

## Apparency revisited

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### Abstract

How easy a plant is to find, or its apparency, is thought to shape plant defenses. Recent meta-analyses suggest that the types of plant defenses employed are not well-predicted by apparency, or apparency can be confounded with life history traits like woodiness and stature. Here, we suggest that the searching environments in which plants grow also influence plant apparency and should thus affect investment in plant defense. Specifically, bare, unvegetated environments may result in greater apparency of inhabitants of all statures to enemies, as a result of loss of associational resistance. We make several predictions about plant defenses in simple searching environments. (1) Plants living in simple searching environments should be more highly defended than plants living in more vegetated, complex searching environments. (2) Plant defenses involving signals—both, signals serving to hide plants and aposematic signals—should be favored in simple searching environments. (3) Levels of damage from enemies in simple searching environments should be related to defensive strategy (resistance, aposematism, mimicry, or crypsis); apparent plants should have low damage, because, as they are easily found, they should be well-defended through physical or chemical defense. In contrast, predictions about damage levels in cryptic plants are harder to make, as damage reflects both whether plants are encountered or not, as well as overall palatability. If crypsis is favored in more palatable species, as has been suggested previously, we predict that cryptic plants should have greater variance in damage and greater maximum damage, if, once found, plants are palatable. (4) Organisms from diverse evolutionary lineages inhabiting the same simple searching environments should adapt to selection from apparency by converging on similar background matching or aposematic defenses. We then test some of these predictions with descriptive data collections in two simple searching environments: largely unvegetated graywacke scree mountaintops of New Zealand and serpentine barrens of northern California (USA). We find that plants that are more apparent (i.e., do not match local rock color as measured across 300–700 nm wavelengths) are more defended, as inferred from mean damage received. In contrast, cryptic species in the same habitats get 7× more heavily damaged, once found, suggesting overall greater palatability. There was no evidence of greater variation in damage, as measured by coefficient of variation, but maximum damage was much greater on cryptic species in both habitats. Convergence on gray substrate is found in diverse species of plants in New Zealand, as well as by scree-living grasshoppers; in California, grasshoppers have also converged on substrate color, and seed color of a non-cryptic plant also matches local outcrops. Considering searching environment and enemy searching abilities when evaluating plant apparency to enemies may shed more light on this challenge to plants.

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### Introduction

How easy a plant is to find, or its apparency, is a characteristic that has been thought to shape plant defenses (Feeny, 1976; Rhoades & Cates, 1976). Apparent plants are those that are predictably or easily found. As originally framed,

apparency is also linked to plant life history; it is argued that larger perennial plants like trees are reliably found in the same places year after year, and may be oriented to from great distances by herbivores. In contrast, plants that are in the landscape only under some conditions (e.g., after disturbance or fire) are annually variable in densities or small in stature, may be less apparent to enemies and less reliably found.

Apparency theory predicts that apparent and unapparent plants are defended in different ways. Apparent plants must be able to ward off all comers, whereas unapparent plants are expected to have defenses primarily against more generalized herbivores, while escaping specialists through unpredictability in space and time. Apparent plants are predicted to have tough, well-defended leaves that contain energetically expensive defenses that act against all herbivores ('quantitative' defenses). Less apparent plants are predicted to employ less costly defenses that act primarily against generalized herbivores ('qualitative' defenses) (Feeny, 1976; Rhoades & Cates, 1976).

Recent meta-analyses have refuted the ability of apparency theory to predict the types of defenses employed (Endara & Coley, 2011; Massad et al., 2011). Both of these meta-analyses found that plant defenses might be better predicted by resource availability than apparency, and Massad et al. (2011) did not find consistent support that specific compound classes were selective in their efficacy against specialists vs. generalists herbivores (as predicted by apparency theory). Turcotte et al. (2014), in another recent meta-analysis, found that woody plants suffered greater levels of damage than herbaceous species, and they attributed this result to woody plant apparency. Almost by definition, apparency, as originally framed, is confounded with life history, comparing trees with herbs, for example. Leaf traits are influenced by a constellation of factors including life history, nutrient, light, and water availability (e.g., Wright et al., 2004), as well as herbivores. Moreover, life history, leaf anatomy, and growth form can be phylogenetically conserved (e.g., Zhang & Cao, 2009), as can the identity of chemical defenses at the family level (Ehrlich & Raven, 1964). For example, perennial herbs are generally larger in stature than annuals, occur in the same place for many years, and thus fit the original definition of apparent, yet their chemical defenses are not typically the same types as those found in trees. Woodiness, rather than apparency, might contribute to explain the types of defenses and attack levels found in trees and shrubs (e.g., Silvertown & Dodd, 1996).

Although apparency may not predict the types of defenses employed by plants, there is a large body of evidence supporting the idea that apparency has an important influence on the likelihood of herbivore attack

(reviewed in Barbosa et al., 2009). A big challenge has always been that apparency is in the eye, nose, or antenna of the beholder. Associational resistance, a reduction in attack rates when a plant grows intermingled with others, has been repeatedly shown (Miller et al., 2006; Barbosa et al., 2009; Castagneyrol et al., 2013) and the mechanisms can be both through olfactory or visual masking (e.g., Finch & Collier, 2000; Miller et al., 2006; Castagneyrol et al., 2013). Thus, apparency might not result in consistently similar suites of defenses across groups, nor in consistently differing communities of herbivores, but might require greater amounts of defense, and would therefore result in any accompanying trade-offs that come with defense costs.

Apparency as initially proposed was defined on the basis of encounter rates between herbivores and plants. To broaden the concept of apparency, it is useful to think not only about the inherent traits of species, but also about the environmental contexts in which these species grow. Searching environments may affect plant encounter rates with herbivores and hence plant apparency. Generally, one could predict that plants growing in areas with high encounter rates with herbivores, either because of high herbivore densities, or because of simpler (more homogeneous or more bare) searching environments, should be more defended. That increased frequency of encounters with herbivores shapes antiherbivore defense traits is supported by location of spines and physical defenses on woody plant parts eaten by large vertebrate herbivores (see Burns, 2014) and by decreased investment in defenses on islands with low herbivore densities (Vourc'h et al., 2001; Stenberg et al., 2006). In more diverse or more vegetated areas, where visual and olfactory cues are obscured by neighbors and thus where associational resistance reduces the frequency of encounters with herbivores (Floater, 2001; Barbosa et al., 2009), we would expect relaxed selection for defense (Agrawal et al., 2006). In our own work, we found that removing vegetation from around individual plants increased rates of attack from herbivores in serpentine outcrops (Strauss & Cacho, 2013), a similar result was found by Heard & Sax (2013). Below, we make a number of predictions about plant defense and apparency, focusing on herbaceous plants growing in sparsely vegetated searching environments. We then use descriptive data collections to test some of these predictions in two open habitats, graywacke scree in New Zealand, and serpentine barrens in California (USA).

We predict that plants inhabiting bare or simple environments should be more defended than plants in highly vegetated environments, owing to higher encounter rates with enemies mediated by low associational resistance. In plants, various types of defensive adaptations may be

favored in open habitats, including toxicity, aposematism, mimicry, and crypsis. We note that although these arguments are made for plants, the same effects of apparency should apply to animal defenses. For example, attack rates on plasticine caterpillars by birds were greater in less vegetated serpentine barrens than in adjacent grassland habitats (Strauss & Cacho, 2013). Carnivores living in open habitats are typically more defended by noxious secretions, presumably because they are more apparent (Stankowich et al., 2011).

As detection is context dependent, visual or chemical signals, either to hide or to advertise, may be especially important in environments where plants are easily found. Specifically, we predict (1) greater incidence of crypsis (background matching) or mimicry of inedible things when species are not well-defended (Burns, 2010), or (2) greater incidence of aposematic coloration when species are well-defended in easy searching environments. In an analysis of swallowtail butterfly aposematism, Prudic et al. (2007) showed that the signal environment where larvae feed, i.e., the shape of the leaf on which they fed, was more closely associated with aposematic coloration than was the toxicity of host plant species. Similarly, warning coloration is more common in mammalian carnivores occupying open rather than closed habitats (Stankowich et al., 2011). Thus, the environment in which an organism lives, not just its traits, has an impact on its apparency and on encounter rates with enemies.

Background matching, although often associated with animals (Vignieri et al., 2010; Robertson et al., 2011; Isaac & Gregory, 2013), has also been shown to be a visual defense of plants in bare or open environments (Givnish, 1990; Lev-Yadun, 2006; Burns, 2010; Strauss & Cacho, 2013; Niu et al., 2014). In rocky Californian serpentine soil habitats, brown and gray leaf coloration of mustards in the genus *Streptanthus* match the local rocky serpentine substrates (Strauss & Cacho, 2013). Experimentally mismatching plants from soils by placing sand or sifted soils beneath leaves increased rates of attack from herbivores. In the same environments, seeds of *Acmispon wrangelianus* (Fisch. & CA Mey.) DD Sokoloff (Fabaceae) also match local rock outcrop color (Porter, 2013). In other systems, the mottled leaves of understory spring ephemerals that leaf out before the forest canopy are proposed to serve to visually blend plants into the background of leaf litter (Givnish, 1990; see also Fadzly et al., 2009; Fadzly & Burns, 2010). In China, gray-leaved plants suffered less attack than green-leaved conspecifics on gray scree slopes (Niu et al., 2014), potentially a crypsis defense. In addition to visual crypsis, plants might also exhibit chemical crypsis by reducing emissions of volatile organic compounds,

but to our knowledge, this possibility has yet to be tested.

Aposematism in plants may also be chemical (Weldon, 2013). In Californian mediterranean grasslands, prolonged drought in summer results in vegetation that is dry and golden brown, typically from late May through October. A few herbaceous plant species, of diverse families, can grow in these dry hot summer conditions, for example: tarweeds [*Hemizonia* and *Madia* spp. (Asteraceae)], gumplant [*Grindelia camporum* Greene (Asteraceae)], vinegarweed [*Trichostema lanceolatum* Benth. (Lamiaceae)], locoweed [*Datura wrightii* Regel (Solanaceae)], to name a few, and these green plants are quite conspicuous against a background of dry vegetation. As indicated by their common names, these plants are extremely resinous and noxious. Although resins may aid in drought tolerance (Moreira et al., 2014; but see Tognetti et al., 1997; Gonzalez et al., 2008; Krol et al., 2014), they also play a role in herbivore deterrence (e.g., Moreira et al., 2014). These plants are also all highly aromatic and produce quite different arrays of organic compounds, as they are phylogenetically diverse. Their intense aromas may serve as olfactory aposematism. In sum, in the context of apparency, we suggest that both aposematism and ‘hiding’ signals should be more common defenses in easier searching environments.

This prediction is our most tenuous, as damage levels are dependent on defensive strategy, palatability, and encounter rates. If visually obvious plants are easily found in simple searching environments then they should only survive if chemically or physically well-defended (see prediction 1). Thus, we predict that ‘obvious’ plants should be unpalatable or unsuitable rejected by herbivores, and, consequently, have very low levels of damage (prediction 3a).

In contrast, inferences on the relationship between damage levels experienced by plants with ‘hiding’ defenses, aimed at reducing the number of plant interactions with herbivores, might require more caution. Crypsis may be favored as a defense for species that are inherently more edible than their surrounding community (Burns, 2010). Many cryptic plants would thus avoid damage through hiding, but cryptic plants that were found would receive relatively high amounts of damage, resulting in high variance in damage in a population (not found = zero damage, or, if found, then high levels damage) (prediction 3b). In addition, if cryptic plants are poorly defended physically or chemically, we might expect greater maximum damage (prediction 3c), owing to their overall greater edibility once found.

If apparency in simple searching environments exerts strong selection, we predict that plants from different lineages and animals living in those same simple searching

environments should converge on similar visual defenses aimed at either decreased detection or aposematism.

We address some of these predictions with descriptive data collections from two open, bare systems: serpentine outcrops in California (CA) and barren scree slopes in New Zealand (NZ). Previous work has shown that leaves that match the rock color provide a defense through decreased apparency (e.g., Strauss & Cacho, 2013; Niu et al., 2014). Specifically, we first document through reflectance analysis that plants that seem unapparent (rock-colored) to human eyes are rock-colored across a range of spectral wavelengths, and explore specific wavelengths at which plants are best matched to rocks. We then test prediction 3 by asking: do apparent and unapparent plants, as defined by their degree of substrate-matching, experience different levels of herbivory? Specifically, do apparent plants experience low damage levels (prediction 3a)? And is there greater maximum damage and more variation in damage in cryptic plants than in co-occurring plants that are less well-matched to their substrate (predictions 3b and 3c)? We also describe parallel adaptations by plants and animals to these environments (prediction 4).

## Materials and methods

### The systems

In NZ scree habitats, gray-leaved plant species are from diverse families (in this study, Ranunculaceae, Caryophyllaceae, Brassicaceae, Apiaceae, Asteraceae; Figure 1, Table S1). In CA rocky outcrops, we have previously investigated two brown-leaved mustard species in the genus *Streptanthus* [(s.l. (Brassicaceae) Cacho et al., 2014], *Streptanthus breweri* Gray and *Streptanthus hesperidis* Jeps. (Strauss & Cacho, 2013). Several other species in this group also have rock-colored brown or gray leaves (*Streptanthus drepanoides* Kruckeb. & JL Morrison, *Streptanthus barbiger* Greene, *Caulanthus amplexicaulis* S Watson), as well as the legume *Acmispon humistratus* (Benth.) DD Sokoloff (Fabaceae), growing in these same rocky areas. For many of these species, the rock-like coloration of leaves has an ontogenetic component, being primarily found in vegetative rosette stage, and often lost at flowering (see also Fadzly et al., 2009). In both regions, plants are fed on by a variety of vertebrate and invertebrate herbivores (for the CA system, see Strauss & Cacho, 2013).

In NZ, we found many moth larvae on *Notothlaspi rosulatum* Hook. f. (Brassicaceae) and insect damage to *Haastia recurva* Hook. f. (Asteraceae) apices; we also saw aphids on *Lignocarpa carnosula* (Hook. f.) JW Dawson (Apiaceae) and grasshoppers feeding on plants. Extant vertebrate herbivores are mainly introduced (rabbits and deer), but we saw relatively little browsing in our surveys. Until a

couple of 100 years ago, moas, large emu-like herbivorous ratites, were important herbivores in New Zealand. Reconstruction of habitat use from plant fossils in moa coprolites has placed two of the four species as feeders in alpine herbfields, one of them, *Pachyornis elephantopus* (Owen), as an alpine herbfield specialist (Wood et al., 2013). The visual capabilities of various bird classes have recently been reviewed; no extant ratites can see in the UV (Hart, 2001a,b), unlike passerines, and they seem to have spectral sensitivity in the 500–560 nm range. Insects can see in the UV.

### Determining apparency

*Are gray-leaved plants better matched to scree than non-gray leaved plants across a range of spectra?* Here, to classify plants as apparent or unapparent, we examined the degree to which plant species matched the color reflectance of the rock environments in which they grew across wavelengths encompassing UV to infrared (300–700 nm). We also evaluated spectral reflectance mismatch at specific portions of the spectrum, for example, to isolate UV from other spectral components. In a previous study, brown-leaved *S. breweri* species were indeed more closely matched to their substrate than were green-leaved species growing on the same outcrops, averaged across all wavelengths (Strauss & Cacho, 2013; Figure 2). Olfactory apparency was beyond the scope of this study.

To determine whether NZ gray-leaved plants matched the scree more than other-colored leaved plants, and at which portions of the spectrum the match was closest, we measured leaf reflectance spectra for 5–20 individuals per species using a USB Ocean Optics 2000 spectrometer and Xenon Pulse X2 lamp Ocean Optics light source (Ocean Optics, Dunedin, FL, USA). Across four sites, we collected plants and rocks adjacent to plants and measured reflectance of rocks and leaves. Reflectance properties were measured as the proportion of reflectance calibrated against white and black standards. The fiber optics probe was placed directly on the leaf or rock. Reflectance readings were averaged across 20-nm intervals from 300 to 700 nm with SpectraSuite software (Ocean Optics). We measured deviation from rock color by using leaf—rock reflectance across the spectrum. We then examined overall deviation of leaf from rock color averaged across the whole 300–700 nm spectrum, as well as over subsets of the spectrum determined a priori based on visual capabilities of different herbivore groups. We analyzed separately 300–340 (UV; insects and some birds), 400–500 (ratites), and 550–650 nm (green and longer wavelengths).

We used Standard Least Squares models to test whether gray-leaved NZ species were better matched to surrounding rocks averaged across the spectrum, and to determine

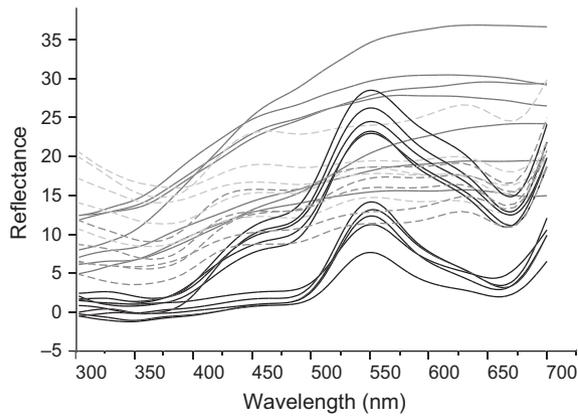


**Figure 1** Unapparent and apparent plants on graywacke scree in New Zealand. From top left: *Lobelia roughii*, *Lignocarpa carnosula*, *Notothlaspi rosulatum* (photo by M Walker), *Epilobium* spec. Landscape with many apparent *Epilobium* spp. and unapparent (invisible here) *L. carnosula* in this picture. Gray scree grasshopper, likely *Brachaspis nivalis* (photos by SY Strauss & MW Schwartz, unless noted differently).

whether there were particular parts of the spectrum in which leaves were more closely matched to surrounding rocks. Our response variable was the deviation of leaf from rock color measured in nm as described above and predictors were: fixed effect leaf color (gray/non-gray) and species nested within leaf color as a random factor. All

analyses were done using JMP Pro 10.0.2 (SAS Institute, Cary, NC, USA, 2012).

*Do rock-colored plants experience greater mean or more variable damage than other species growing in the same areas?* To test whether substrate-matching plants receive



Scree (dark gray, solid high)  
*Notothlaspi rosulatum* (light gray, dashed)  
*Lignocarpa carnosula* (dark gray, dashed)  
*Epilobium crassum* (black, solid high)  
*Wahlenbergia albomarginata* (black, solid)

**Figure 2** Reflectance of pieces of scree, gray-leaved *Lignocarpa carnosula*, gray-leaved *Notothlaspi rosulatum*, and green-leaved species *Wahlenbergia albomarginata* and *Epilobium crassum*. Note distinct peak at 550 nm (green) and lower reflectance in the UV (300–375 nm).

more damage or more variable damage than co-occurring, less-matching plants, we examined natural damage levels in rock-colored plants (gray or brown-leaved) and nearby green- or non-rock colored plants (some of these were deep red in NZ). In both ecosystems, we visually estimated the damage to every leaf and then took the average percent leaf removal across all leaves on the plant. These estimates were done in the field (NZ) and in CA, estimates of leaf damage were made from images of cryptic and non-cryptic species at the same field sites, often in the same image (Table S1). In NZ, we examined damage to six species of gray-leaved plants: *N. rosulatum*, *H. recurva*, *L. carnosula*, *Ranunculus paucifolius* Kirk (Ranunculaceae), *Gingidia enysii* (Kirk) JW Dawson (Apiaceae), and *Stellaria roughii* Hook. f. (Caryophyllaceae) and non-scrree-matching species from four other families and across six sites on the South Island: Broken River ski area, Foggy Peak, Craigieburn Ski Area, Mt. Cheeseman, Mt. Robert, and Castle Hill (Table S1). In CA, we assessed matching of five soil-colored *Streptanthus* and *Caulanthus* species (Brassicaceae), and several green-leaved species, including one green-leaved *Streptanthus*, across 11 sites in Lake, Napa, Butte, and San Bernardino counties.

We used restricted maximum likelihood analyses with the response variable mean % damage (arcsine  $\sqrt{x}$ -transformed) and with predictors leaf color (rock-colored: yes or no) as a fixed factor with site (random factor) and species nested within leaf color (random factor). To

test whether soil-colored species received greater maximum or more variable damage, we calculated the maximum damage as well as coefficient of variation (CV) of damage for each species by site (only for cases with  $n > 4$  observations per species) and then compared mean maximum and mean CV of rock-colored species to that of other species using the model: CV = leaf color and site (fixed effects) with species (leaf color) as a random factor.

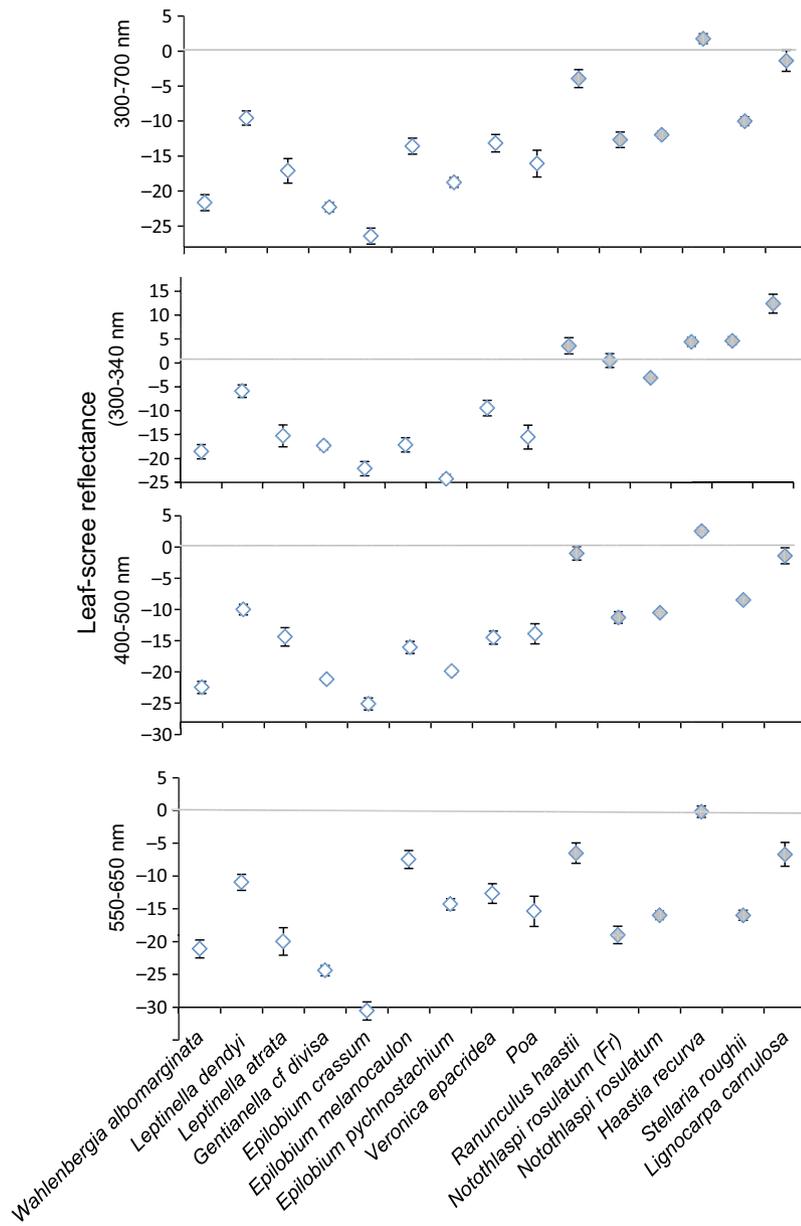
## Results

### Are gray-leaved species more closely matched to scree than other species, and are there specific wavelengths where matching is closest?

Scree in NZ had some reflectance in the UV (Figures 2 and 3, Table S2). In all comparisons of gray- vs. other color-leaved species, the gray species were significantly more closely matched to scree color ( $P < 0.0001$  in all comparisons; Table S2). However, inspection of data reveals that matching was especially close in the UV (300–340 nm) across all species (Figures 2 and 3), suggesting a selective role of insects, birds, or other herbivores that see in the UV. At longer wavelengths (400–500, 550–650 nm), three gray species remain tightly matched to scree color as evidenced by their near-zero deviation from rock color (Figure 2; *H. recurva*, *Ranunculus haastii* Hook. f., and *L. carnosula*), whereas *N. rosulatum* and *S. roughii* were less matched. Only one non-gray species, with green-gray leaves, *Leptinella dendyi* (Cockayne) DG Lloyd & CJ Webb (also Asteraceae), had comparable substrate matching at these longer wavelengths. To the human eye, *N. rosulatum* was the most cryptic, because of its scree-like, wedge-shaped leaves in addition to its gray coloration; other species had leaf shapes that were much more different from scree shapes (Figure 1); leaf shape may represent another axis of visual defense not assessed here. The three matching species at green wavelengths (within moa visual range) belong to families Asteraceae and Apiaceae and genus *Ranunculus*, all of which are recorded from moa coprolites (Wood et al., 2013).

### Are 'apparent' plants inferred to be well-defended chemically or physically? Do rock-colored species receive more variable damage or greater maximum damage than 'apparent' species?

Apparent plants in NZ scree received, on average, 0.3% damage, substantially lower than the global average level of damage recorded in meta-analyses (5.3%; Turcotte et al., 2014), and lower than damage to the cryptic species (see below). These results suggest that apparent plants are well-defended chemically or physically (prediction 1; Figure 4). In CA serpentine environments, green-leaved apparent species received an average of 3% damage, again lower



**Figure 3** Leaf-rock matching (mean difference in reflectance  $\pm$  SE) across wavelengths; zero is perfectly matched (see Materials and methods). From top: average across all wavelengths 300–700 nm, near UV wavelengths 300–340 nm (insect and some bird vision), and other portions of spectrum. Species with a gray symbol are gray to human eye. Gray-leaved species are better matched to rock averaged across all wavelengths. All are well-matched at UV, some (*Ranunculus haastii*, *Haastia recurva*, and *Lignocarpa carnosula*, all from different families) are well-matched across the spectrum.

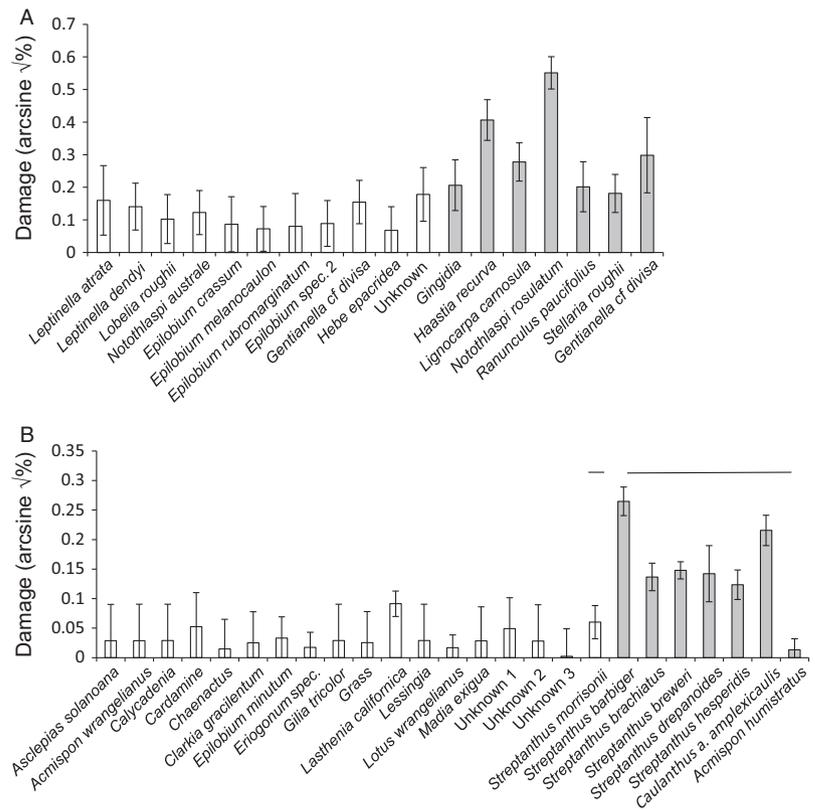
than the average from meta-analyses. Together, these data suggest that ‘apparent’ plants in open searching environments are well-defended (prediction 1).

In both NZ scree and CA serpentine bare environments, rock-colored species were more damaged, on average, than green- or other color-leaved species. In NZ, the model explained 33% of the variance in damage and gray-leaved species received an average of 13% damage vs. 0.3% in apparent species ( $P < 0.003$ ,  $n = 447$ ; Figure 4, Table S3). In CA serpentine outcrops, the *Streptanthus* clade (Brassicaceae) dominated these rock-colored species (Table S1). To examine whether higher levels of damage in CA rock-

leaved species was a result of a greater susceptibility to damage of Brassicaceae compared to other plant families, we conducted a contrast comparing just green-leaved *Streptanthus morrisonii* FW Hoffmann with the other rock-colored *Streptanthus* (s.l.) species. Green-leaved *S. morrisonii* received significantly less damage than the cryptic *Streptanthus* species (0.03 vs. 15%;  $P < 0.01$ ), and had the lowest mean damage of any *Streptanthus* (Figure 4), suggesting more chemical or physical defenses in this green-leaved *Streptanthus*.

Cryptic species did not experience greater variance in damage in either CA (CV: d.f. = 1,10.8,  $P = 0.33$ ) or NZ

**Figure 4** Mean ( $\pm$  SE) leaf damage (arcsine  $\sqrt{\%$ ) for background matching and non-matching (apparent) species from New Zealand and California. Species with soil-colored leaves (gray bars) receive more damage than other, co-occurring, unmatched species in the same habitats (white bars). (A) Gray-leaved species get more damage in New Zealand scree habitats (F-test: see results). (B) Brown- or gray-leaved species get more damage than green-leaved species in serpentine soil outcrops of California. Green-leaved *Streptanthus morrisonii* gets significantly less damage ( $P = 0.01$ ; 1 d.f. contrast denoted with lines) than brown- or gray-leaved species in the same *Streptanthus* (s.l.) clade, often growing in the same rock outcrops.



(d.f. = 1,16,  $P = 0.53$ ), contrary to our predictions. Six non-cryptic species in CA and one non-cryptic species in NZ had mean of zero damage with  $n > 5$  individuals censused; no cryptic species had zero mean damage, in either CA or NZ. These no-variance, zero-damage species could not be included in the CV analyses (as CV of mean = 0 is undefined).

Cryptic, unapparent species experienced greater (ca. 7 $\times$ ) maximum damage than did non-cryptic species [NZ: d.f. = 1,16.65,  $P < 0.0001$ ; gray-leaved: mean ( $\pm$  SD) maximum damage =  $63.6 \pm 8\%$ ; apparent species:  $9.27 \pm 6.4\%$ ; CA: d.f. = 1,26.2,  $P < 0.001$ ; rock-colored:  $25.4 \pm 4.6\%$ ; green:  $5.95 \pm 4.6\%$ ]. This result suggests that, once found, cryptic species are less defended than apparent species growing in the same habitats. It supports the hypothesis that crypsis is favored in plant species that are less defended than the surrounding plant species (Burns, 2010).

## Discussion

Although apparency theory might not predict the kinds of defenses exhibited by plants (Endara & Coley, 2011; Mas-sad et al., 2011), plant apparency may predict the degree to which plants are defended. A fruitful way forward is to

consider apparency in light of searching environments and how environments might affect encounter rates with enemies. It is clear from a large body of literature that plants gain refuge from herbivores not just from their inherent qualities but also from their neighborhoods (reviewed in Barbosa et al., 2009). Simple searching environments will increase encounter rates between herbivores and host plants, and between predators and prey. We suggest that this increased likelihood of encounter may impose strong selection for increased defense and increased signaling—visual, chemical, and physical—against enemies.

Obviousness to enemies may be a strong selective pressure favoring defense in bare environments. Examples of background matching in non-green leaved plants are exclusively found in habitats with minimal green vegetation (Porter, 2013; Strauss & Cacho, 2013; Fadzly et al., 2009; Niu et al., 2014). Recently, Cacho & Strauss (2014) have shown that the evolution of the ability to inhabit serpentine soils, chemically stressful soils that are relatively devoid of vegetation, was preceded not by use of chemically similar soils, but rather by use of bare habitats. Adaptation to ‘bareness’ in the *Streptanthus* clade was more conserved than any elemental property of soil. Occupation of bare environments is likely the result of a large number of adaptations, including those needed to deal with ene-

mies and apparency in these simplified searching environments.

The same challenge of apparency to enemies in easy searching environments is also present in animals. We found that attack rates by birds on plasticine caterpillars were greater in more open, less vegetated serpentine habitats than in adjacent grassland habitats (Strauss & Cacho, 2013). Noxious defensive secretions in mammalian carnivores (e.g., skunks) are also associated with inhabiting open habitats, again supporting the hypothesis of a greater need for defense when organisms are more easily encountered by enemies (Stankowich et al., 2011).

We predict that organisms that are conspicuous in easy searching environments are unpalatable, physically defended, or Batesian mimics. We found in both CA rocky outcrops and in NZ scree that non-matching ‘apparent’ plants received less damage than the average damage recorded across all systems—0.3% (NZ) and 3% (CA) vs. 5.3% (global)—suggesting selection for greater defense. In contrast, substrate-matching plants living in the same areas received 7× greater mean and even more maximum damage than species whose leaves did not match, suggesting that crypsis is favored in more edible (i.e., less chemically or physically defended) species. We had also predicted that variation in leaf damage might be greater for cryptic species, but we did not find support for this prediction in either site as measured by CV (we note that six non-cryptic species had 0 damage on all individuals and thus could not be included in the analysis). Both cryptic and non-cryptic plants had many individual plants that received no damage. These results are purely descriptive, and, especially for cryptic species, it is difficult to infer what damage patterns mean, as they include both encounter rates and palatability. Next steps will require testing palatability of ‘apparent’ and ‘unapparent’ species experimentally, as well as manipulating apparency in the field and examining changes to damage levels (e.g., Strauss & Cacho, 2013).

Selection for background matching in response to apparency might result in diverse lineages converging on the same coloration (prediction 4). In NZ, we already noted that many species from a wide variety of plant families exhibit gray leaves—Apiaceae, Asteraceae, Brassicaceae, Caryophyllaceae, Ranunculaceae—just in our study. In northern CA serpentine, *Streptanthus* in Brassicaceae is the primary group exhibiting leaf background matching, though there are other species, like legume, *Acmispon humistratus* (Benth.) DD Sokoloff, and possibly some species of *Eriogonum*, that also seem to match their local substrates. In addition, in CA, *A. wrangelianus* does not have cryptic leaves, but it does produce cryptic seeds that are either gray-green or brown, depending on local rock out-

crop color (Porter, 2013). The convergence of plant and animal species to match their backgrounds suggests that open or simple searching environments exert similar pressures and result in similar adaptations to avoid being eaten. We find background matching coloration in response to predation in mice (e.g., Vignieri et al., 2010), lizards (Rosenblum & Harmon, 2011), gull eggs (Lee et al., 2010), and grasshoppers (Gillis, 1982; Eterovick et al., 1997), among others. In our systems, grasshoppers seem to have also responded to selection from encounters with enemies in open habitats to background match, with gray grasshoppers in NZ and rocky colored and textured ones in CA.

Other adaptations to apparency in easy searching environments may be convergence on aposematism (though organisms may not have the same aposematic look, they typically converge on the colors black, white, yellow, orange, and red; e.g., Kikuchi et al., 2014). In NZ, several *Epilobium* species are completely red (*Epilobium melanocaulon* Hook., *Epilobium pychnostachyum* Hausskn.) or have deep red edges of leaves (*Epilobium rubro-marginatum* Cockayne). These species are very visible from long distances on the gray scree. Although anthocyanins play a role in UV defense (Gould, 2004), they are being increasingly recognized as serving in direct defenses against herbivores (Manetas, 2006; Cooney et al., 2012). They also serve as aposematic signals: not only purple and white bract flags on floral displays served not just as defense but also as a signal of unpalatability in *Salvia viridis* L. (Gerchman et al., 2012). Olfactory (or more broadly, chemical) aposematism, through volatile compounds that advertise distastefulness or toxicity, may also be favored in bare environments, but these attributes were not tested. Aposematism in the form of black and white coloration in noxious carnivores is also associated with bare and open habitats (Stankowich et al., 2011).

A challenge in the study of apparency will always be that apparency depends on the sensory and dispersal abilities of the enemy. The nature of apparency will vary not only with different ways of seeing or smelling but also in whether searching environments are ‘simple’ or ‘complex’. A flying predator can traverse large distances and see from above, a small ground-dwelling predator may not find the same searching environment ‘simple’. Despite these large differences in detection abilities, enemies may overlap in some sensory aspects, and plants/animals may adapt to multiple sensory abilities. Emergence of plants from the mean canopy layer increases attack by both insect and mammalian herbivores (Miller et al., 2006; Castagnayrol et al., 2013) (though plant vigor or quality must be ruled out in these comparisons). Chemical defenses may work

against a large suite of species, from invertebrates to mammals (e.g., Lindroth & St Clair, 2013). Plants or plant parts can evolve to be cryptic to human eyes as well as cryptic to other species (Burns, 2010), including invertebrates.

To date, apparency theory has confounded apparency with woodiness and large stature. In simple searching environments, even small organisms like caterpillars or herbaceous plants can be quite apparent (Strauss & Cacho, 2013). Turcotte et al. (2014) found that woody perennial species experienced significantly greater attack than herbaceous species and they attributed this result to apparency. Herbaceous perennials, however, did not receive significantly more damage than herbaceous annuals in their study, as would be expected given that perennials are predicted to be more apparent than annuals, owing to their predictability in time and space. Taking into account searching environments might also shed light on some of these discrepancies.

In sum, the initial formulations of apparency theory were valuable in provoking us to think about encounter rates between herbivores and their hosts. Although the predictions on the kinds of defenses used by apparent and unapparent plants have not been well supported (Endara & Coley, 2011; Massad et al., 2011), perhaps because they suffered from confounding attributes of life history and phylogeny (Turcotte et al., 2014), we believe that the kernel of the ideas suggesting that encounter rates shape plant defense traits, is still valid and informative. We suggest that considering plant defenses and apparency in light of searching environments and the searching abilities of enemies may provide new predictions about defense in light of apparency.

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## References

- Agrawal AA, Lau JA & Hambäck PA (2006) Community heterogeneity and the evolution of interactions between plants and insect herbivores. *Quarterly Review of Biology* 81: 349–376.

- Barbosa P, Hines J, Kaplan I, Martinson H, Szczepaniec A & Szendrei Z (2009) Associational resistance and associational susceptibility: having right or wrong neighbors. *Annual Review of Ecology Evolution and Systematics* 40: 1–20.
- Burns KC (2010) Is crypsis a common defensive strategy in plants? Speculation on signal deception in the New Zealand flora. *Plant Signalling & Behavior* 5: 9–13.
- Burns KC (2014) Are there general patterns in plant defence against megaherbivores? *Biological Journal of the Linnean Society* 111: 38–48.
- Cacho NI & Strauss SY (2014) Occupation of bare habitats, an evolutionary precursor to soil specialization in plants. *Proceedings of the National Academy of Sciences of the USA* 111: 15132–15137.
- Cacho NI, Burrell AM, Pepper AE & Strauss SY (2014) Novel nuclear markers inform the systematics and the evolution of serpentine use in *Streptanthus* and allies (Thelypodieae, Brassicaceae). *Molecular Phylogenetics and Evolution* 72: 71–81.
- Castagneyrol B, Giffard B, Pere C & Jactel H (2013) Plant apparency, an overlooked driver of associational resistance to insect herbivory. *Journal of Ecology* 101: 418–429.
- Cooney LJ, van Klink JW, Hughes NM, Perry NB, Schaefer HM et al. (2012) Red leaf margins indicate increased polygodial content and function as visual signals to reduce herbivory in *Pseudowintera colorata*. *New Phytologist* 194: 488–497.
- Ehrlich PR & Raven PH (1964) Butterflies and plants: a study in coevolution. *Evolution* 18: 586–608.
- Endara MJ & Coley PD (2011) The resource availability hypothesis revisited: a meta-analysis. *Functional Ecology* 25: 389–398.
- Eterovick PC, Figueira JEC & Vasconcelos Neto J (1997) Cryptic coloration and choice of escape microhabitats by grasshoppers (Orthoptera: Acrididae). *Biological Journal of the Linnean Society* 61: 485–499.
- Fadzly N & Burns KC (2010) Hiding from the ghost of herbivory past: evidence for crypsis in an insular tree species. *International Journal of Plant Sciences* 171: 828–833.
- Fadzly N, Jack C, Schaefer HM & Burns KC (2009) Ontogenetic colour changes in an insular tree species: signalling to extinct browsing birds? *New Phytologist* 184: 495–501.
- Feeny P (1976) Plant apparency and chemical defense. *Biochemical Interaction between Plants and Insects* (ed. by JW Wallace & RL Mansell), pp. 1–40. Plenum, New York, NY, USA.
- Finch S & Collier RH (2000) Host-plant selection by insects – a theory based on ‘appropriate/inappropriate landings’ by pest insects of cruciferous plants. *Entomologia Experimentalis et Applicata* 96: 91–102.
- Floater GJ (2001) Habitat complexity, spatial interference, and ‘minimum risk distribution’: a framework for population stability. *Ecological Monographs* 71: 447–468.
- Gerchman Y, Dodek I, Petichov R, Yerushalmi Y, Lerner A & Keasar T (2012) Beyond pollinator attraction: extra-floral displays deter herbivores in a Mediterranean annual plant. *Evolutionary Ecology* 26: 499–512.
- Gillis JE (1982) Substrate colour-matching cues in the cryptic grasshopper *Circotettix rabula rabula* (Rehn & Hebard). *Animal Behaviour* 30: 113–116.

- Givnish TJ (1990) Leaf mottling – relation to growth form and leaf phenology and possible role as camouflage. *Functional Ecology* 4: 463–474.
- Gonzalez WL, Negritto MA, Suarez LH & Gianoli E (2008) Induction of glandular and non-glandular trichomes by damage in leaves of *Madia sativa* under contrasting water regimes. *Acta Oecologica* 33: 128–132.
- Gould KS (2004) Nature's Swiss army knife: the diverse protective roles of anthocyanins in leaves. *BioMed Research International* 2004: 314–320.
- Hart NS (2001a) Variations in cone photoreceptor abundance and the visual ecology of birds. *Journal of Comparative Physiology A* 187: 685–697.
- Hart NS (2001b) The visual ecology of avian photoreceptors. *Progress in Retinal and Eye Research* 20: 675–703.
- Heard MJ & Sax DF (2013) Coexistence between native and exotic species is facilitated by asymmetries in competitive ability and predator tolerance. *Ecology Letters* 16: 206–213.
- Isaac LA & Gregory PT (2013) Can snakes hide in plain view? Chromatic and achromatic crypsis of two colour forms of the western terrestrial garter snake (*Thamnophis elegans*). *Biological Journal of the Linnean Society* 108: 756–772.
- Kikuchi DW, Seymoure BM & Pfennig DW (2014) Mimicry's palette: widespread use of conserved pigments in the aposematic signals of snakes. *Evolution & Development* 16: 61–67.
- Krol A, Amarowicz R & Weidner S (2014) Changes in the composition of phenolic compounds and antioxidant properties of grapevine roots and leaves (*Vitis vinifera* L.) under continuous of long-term drought stress. *Acta Physiologiae Plantarum* 36: 1491–1499.
- Lee WS, Kwon YS & Yoo JC (2010) Egg survival is related to the colour matching of eggs to nest background in black-tailed gulls. *Journal of Ornithology* 151: 765–770.
- Lev-Yadun S (2006) Defensive functions of white coloration in coastal and dune plants. *Israel Journal of Plant Sciences* 54: 317–325.
- Lindroth RL & St Clair SB (2013) Adaptations of quaking aspen (*Populus tremuloides* Michx.) for defense against herbivores. *Forest Ecology and Management* 299: 14–21.
- Manetas Y (2006) Why some leaves are anthocyanic and why most anthocyanic leaves are red? *Flora* 201: 163–177.
- Massad TJ, Fincher RM, Smilanich AM & Dyer L (2011) A quantitative evaluation of major plant defense hypotheses, nature versus nurture, and chemistry versus ants. *Arthropod-Plant Interactions* 5: 125–139.
- Miller AM, McArthur C & Smethurst PJ (2006) Characteristics of tree seedlings and neighbouring vegetation have an additive influence on browsing by generalist herbivores. *Forest Ecology and Management* 228: 197–205.
- Moreira X, Mooney KA, Rasmann S, Petry WK, Carrillo-Gavilan A et al. (2014) Trade-offs between constitutive and induced defences drive geographical and climatic clines in pine chemical defences. *Ecology Letters* 17: 537–546.
- Niu Y, Chen G, Peng DL, Song B, Yang Y et al. (2014) Grey leaves in an alpine plant: a cryptic colouration to avoid attack? *New Phytologist* 203: 953–963.
- Porter SS (2013) Adaptive divergence in seed color camouflage in contrasting soil environments. *New Phytologist* 197: 1311–1320.
- Prudic KL, Oliver JC & Sperling FAH (2007) The signal environment is more important than diet or chemical specialization in the evolution of warning coloration. *Proceedings of the National Academy of Sciences of the USA* 104: 19381–19386.
- Rhoades DF & Cates RG (1976) Toward a general theory of plant antiherbivore chemistry. *Recent Advances in Phytochemistry* 10: 168–213.
- Robertson JM, Hoversten K, Gründler M, Poorten TJ, Hews DK & Rosenblum EB (2011) Colonization of novel white sands habitat is associated with changes in lizard anti-predator behaviour. *Biological Journal of the Linnean Society* 103: 657–667.
- Rosenblum EB & Harmon LJ (2011) “Same same but different”: replicated ecological speciation at White Sands. *Evolution* 65: 946–960.
- Silvertown J & Dodd M (1996) Comparing plants and connecting traits. *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences* 351: 1233–1239.
- Stankowich T, Caro T & Cox M (2011) Bold coloration and the evolution of aposematism in terrestrial carnivores. *Evolution* 65: 3090–3099.
- Stenberg JA, Witzell J & Ericson L (2006) Tall herb herbivory resistance reflects historic exposure to leaf beetles in a boreal archipelago age-gradient. *Oecologia* 148: 414–425.
- Strauss SY & Cacho NI (2013) Nowhere to run, nowhere to hide: the importance of enemies and apparency in adaptation to harsh soil environments. *American Naturalist* 182: E1–E14.
- Tognetti R, Michelozzi M & Giovannelli A (1997) Geographical variation in water relations, hydraulic architecture and terpene composition of Aleppo pine seedlings from Italian provenances. *Tree Physiology* 17: 241–250.
- Turcotte MM, Davies TJ, Thomsen CJ & Johnson MT (2014) Macroecological and macroevolutionary patterns of leaf herbivory across vascular plants. *Proceedings. Biological sciences* 281: pii: 20140555.
- Vignieri SN, Larson JG & Hoekstra HE (2010) The selective advantage of crypsis in mice. *Evolution* 64: 2153–2158.
- Vourc'h G, Martin JL, Duncan P, Escarre J & Clausen TP (2001) Defensive adaptations of *Thuja plicata* to ungulate browsing: a comparative study between mainland and island populations. *Oecologia* 126: 84–93.
- Weldon PJ (2013) Chemical aposematism. *Chemoecology* 23: 201–202.
- Wood JR, Wilmshurst JM, Richardson SJ, Rawlence NJ, Wagstaff SJ, et al. (2013) Resolving lost herbivore community structure using coprolites of four sympatric moa species (*Aves: Dinornithiformes*). *Proceedings of the National Academy of Sciences of the USA* 110: 16910–16915.
- Wright IJ, Reich PB, Westoby M, Ackerly DD, Baruch Z, Bongers F, et al. (2004) The worldwide leaf economics spectrum. *Nature* 428: 821–827.

Zhang JL & Cao KF (2009) Stem hydraulics mediates leaf water status, carbon gain, nutrient use efficiencies and plant growth rates across dipterocarp species. *Functional Ecology* 23: 658–667.

### **Supporting Information**

Additional Supporting Information may be found in the online version of this article:

**Table S1.** Localities and species.

**Table S2.** Restricted maximum likelihood (REML)

analysis of deviation leaf—rock reflectance across wavelengths (nm). Mean deviation was analyzed as a function of random effects of site and species [leaf color] and leaf color. Gray-leaved plants were more closely matched to scree in all comparisons and across all wavelengths considered (Figure 4).

**Table S3.** Analysis of mean percent leaf damage to plants in the field with respect to whether leaves matched rock color (by spectral analysis).