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Plant structural complexity mediates trade-off in direct and indirect plant defense by birds

COLLEEN S. NELL ^{1,3,4} AND KAILEN A. MOONEY ^{1,2}

¹*Department of Ecology & Evolutionary Biology, UC Irvine, 321 Steinhaus Hall, Irvine, California 92697 USA*

²*Center for Environmental Biology, UC Irvine, Irvine, California 92697 USA*

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Abstract. Direct and indirect defenses are predicted to trade-off due to costs associated with redundancy in plant defense, but the factors mediating a plant's position along this trade-off axis are unknown. We conducted a bird exclusion experiment of nine sympatric shrub species to assess convergent associations among direct defense, indirect defense from birds, and shrub structural complexity, a trait predicted to influence bird foraging. We found high variation in defense; direct resistance varied four-fold, with indirect defense ranging from a 59% reduction to a 32% increase in herbivore density. These resistance strategies traded off and were mediated by plant structure; high complexity was associated with weaker indirect defense from birds, strong direct defense, and more predatory arthropods. Our findings suggest that species with growth forms that inhibit bird foraging invest more in direct defense and may provide refuge for arthropod predators. Accordingly, we provide evidence for a potentially widespread mechanism underlying the evolution of plant defenses.

Key words: *coastal sage scrub; herbivore resistance; indirect defense; insectivorous birds; structural complexity; trade-off.*

INTRODUCTION

Plants have evolved a myriad of strategies to protect themselves against herbivores (Heil 2008, War et al. 2012). Plant defense theories are often framed in terms of trade-offs in which investment in anti-herbivore strategies are negatively associated with critical plant functions like growth and reproduction, or contrasting defensive traits due to resource allocation constraints (Coley et al. 1985, Koricheva 2002, Mooney et al. 2010b, Züst and Agrawal 2017). As such, plant defense traits that are redundant in function and costly to produce may be unfavorable.

In addition to resistance traits that directly reduce herbivore performance (e.g., chemical and physical defenses), plants employ a variety of indirect defenses that increase predator attraction and retention and, subsequently, promote plant fitness by reducing herbivore pressure (Kessler and Heil 2010). Direct and indirect

plant defenses are potentially redundant and have been predicted to trade off (Janzen 1966, Rudgers et al. 2004, Llandres et al. 2010), however, the evidence of negative correlations between individual defense traits has been mixed (Heil et al. 2002, Ballhorn et al. 2008, Rasmann et al. 2011, Koricheva and Romero 2012, Kersch-Becker et al. 2017). This has contributed to the broader understanding that plant defense is multivariate and characterized by suites of complementary traits shaped by diffuse selection from complex interactions involving both herbivores and their natural enemies (Agrawal and Fishbein 2006, Agrawal 2011, Singer et al. 2012).

Indirect defense from predators should covary in predictable ways with plant traits that directly affect predator foraging, or plant traits that mediate multitrophic arthropod community structure in ways that affect top-down control of herbivores (Marquis and Whelan 1996, Krivan and Schmitz 2004, Griffin and Thaler 2006). Studies of indirect defense have focused primarily on traits that directly recruit natural enemies (e.g., volatile organic compounds; Dicke and Baldwin 2010, Amo et al. 2013) or increase the retention of predatory ants (e.g., domatia, extra-floral nectaries; Rosumek et al. 2009) and other arthropod predators, but it is likely that plant mediation of predator foraging extends to a wider array of traits and

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³Present address: Department of Biological Sciences, George Washington University, 800 22nd Street NW, Science and Engineering Hall 6000A, Washington, D.C., 20052 USA.

⁴E-mail: coll.s.nell@gmail.com

predator taxa (Rudgers 2004, Kessler and Heil 2010). For instance, plant morphologies that make herbivores more accessible and influence the functional response of predators could mediate the magnitude of indirect defense (Marquis and Whelan 1996, Smout et al. 2010, Reynolds and Cuddington 2012), and as a result mediate a plant's position along a direct-indirect defense trade-off.

Despite fundamental differences in the foraging ecology of predator taxa, trade-offs between direct and indirect plant defense have mainly focused on arthropod predators and parasitoids (Koricheva et al. 2004, Kersch-Becker et al. 2017), ignoring the role of vertebrate insectivores and intraguild predation in plant defense. In particular, insectivorous birds are critical predators of both herbivorous and predatory arthropods, whose top-down effects can indirectly affect plant performance (Whelan et al. 2008, Mooney et al. 2010a, Singer et al. 2012). Predatory birds are highly mobile generalists that forage on larger spatial scales than their arthropod counterparts and exhibit prey-switching behaviors that allow them to track resources. Thus, due to the nature of their foraging behavior, indirect defense from birds should be negatively associated with direct herbivore resistance and other plant traits that determine herbivore density and capture rates (Whelan 1989, Singer et al. 2012). Although the density-dependent effects of natural enemies on their prey are well studied in an ecological bi-trophic context (Holling 1965, Smout et al. 2010), the evolutionary implications of these higher trophic level interactions for plant defense are unknown. Moreover, we predict that with respect to indirect defense from vertebrate insectivores, complex branching morphologies can inhibit foraging by restricting predator movement thus encounter rates with prey. If this is the case, complexity may also mediate indirect defense from predatory arthropods by reducing predator–predator interactions (Jeffries and Lawton 1984, Langellotto and Denno 2004) and potentially increasing the dominance of arthropod predators (Rogers et al. 2012).

Here, we examine whether plant morphology mediates the top-down effects of birds, and consequentially a trade-off between indirect defense and herbivore defense strategies. To do so, we use nine sympatric shrub species of the coastal sage scrub ecosystem of southern California and assess evolutionary convergent associations among direct defense, indirect defense from birds, and structural complexity. We measured direct herbivore defense and the effects of bird predators on herbivores for each shrub species to test the following three predictions: (1) structural complexity mediates the top-down effects of bird predators; (2) interspecific variation in direct and indirect defense trade-off; and (3) based on the above, structural complexity mediates plant species strategies along this axis of variation in direct vs. indirect defense. Further, we assessed variation in predatory arthropods to infer their potential role in plant indirect defense. In doing so, we test for a novel mechanism underlying potentially widespread trade-offs in defense.

MATERIALS AND METHODS

Experimental system

We assess plant structural complexity, herbivore resistance, and indirect defense (via bird exclusion) for nine plant species that co-occur in the coastal sage scrub ecosystem (CSS); *Artemisia californica* Less. (Asteraceae), *Artemisia douglasiana* Besser (Asteraceae), *Encelia californica* Nutt. (Asteraceae), *Ericameria palmeri* H. M. Hall (Asteraceae), *Eriogonum fasciculatum* Benth (Polygonaceae), *Isocoma menziesii* G. L. Nesom (Asteraceae), *Lupinus albifrons* Benth (Fabaceae), *Salvia apiana* Jepson (Lamiaceae), and *Salvia mellifera* E. Greene (Lamiaceae). CSS is a shrub-dominated ecosystem that is limited to a narrow climatic band along the Pacific Coast of southern California, and is home to many endemic species threatened by habitat loss and associated anthropogenic (Davis et al. 1994, Talluto and Suding 2008). Among its inhabitants are several species of insectivorous birds, including the California Thrasher (*Toxostoma redivivum*), and the threatened California Gnatcatcher (*Poliophtila californica*) and Cactus Wren (*Campylorhynchus brunneicapillus*), which depend on CSS shrubs as a source for their insect diet. The nine shrub species in this study encompass the most common shrubs in CSS and exemplify the phenotypic range of species in this ecosystem (Westman 1981).

Direct and indirect defense

To quantify direct and indirect defenses, we conducted a bird exclusion experiment at the Irvine Ranch Conservancy's native seed farm, located in Orange County, California, USA (33°43'9.9624" N, 117°43'35.2452" W). We selected approximately 13 individuals of each plant species, eight of which we applied a bird exclusion treatment (1.9 cm mesh netting) and five or six individuals selected as control plants. At this site, plants of similar age (4 yr) and thus size were grown in large monospecific blocks and supplemented with irrigation and weed control until 6 months prior to the experiment. Bird exclusion netting remained on the plants for 3 months during peak bird nesting season (March to June). After 3 months, arthropod communities were vacuum sampled from each plant at a constant effort. All arthropods were measured in length, assigned a trophic level based upon identification to order, with the exception of Hemipterans and Coleopterans, which required further characterization to determine trophic level (Hemiptera identified to suborder as Auchenorrhyncha, Heteroptera, or Sternorrhyncha; Coleoptera identified to family, with Coccinellidae and Carabidae designated as predators).

Using the measured lengths of each arthropod, we estimate the total biomass of herbivorous and predatory arthropods collected from each plant (Hóðar 1996). For each plant, herbivore density was quantified as total herbivore biomass standardized by plant dry mass. Plant dry mass was estimated by quantifying the size of each

plant relative to two different branches cut from non-experimental plants. Branches were weighed after drying for 120 h at 60°C. The dry biomass weight of each branch was then multiplied by the relative plant size and averaged across the two branch estimates for a final dry biomass value for each plant.

We measure direct defense for each species, herbivore resistance, as the inverse of mean herbivore density in bird exclusion (mg/kg), such that high resistance is reflective of low herbivore density. For each species, we measure indirect defense as the log response ratio of herbivore density on bird exclusion plants compared to control plants ($\ln[\text{exclusion/control}]$), where positive values indicate stronger indirect defense via reduced herbivore density when exposed to birds. The trophic composition of arthropod communities was characterized as the ratio of predatory arthropods to herbivores from bird exclusion plants (IP:H).

Plant traits

To examine plant traits that may be related to a trade-off in direct and indirect defense, we measured plant structural complexity and host plant quality. To measure plant complexity, we counted the number intersections in which woody plant material contacted an axis (2 cm in diameter) projected through the plant center, standardized to the length of the axis in meters (i.e., contact points per meter). Three such measurements per plant were taken on a horizontal plane through the center or main stem of the plant at 3 angles (45, 0, and 135 degrees). For each species, structural complexity is calculated as the mean of the total number of contact points divided by the summed widths of each axis.

In the absence of birds, variation in herbivore resistance associated with structural complexity could be due to changes in plant quality, but also potentially due to changes in the abundance of unmanipulated predatory arthropods (Mooney et al. 2010a). To confirm our assumption that herbivore density under bird exclusion is a metric of direct defense, we performed a laboratory bioassay using a generalist leaf-chewing herbivore, *Spodoptera exigua* (Lepidoptera: Noctuidae), to assess host plant quality and test for an association between plant quality and resistance measured in the field. In this bioassay, three fresh leaves (or branches for small leaf morphologies) were collected from three separate plants of each species at the field site. In the lab, first instar larvae were placed on each leaf in separate petri dishes nine larvae per species. Larvae fed for 10 d in which they were checked twice per day and leaves were replaced with fresh material once after 4 d. At the end of the feeding trial, total mass gain was measured to reflect host plant quality for all of the shrub species, based on the assumption that growth from feeding on leaves under lab conditions indicates food quality (Awmack and Leather 2002, Singer et al. 2012). Ten individuals did not survive for all 10 d and their mass at mortality is used.

Statistical analyses

Using species means, we conducted trait-trait correlations to assess all of the pairwise relationships among indirect defense, direct defense, and structural complexity, as well as the pairwise comparison between lab vs. field host plant quality/resistance. In addition, phylogenetic independent contrasts were used to account for statistical non-independence of species due to shared evolutionary history (Felsenstein 1985, Cooper et al. 2016). The phylogenetic relationships among our study species are based upon the Zanne et al. (2014) time-calibrated, species-level, angiosperm backbone (Zanne et al. 2014) (Appendix S1: Methods).

We use a randomization test to determine the statistical significance of the correlation between species-level means for direct herbivore resistance and indirect defense from birds, because these two metrics are mathematically coupled (both based upon herbivore density in exclusion) (Pearson 1896). In this test, we compared our observed correlation coefficient ($r = -0.72$) to a null distribution of correlation coefficients generated from 10,000 simulations of our data where treatments were randomized across species (Jackson and Somers 1991). The empirical correlation under the null hypothesis was -0.145 (2.5 and 97.5 centiles; $-0.67, 0.48$) indicating that the observed correlation (-0.72) was more negative than under a null expectation. We report the significance of our observed correlation as the proportion of simulations that were more extreme than the observed relationship after 10,000 trials.

Our hypotheses offer clear predictions for the nature (positive, negative) of the trade-offs among the measured traits specifically, we hypothesized a negative association between direct resistance and indirect resistance, a negative association between structural complexity and indirect resistance, and a positive association between structural complexity and direct resistance. Accordingly, we report one-tailed statistical tests, although the two-tailed P values are simply double these values.

RESULTS

Across our experimental plants, we collected and identified 2,910 individual arthropods belonging to 16 different orders. On average, $79.9\% \pm 1.2\%$ (mean \pm SE) of arthropods on a plant were herbivorous. Direct herbivore resistance varied among shrub species; mean herbivore density was 4.2 times higher on *A. douglasiana* (38.7 ± 9.18 mg/kg) than to the most well-defended species, *E. palmeri* (9.2 ± 2.03 mg/kg; Appendix S1: Fig. S2).

Indirect defense from birds reduced herbivore densities by $48\% \pm 17.9\%$ (mean LRR = 0.336 ± 0.122), with a mean herbivore density of 21.8 ± 1.8 mg/kg in bird exclusion compared to 14.9 ± 1.4 mg/kg on control plants. However, the magnitude and direction of bird effects differed with shrub species. Indirect defense was strongest on *L. albifrons*, where birds effectively lowered

herbivore densities by 59% ($LRR = 0.89 \pm 0.242$) ranging to a 32% increase in herbivore density on *I. menziesii* ($LRR = -0.28 \pm 0.252$; Appendix S1: Fig. S2a). Of the shrubs, *I. menziesii* was the most complex (8.51 ± 0.767 intersections/m) and *A. douglasiana* the lowest (2.39 ± 0.466 intersections/m; Appendix S1: Fig. S2c).

Interspecific variation in herbivore resistance traded off (was negatively correlated) with indirect defense by birds based upon raw means (raw) and phylogenetically corrected correlations (PIC) ($R_{\text{raw}}^2 = 0.52$, $P_{\text{raw}} = 0.032$; $R_{\text{PIC}}^2 = 0.35$, $P_{\text{PIC}} = 0.048$) (Fig. 1a, Appendix S1: Fig. S3a), and based upon the randomization test (observed $r = -0.72$; $P = 0.032$). Plant structural complexity was negatively associated with indirect defense ($R_{\text{raw}}^2 = 0.72$, $P_{\text{raw}} = 0.001$; $R_{\text{PIC}}^2 = 0.71$, $P_{\text{PIC}} = 0.002$; Fig. 1c, Appendix S1: Fig. S3a) and positively associated with herbivore resistance ($R_{\text{raw}}^2 = 0.51$, $P_{\text{raw}} = 0.015$; $R_{\text{PIC}}^2 = 0.42$, $P_{\text{PIC}} = 0.030$; Fig. 1b, Appendix S1: Fig. S3b), although the phylogenetically corrected association appears to be driven by one particular contrast. Plant structural complexity was also positively associated with the ratio of arthropod predators to herbivores (Fig. 2) ($P_{\text{raw}} = 0.039$, $R_{\text{raw}}^2 = 0.38$; $P_{\text{PIC}} = 0.065$, $R_{\text{PIC}}^2 = 0.29$). Accordingly, structurally complex (vs. simple) plants had lower indirect defense from birds, more arthropod predators relative to herbivores, and higher herbivore resistance (lower herbivore density).

Furthermore, there was a negative association between herbivore resistance (herbivore density in the field) and host plant quality (herbivore growth in lab bioassay; $R_{\text{raw}}^2 = 0.46$, $P_{\text{raw}} = 0.022$; $R_{\text{PIC}}^2 = 0.67$, $P_{\text{PIC}} = 0.003$; Appendix S1: Fig. S4) and no observed relationship between indirect defense from birds and the ratio of intermediate predators to herbivores ($P_{\text{raw}} = 0.18$; $P_{\text{PIC}} = 0.33$), suggesting that species variation in herbivore resistance was due in large part to changes in plant quality (vs. variation in indirect defense from arthropod predators).

DISCUSSION

Plant resistance strategies traded off and were mediated by plant structure; high complexity was associated with weaker indirect defense from birds, strong direct defense, and more predatory arthropods. Insectivorous

bird predation of herbivores was positively density dependent, resulting in a trade-off between direct and indirect defenses; the shrub species with lowest direct resistance (*A. douglasiana*) received strong indirect

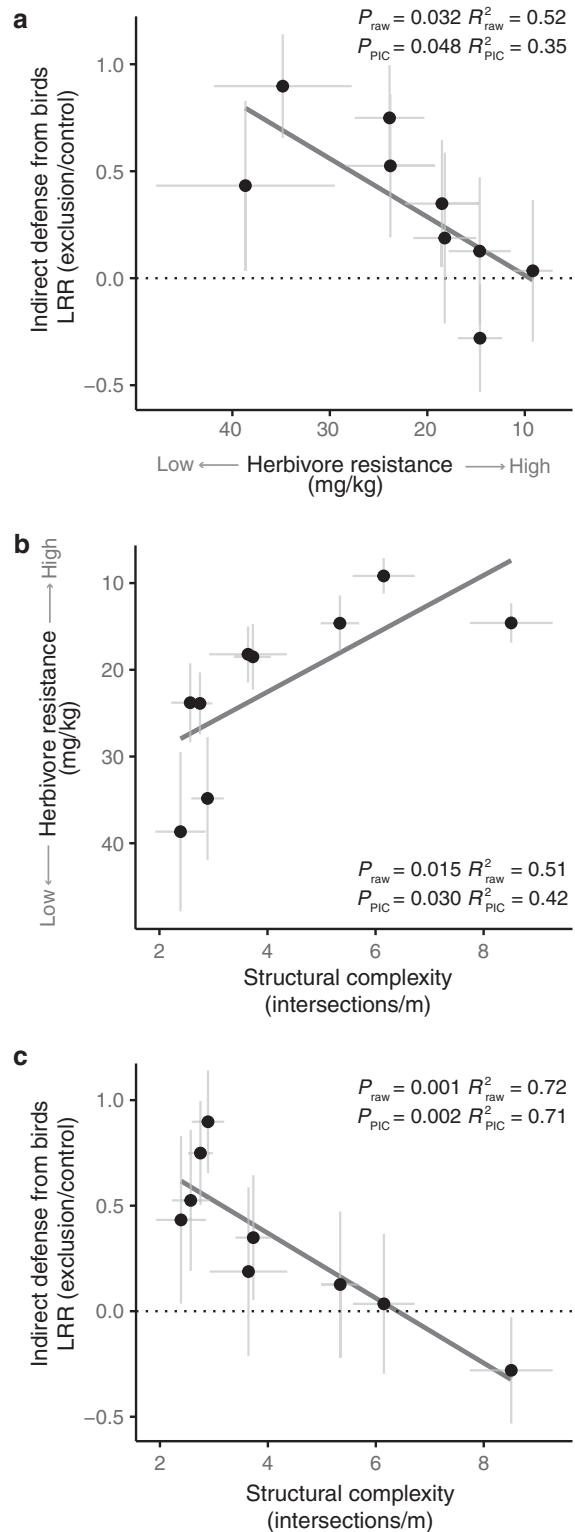


FIG. 1. Trade-off between (a) direct herbivore resistance and indirect defense from birds and underlying relationships between (b) plant structural complexity and herbivore resistance and (c) structural complexity and indirect defense. Direct herbivore resistance is measured as herbivore density in bird exclusion (mg/kg), such that high resistance is reflective of low herbivore density. Indirect defense from birds is the log response ratio (LRR) of herbivore densities in bird exclusion compared to control plants ($LRR = \ln[\text{exclusion/control}]$). Statistical significance for the trade-off in direct and indirect defense (a) is based upon a randomization test because these two variables are both based upon herbivore density with bird exclusion, and statistically non-independent. R-squared and P-values using raw species' means (raw) and phylogenetic independent contrasts (PIC) are provided. Error bars show the SE of species means

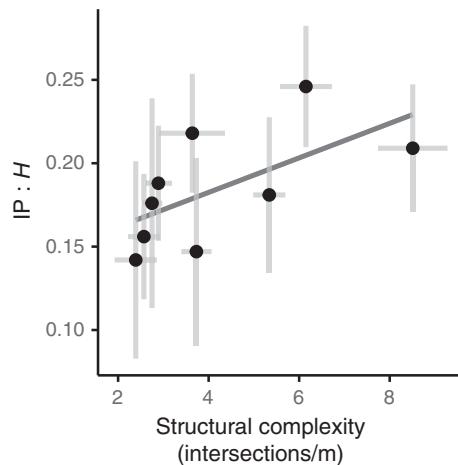


FIG. 2. Relationship between shrub structural complexity and the trophic composition of arthropod communities (IP:H; $P_{\text{raw}} = 0.039$, $R^2_{\text{raw}} = 0.38$; $P_{\text{PIC}} = 0.065$, $R^2_{\text{PIC}} = 0.29$), measured as the ratio of predatory arthropod density (IP) to herbivore density (H) with bird exclusion. Error bars show the SE around species' means

defense from birds, a 35% reduction in herbivore density, while the species with the highest direct resistance (*E. palmeri*) received no effect. Accordingly, the plant's costs of reducing investment in direct resistance are at least partially mitigated by predator foraging behavior. A plant's position along this interspecific trade-off between direct and indirect defense from birds was in turn mediated by plant structural complexity. Structurally complex plants were associated with lower indirect defense from birds and lower herbivore densities, suggesting stronger direct resistance. Structurally complex plants were also associated with a higher ratio of arthropod predators to herbivores, suggesting that lower herbivore densities might be due to increased predation from arthropod predators. Nevertheless, species with growth forms that inhibit indirect defense from birds in turn increase investment in direct defense or interactions with other predator taxa. Accordingly, we provide novel evidence for a potentially widespread mechanism underlying the evolution of plant defense trade-offs driven by density dependence and access for foraging by birds.

Density-dependence leading to a trade-off between direct and indirect defense is likely a common dynamic shaping indirect defense traits and community stability (Griffin and Thaler 2006, Singer et al. 2012, Kersch-Becker et al. 2017). Further, stronger top-down effects on low resistance plants may be driven in part by the density relationships with plant signals that directly recruit predators indirectly increase their fitness (e.g., herbivore-induced plant volatiles). There is a growing appreciation that insectivorous birds, in addition to arthropod predators and parasitoids, respond to volatile cues from damaged plants as well as visible signs of damage (Mäntylä et al. 2008, Amo et al. 2013). If herbivore density is positively related to visible or olfactory signals, low resistance

plants will provide reliable information on prey availability and increase predator efficacy (Kersch-Becker et al. 2017). As such, interactions with predators could reinforce both inducible and constitutive indirect traits (e.g., complexity) to regulate herbivore populations and as a result trade-off with direct resistance traits.

Plant complexity can affect arthropods in a multitude of ways distinct from bird predators that operate on different spatial scales. For both arthropod predators and herbivores, plant complexity and fine-scale variation in morphology may provide a greater diversity of foraging niches and microhabitats to support larger and more diverse arthropod communities (Root 1973, Price et al. 1980, Langelotto and Denno 2004), while concurrently modifying the identity and efficacy of foraging birds (Robinson and Holmes 1984, Whelan 2001). Similarly, complex shrubs may provide more suitable conditions for both arthropod predators and herbivores because they offer more moderate microclimatic conditions by limiting direct sunlight and buffering abiotic extremes. Across our nine species, we did find that complexity was associated with relatively higher densities of predatory arthropods but lower herbivore density (strong direct resistance) where bird effects were negligible. Thus by weakening the impact of birds on arthropods, arthropods predators may benefit from increased enemy free space on complex plants due to lower intraguild predation (Marquis and Whelan 1996), and subsequently plant morphology may provide an axis by which top-down effects differ. It is worth noting that some inhabitants of CSS, like the California Cactus Wren, are highly skilled at moving and foraging through dense foliage. The avifauna of this system is characterized by many ground-feeding species that likely gain refuge from aerial predators by foraging in complex vegetation. However, in this study indirect defense from birds was weaker with complexity indicating a cost to foraging at the interior of dense shrubs.

This work advances plant defense theory in suggesting a fundamental trade-off between direct herbivore resistance and indirect defense by birds driven by bird behavior and plant traits. This is important because it demonstrates that both the behavioral ecology of predators and lesser recognized plant morphological traits can influence the dynamics of biological control.

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