green-leaved members of the local community. We measured reflectance spectra from 300 (UV) to 750 (IR) nm using an Ocean Optics USB2000 spectrometer and a deuterium/tungsten halogen light source (Ocean Optics, Dunedin, FL) with a 3-s integration time and boxcar of 12. We averaged three independent scans per sample for 15 plants per population of brown-leaved *S. breweri* (two populations), 10–15 plants of each of 1–4 other members of the same outcrop communities (*Allium diabolense*, *Clarkia gracilentum*, *Epilobium minutum*, and *Eriogonum* sp.), and three rocks in the immediate vicinity of each plant measured. We then sub-

tracted the spectral curves of leaves of each plant from those of the rocks with which each plant was growing to quantify the degree to which leaves and substrate matched across the spectrum measured. Matching was assayed by calculating the mean | leaf-substrate | reflectance from 305 to 750 nm averaged over 5-nm increments (i.e., 90 wavelength categories), as we had no a priori reasons to focus on specific wavelengths. We also measured spectra of 15 plants of *Streptanthus morrisonii* (one population) and associated rocks because it is a green-leaved close relative that grows in outcrops nearby and often co-occurs with *S. breweri* (Jepson herbarium accessions; S. Y. Strauss and N. I. Cacho, personal observation).

Observation 2B: Images. Because the mottling of leaves and substrate are at scales larger than the sample probe for the spectrometer, because there was no UV reflectance (figs. S1, S2) and because we were interested in assessing leaf-substrate matching under natural light in field conditions, we also used digital images to compare the similarity of leaf and substrate colors within and across sites. Under selection for crypsis, differences in substrate and leaf color should be smaller between leaves and substrates at the same site than between leaves and substrates at different sites; in contrast, differences between leaf color and a standard brown color square used at all sites should be the same whether sampled within sites or across sites.

Images of *S. breweri* plants and substrate were taken in full sunlight, a typical light environment of these serpentine barrens in California's sunny, mediterranean climate. We photographed 12–47 plants from three outcrops with surrounding substrate, depending on population size. In each photograph, we included an Xrite Colorchecker Mini (fig. 1) to calibrate images for changing light conditions using the gray color square and following established methods (Bergman and Beehner 2008). Calibrated images were then sampled in ImageJ (Rasband 1997–2011) by choosing three leaves from a plant at random and sampling a square that was as large as possible within leaf margins; squares of the same size were then randomly selected from the substrate in the same photograph. We subtracted the mean red, green, and blue (hereafter RGB) values of the random samples of substrate from those of leaves in the same image (LF-SUB_{Same}). We then compared these differences to differences between leaf and substrate RGB drawn at random from other images (LF-SUB_{Rand}). To ensure that any similarities between leaf and substrate in the same image did not arise from residual uncorrected light environments between pictures, we also analyzed the difference of mean leaf RGB in the picture from RGB values of a brown Colorchecker square (LF-BSQ_{Same}), which we knew to be identical across all images. We then compared the LF-BSQ_{Same} difference to the difference between the

same leaf and the RGB of the same brown square drawn at random from other images (LF-BSQ_{Rand}).

Experiment 2A: Background Mismatching. If mottled brown leaf coloration serves as a crypsis defense, then experimentally mismatching leaves from substrate should increase damage rates to plants. This experiment also more specifically addresses apparency per se, as encounter rates and at least larger-scale thermal environments should be similar for these treatments. Additions of sand or sifted soil covering the litter and rocks directly beneath a plant would result in a substrate of more uniform color and texture (fig. 1F, 1G), which we predicted would increase contrast of the plants against their background, making them more visible (Uy and Endler 2004) and more susceptible to damage.

Because populations of our target species are sparse and plants are difficult to locate, we conducted the same basic experiment for *S. breweri* at five outcrops in 2009 and three outcrops in 2008 (all located in Napa and Lake Counties); for *S. hesperidis*, we conducted this experiment once each at three different outcrops in three different years (2008, 2009, and 2011). At each site, we selected sets of seedlings assigning one at random to be an unmanipulated control. The other seedling received at its base a thin surface application of either sterilized sand (2008, 2009) or sieved (2.0-mm mesh) serpentine soil (2008, 2011) extending ~9 cm beyond the outline of the leaves. The number of sets per site per experiment ranged from 7 to 25, depending on population size and our ability to find plants. Sand additions were lighter than base soil and could have had other effects, such as possible changes in microsite temperature (fig. 1G). We monitored plants for damage and reestablished treatments every 10–14 days if rain had washed them away.

Statistical Analyses

1. Do Palatable Organisms Living on Bare Substrates Experience High Rates of Enemy Attack?

Observation 1: Damage Surveys. We predicted that, after accounting for size, plants in barer habitats should be more obvious and receive more damage. We examined the relationship between bare ground and damage by analyzing arcsine square root transformed mean damage to plants using restricted maximum likelihood standard least squares (REML SLS in JMP 9.0) with predictors: site (as a random effect), and percent bare ground using plant maximum height as a covariate to remove effects of size. We used lowest corrected Akaike Information Criteria (AICc) to select the best model predicting damage; this approach is appropriate for descriptive data.

Experiment 1A: Transplant/Neighbor Removal. We predicted that removing neighbors would increase damage to plants, after the effects of neighbor removal on plant size were accounted for. We analyzed the mean percent damage received by plant (arcsine square root transformed) as a function of location (two levels, on or off outcrop, reflecting the absence or presence of a tall exotic grass cover), position (location), weeding treatment, and location × weeding, with two covariates [log vegetative biomass removed from each pair's site [this provides an estimate of associational resistance of the unweeded partner], and plant height [for reasons as above]], and with outcrop as a random factor. While we evaluated the best model based on lowest AICc, we also present *P* values from our a priori model, an appropriate approach in randomized experiments (Burnham and Anderson 2002).

Experiment 1B: Attack Rates on Caterpillar Models. A χ^2 test was used to compare the frequency of attacks on caterpillar models on and off the serpentine outcrop.

2. Does Coloration Serve as a Defense?

Observation 2A: Reflectance. To determine whether brown-leaved plants more closely match their substrate than green-leaved plants, we analyzed the average mean difference in leaf-substrate spectra using expected mean squares (EMS SLS in JMP v.9.0) with the model mean | (leaf-substrate spectral reflectance across 300–750 nm) | as a function of species. A priori contrasts were used to compare *S. breweri* to all co-occurring green-leaved species and separately to green-leaved close relative *S. morrisonii*.

Observation 2B: Images. To determine whether leaves of *S. breweri* plants match the substrate of their home outcrop more closely than that of other outcrops, we compared the differences in RGB between *S. breweri* leaves (LF) and substrate (SUB) from the home outcrop (same image), other outcrops (image drawn at random), and a standard brown square control (BSQ; see “Material and Methods”). Mean summed differences were analyzed by a one-way ANOVA comparing “treatments” with Tukey's HSD. Treatments were (1) LF-SUB_{Same}, (2) LF-SUB_{Rand}, (3) LF-BSQ_{Same}, and (4) LF-BSQ_{Rand}.

Experiment 2A: Background Mismatching. Damage levels varied significantly across species and site, and were non-normally distributed, with excess numbers of plants with both very low and very high damage levels; in addition, there were unequal sample sizes across sites and years. Because nonparametric methods are not available to analyze random factors and nested designs, we generated residuals from a generalized linear mixed model in which

Results

1. Does Bare Ground Increase Attack Rates?

Observation 1: Damage Surveys. We found that herbivore damage to naturally occurring plants was best predicted (based on AICc) by increased amounts of surrounding bare ground, smaller height, and species (fig. 2, table S1a; tables S1–S5 available online). Greatest fruit production (a measure of fitness in an annual plant) occurred in plants that had less herbivore attack but greater surrounding bare ground (table S1b).

Experiment 1A: Neighbor Removal/Seedling Transplants. Transplanted seedlings growing off outcrops were surrounded by threefold greater vegetative biomass than plants on outcrops (mean dry mass on outcrops 1.02 g [SE 0.10]; mean dry mass off outcrops 2.90 [SE 0.12]; $t = 24.54$, $df = 1, 212$; $P < .001$), and this measure is very conservative, as biomass was measured early in the season when maximum biomass and canopy height of neighbors had not been attained.

Experimental neighbor removal increased levels of attack on plants on serpentine outcrops but not in adjacent grasslands (a significant weeding \times location on outcrop interaction; fig. 3; table S2a). Plant height was included in the best model based on AICc (table S2b), where it was negatively associated with damage, as with our observational data. Final biomass, like fruit set, was significantly greater for plants receiving less herbivore damage (table S2c; $P < .0008$). That damage decreases biomass and fruit

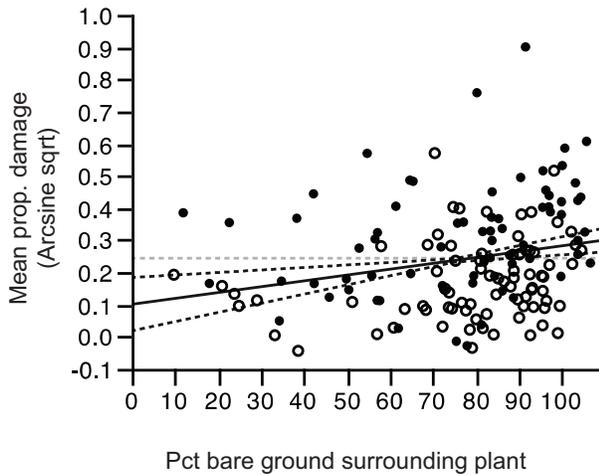


Figure 2: Leverage plot showing the amount of bare ground surrounding a plant was positively related to mean herbivore damage over 5 months (incorporating random effects of site and plant height under best model in table S1, available online; gray line is expectation under no effect). Filled circles: *Streptanthus breweri*; open circles: *Streptanthus hesperidis*.

damage was the response variable and predictors were year, species, and site nested within species as a random factor. This procedure removed variation owing to factors independent of our treatments, but the distribution of residuals was still nonnormal. We then used residuals to compare damage levels between our leaf-substrate mismatching and control treatments using ranks and a non-parametric Wilcoxon rank sum test.

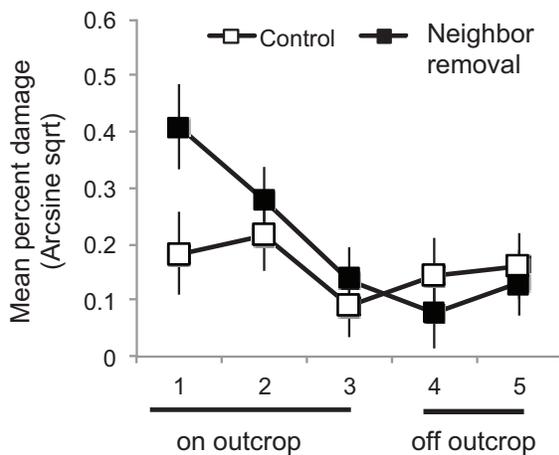


Figure 3: Experimental neighbor removal increased damage to *Streptanthus breweri* and *Streptanthus hesperidis* on serpentine outcrops but not in adjacent more vegetated nonserpentine areas. Pairs were transplanted into positions along replicated transects across a vegetation gradient from serpentine outcrop (positions 1–3) to nonserpentine grassland (positions 4 and 5). The picture illustrates the position variable for a single transect at one outcrop. The best model (table S2, available online) included covariates plant height and the amount of biomass removed in the weeding treatment, as well as position (outcrop), neighbor removal, and their interaction.

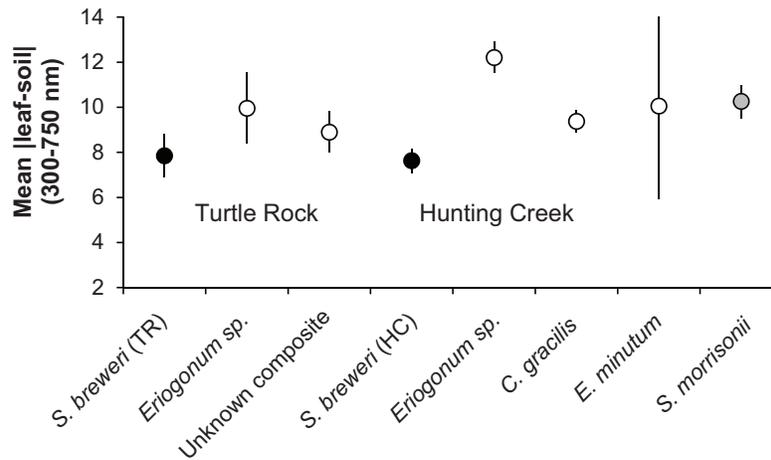


Figure 4: Leaf-soil substrate matching (mean absolute value of difference in reflectance between leaf and substrate color across 300–750-nm wavelengths) across two outcrops is closer in *Streptanthus breweri* than in companion species. Gray symbol: *Streptanthus morrisonii* is a close, green-leaved relative, while the other companion species come from diverse families (table S3, available online).

set supports the role of enemies as selective agents on outcrop-inhabiting *Streptanthus*.

Experiment 1B: Attack Rates on Caterpillar Models. Polymer larval models on serpentine substrates were attacked by birds (as inferred by beak marks left) at five times the rate as in the adjacent grassland over a 3-week period (5/70 [7%] attacked in grassland and 29/83 [35%] attacked on serpentine; $\chi^2 = 15.73$, $df = 1$, $P < .001$; 24 models were missing or ambiguous, but these models did not differ significantly in their frequency across habitat type ($\chi^2 = 0.28$, $df = 1$, $P = .59$)). These results support our hypothesis that ability to survive on outcrops must include effective defense against, at least, vertebrate enemies.

2. Does Coloration Play a Role in Defense?

Observation 2A: Leaf-Substrate Matching with Spectrometer. Reflectance measurements of leaf and soil spectra ranging from UV (300) through IR (750 nm) showed that *S. breweri* plants are more closely matched to their surrounding substrate than are companion green-leaved plant species growing on the same outcrops ($P < .001$; fig. 4; table S3) and than green-leaved relative *S. morrisonii*, with which it often co-occurs. There was no reflectance in the UV for either rocks or leaves, which was confirmed with photographs taken under UV light (figs. S1, S2).

Observation 2B: Leaf-Substrate Matching with Images. From images, RGB spectra of local *S. breweri* plant populations were significantly more similar to the RGB spectra

of their local substrate (same image) than to spectra of substrate from images of other outcrops drawn at random (fig. 5; $P < .001$ for RGB; table S4), supporting a hypothesis of crypsis. Moreover, this similarity is not attributable to bias from being in the same light environment or image, as there were no significant spectral differences between $|LF-BSQ_{\text{Same}}|$ and $|LF-BSQ_{\text{Rand}}|$. Thus, there appears to be some advantage of close leaf matching to substrate, above and beyond brown leaf color.

Experiment 2A: Experimental Mismatching of Leaf and Substrate. Under the “crypsis as defense” hypothesis we predicted that experimental leaf-substrate mismatching should increase damage rates by increasing detection or leaf recognition. After effects of species, site, and year were accounted for, we found significantly higher rates of damage in plants with sifted soil and sand backgrounds than in controls (Wilcoxon rank sum test $Z = -3.197$, $P = .001$; table S5). When analyses were conducted for sand versus controls and sifted soil versus controls separately, plants in both mismatching treatments had significantly higher damage rates than controls ($P < .02$; table S5). Mismatching effects were largely driven by *S. breweri*, which incurred, on average, 8% more damage in mismatched than control treatments; plants of this species emerge earlier, are typically at least twice as large as *S. hesperidis*, and received more damage in these experiments (mean 18% vs. 4%) than they did in field surveys.

Discussion

Taken as whole, our results show that enemy pressure is greater in sparsely vegetated areas for both plants and

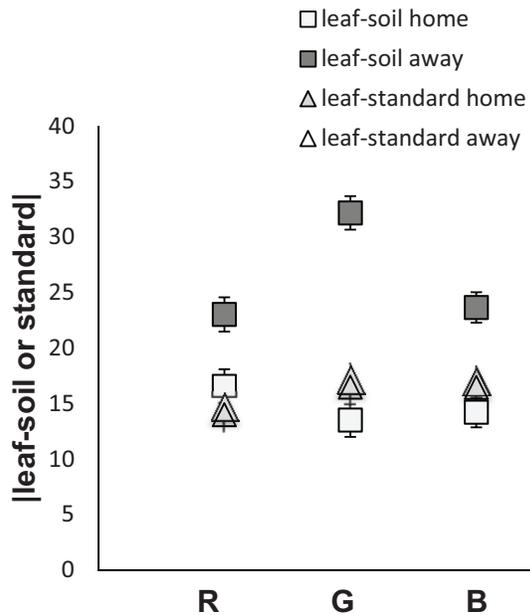


Figure 5: Leaf-soil color matching in *Streptanthus breweri* is closer with home outcrop substrate (open squares) than with other outcrops (filled squares); a control standard brown color square identical across all environments shows no differences between leaf RGB (red, green, blue) and standard RGB in home and away outcrop images (triangles), suggesting that the matching result is not a function of shared light conditions on outcrops or images (table S4, available online).

“undefended” caterpillar models, and that this pressure is, at least in part, due to apparency. We suggest that leaf coloration can serve as a crypsis defense against apparency for palatable plants because (a) increased leaf damage is correlated with reduced plant fitness in both *Streptanthus breweri* and *Streptanthus hesperidis* in both observational and experimental studies, (b) leaves of *S. breweri* populations are more closely matched to their home outcrop than to other outcrops, (c) neighbor removal significantly increased damage rates, and (d) experimental mismatching between leaves and substrate also increased damage, suggesting a role for apparency per se.

While apparency has been a factor invoked to explain patterns of plant defense for decades, it has been difficult to determine its importance because apparency may depend on the herbivore (Parmesan 1991). Moreover, many nonexclusive mechanisms can explain increased attack rates on more isolated plants, a metric commonly used for apparency (Rausher 1981; Karban and Courtney 1987; Masumoto et al 1993). Aside from being more conspicuous, as we have suggested, outcrop plants surrounded by bare ground rather than by vegetation might also experience warmer daytime temperatures. Thus, plants in such

microsites could be experiencing more damage through herbivore preference for warmer microhabitats (Velde et al. 2011). The increased damage that isolated plants suffer could also be the result of herbivore-specific behaviors such as increased time spent on isolated plants (Parker 1984) or host selection consistent with “spreading the risk” behaviors in which ovipositing butterflies do not lay on plants in proportion to their density (Root and Kareiva 1984).

However, increased conspicuousness per se has also been supported as a mechanism through which isolated plants experience increased damage from herbivores. Wiklund (1984) writes, “It is evident that all of the butterflies that never alight on non-host plants during the oviposition flight, like *P. machaon*, *Gonepteryx rhamni*, ... all use visually ‘apparent’ host plants that can be oriented towards from a distance and also approached and alighted on horizontally.” Similarly, Rausher (1981) used experimental neighbor removal as we did and found higher rates of oviposition by pipevine swallowtail females on isolated plants (see also Masumoto et al. 1993); greater susceptibility to discovery was the primary reason underlying this pattern, as neither differences in host plant quality nor predation could explain this pattern. Moreover, butterfly oviposition efficiency decreased by half when surrounding unacceptable nonhost vegetation grew larger later in the season (and was not an effect of butterfly aging). Additionally, in two recent studies of mammalian browsing and lycaenid butterfly oviposition, hosts that were more emergent from local vegetation canopy, and hence also more apparent, suffered more damage (Miller et al. 2007; Sevens 2011). The ratio of host plant height to canopy height was the best (for lycaenids) or one of the best (for mammals) predictors of damage after numerous other variables were considered. In the lycaenid study, when short *Rumex* host plants were obscured from searching butterflies by a tall exotic grass canopy, they were used less often; tall exotic grass canopy might also explain why weeding small areas around short *S. breweri* and *S. hesperidis* in the invaded grassland habitat in our study did not increase damage in our experiments. These two studies and ours also support the idea that despite differences in sensory perceptions of herbivores, plants can be consistently apparent or unapparent to a diversity of herbivores. Finally, we note that many of the mechanisms described above, including apparency, can result in greater attack rates in barer habitats, and all would contribute to selection for increased defense by plants and animals inhabiting barer substrates.

Brown cryptic leaves may be defense against increased apparency and enemy pressure on bare substrates; however, alternative hypotheses for “earthy” leaf coloration other than crypsis must be also considered. The anthocyanins contributing to the gray and brown color of ser-



Figure 6: Possible soil-matching species in greywacke scree in New Zealand. *Notothlaspi rosulatum* (top left) and *Lignocarpa carnulosa* (top right); photographs copyright S. Y. Strauss). *Bottom left*, South African Aizoaceae *Lithops lesliei*; *bottom right*, *Nanathus vittatus* (photographs copyright S. Siebert).

pentine-growing species likely serve multiple functions, including conferring UV protection and drought tolerance (Cooney et al. 2012; Gould 2004), as well as direct defense (Lev-Yadun and Gould 2009; Manetas 2006). Also, increased red coloration in leaves and stems is a general and well-documented stress response of many plant species. We suggest that the pathways leading to reddish coloration serving other functions, including as a stress response, may have been co-opted to serve a crypsis defense role. We do not know of other agents of selection that would specifically favor leaf-substrate color matching, as opposed to the presence of brown leaf color per se. One study has experimentally examined the role of brown bracts as mimics of dead leaves to protect the flowers of a parasitic plant (Klooster et al. 2009). Experimental bract removal increased damage to flowers and stems, supporting a possible role for mimicry of dead leaves.

Crypsis through substrate matching has been suggested in other, diverse plant species, and all these species also grow in areas with little green vegetation (fig. 6). At least

five species from diverse families growing on greywacke scree in New Zealand have gray leaves (suggested as a crypsis defense in Burns 2010; fig. 6), many of the South African Aizoaceae, long thought to be stone mimics, are consumed by rodents (fig. 6; S. Siebert, personal communication). Leaf mottling in forest understory herbs was hypothesized to be a camouflage defense in early spring before leaf-flush of other vegetation (Givnish 1990), and leaf patterning due to variegation has been shown to be favored in open sites in otherwise dense tropical forests (Smith 1986). In none of the latter cases, however, has the adaptive value of leaf coloration (through pigmentation) been experimentally assessed with respect to apparency (Smith 1986 used reciprocal transplant experiments but did not assess apparency per se as a driver of herbivore attack differences).

We suggest that apparency is also a problem for animal species inhabiting bare outcrops. Our caterpillar models suffered higher attack rates from birds on outcrops than in vegetated areas, suggesting that at least for late instars,



Figure 7: *Top left*, *Euchloe hyantis* green cryptic larva on *Streptanthus* fruit (photograph copyright S. Y. Strauss). *Top right*, *Pontia sisymbrii* larva on *Streptanthus hesperidis* (having eaten all flowers/fruits; photograph copyright N. I. Cacho). *Center left*, monarch butterfly larva (*Danaus plexippus plexippus*; photograph copyright K. Mooney). *Bottom left*, grasshopper *Agymnastus ingens* (Gerald and Buff Corsi copyright California Academy of Sciences) in Marin County and (*bottom right*) at our sites (photograph copyright S. Y. Strauss).

coloration may serve in enemy defense against vertebrate predators for several herbivores of *Streptanthus*. Other studies have shown that animal coloration is under selection for substrate matching in vulnerable mice living in sparsely vegetated sand dunes bare habitats. Using models of light- and dark-colored mice in sand habitats, Vignieri et al. (2010) showed that stabilizing selection from enemies maintains coat-substrate matching and crypsis, as mammalian and bird predators selected against models that were both lighter and darker than the local substrate. In contrast, slow-moving mammalian carnivores inhabiting barer habitats more often have warning color and a higher incidence of noxious anal defensive secretions (in phylogenetically controlled contrasts; Stankowich et al. 2011). These patterns support the hypothesis for of a need for greater investment in defense in these barer habitats (see also Stankowich and Caro 2009). In our serpentine system, coloration and apparency also may play a role in animal defense. While the majority of pierid caterpillars, such as *Euchloe hyantis*, are green with a lateral white stripe, rest vertically on stems and are considered cryptic (Kingsolver and Gomulkiewicz 2003; fig. 7), the far more common species at our sites, *Pontia sisymbrii*, is strikingly black, yellow, and white striped. This coloration could be aposematic or possibly mimetic of a model with warning colors such as a monarch butterfly larva, which occurs nearby off serpentine (fig. 7); to date, we do not know whether *P. sisymbrii* is toxic or a Batesian mimic. In addition, female *Agymnastus ingens* grasshoppers at our sites are flightless, sedentary, and appear cryptic and “rock-like” (fig. 7). Thus, animals regularly inhabiting our outcrops may use coloration defense mechanisms reflecting the challenges of apparency in barer sites, as do plants.

In general, if enemy pressure is, or has been, greater on barer soils, then we predict that species successfully inhabiting those habitats must have adapted to apparency by being largely inedible (*a*), or if palatable, by having other defenses such as crypsis, escape, mimicry, etc. (*b*). By this logic, we predict that green-leaved, conspicuous plants on outcrops should be highly defended and suffer low damage. Consistent with this idea, we find low levels of damage on green-leaved, nonmustard companion species and also low levels of damage on green-leaved congener *Streptanthus morrisonii*, which often co-occurs with *S. breweri* (S. Y. Strauss and N. I. Cacho, unpublished data).

In conclusion, we present evidence supporting two major points: (1) both palatable plants and undefended insect models inhabiting bare, stressful soil habitats with low vegetative cover suffer high attack rates from enemies and thus must adapt to high enemy pressure for survival; and (2) apparency per se may favor increased defenses in both plants and animals. Several authors have emphasized the increased costs of replacing plant tissues in stressful low-

nutrient soils as a selective pressure favoring increased defense in these environments (Coley et al. 1985; Fine et al. 2006; Van Zandt 2007). We suggest that increased enemy pressure caused, at least in part, by increased apparency in simplified searching environments could also drive increased investment in defense in plant specialists of bare habitats. Costs of defense, anthocyanin production (Burger and Edwards 1996; Nikiforou et al. 2010), and other defense adaptations may result in trade-offs in plant competitive ability (Fine et al. 2006), thereby limiting plant distributions to harsh soils and ultimately contributing to the high rates of endemism associated with harsh environments. In general, despite diverse sensory abilities of enemies, apparency may be a useful framework to better understand trade-offs experienced by plants and animals living in bare habitats.

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