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Between plant and predator: indirect interactions mediate plant resistance against herbivores

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# Between plant and predator: indirect interactions mediate plant resistance against herbivores

DISSERTATION

submitted in partial satisfaction of the requirements
for the degree of

DOCTOR OF PHILOSOPHY

in Ecology and Evolutionary Biology

by

Colleen S. Nell

Dissertation Committee:
Professor Kailen A. Mooney, Chair
Professor Matt Bracken
Professor Diane Campbell

2018

# DEDICATION

To

Anand, who empowered me to become who I am today.

# TABLE OF CONTENTS

Page

LIST OF FIGURES iv

LIST OF TABLES vi

ACKNOWLEDGMENTS vii

CURRICULUM VITAE viii

ABSTRACT OF THE DISSERTATION ix

INTRODUCTION 1

CHAPTER 1: Trade-off in direct and indirect defense plant defenses underlain by density-dependent bird foraging 5

CHAPTER 2: Toxic hosts provide enemy-free space from insectivorous birds via multiple mechanisms 27

CHAPTER 3: Tropical tree diversity mediates foraging and predatory effects of insectivorous birds 45

REFERENCES 68

# LIST OF FIGURES

| | | Page |
|---|---|---|
| Figure 1.1a | Trade-off between direct herbivore resistance and indirect defense from birds across nine shrub species | 15 |
| Figure 1.1b | Relationship between plant structural complexity and direct herbivore resistance | 15 |
| Figure 1.1c | Species-level correlation between plant structural complexity and indirect defense from birds. | 15 |
| Figure 1.2 | Relationship between shrub complexity and trophic composition of arthropod communities | 17 |
| Figure S1.1 | Phylogenetic relationships among experimental species | 21 |
| Figure S1.2 | Species-level means for indirect defense from birds, direct herbivore resistance, and structural complexity | 22 |
| Figure S1.3 | Species trait-defense correlations using phylogenetic independent contrasts | 24 |
| Figure S1.4 | Relationship between host plant quality and herbivore resistance | 26 |
| Figure 2.1 | Enemy-free space due to aposematism and toxic host plants | 36 |
| Figure 2.2 | Association between neighborhood cycad density and predation risk | 39 |
| Figure 2.3 | Predation risk associated with visible leaf damage due to herbivory | 41 |
| Figure 3.1 | Tree diversity effect on bird communities and model attack rate | 55 |
| Figure 3.2 | Patterns of bird diversity between monoculture and polyculture plots | 56 |
| Figure 3.3 | Partitioning the net effect of tree diversity on model attack rates | 57 |
| Figure 3.4 | Bivariate relationships between plot-level attack rates and bird communities | 60 |
| Figure 3.5 | Structural equation models comparing the indirect effects of tree diversity on model attack rate mediated by the bird community | 61 |

Figure S3.1 Map of the UADY tree diversity experiment plot design 65

Figure S3.2 Plot-level values for net, selection, and complementarity effects 66

Figure S3.3 Positive correlations between bird community metrics 67

# LIST OF TABLES

Page

Table 2.1 Effects of model color and host on bird attack 37

Table 3.1 Comparing bird community metrics as predictors of model attack rates 62

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# CURRICULUM VITAE

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### PUBLICATIONS

3. **Nell, C.S.,** Meza-Lopez, M.M., Croy, J., Nelson, A., Moreira, X., Pratt, J., and Mooney, K.A. (2018). Relative effects of genetic variation and sexual dimorphism on plant traits and associated arthropod communities. Oecologia. doi:10.1007/s00442-018-4065-y
2. Roslin, T., [et al, including **Nell, C.S.**] (2017). Higher predation risk for insect prey at low latitudes and high elevation. Science. 356(6339); 742-744. doi:10.1126/science.aaj1631
1. Moreira, X., **Nell, C.S.,** Rasmann, S., and Mooney, K.A. (2016). Herbivore specificity and the chemical basis of plant-plant communication. New Phytologist. doi:10.1111/nph.14164

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| 2016 | UC Irvine Data Science Initiative Summer Fellowship |
| 2015 | Dissertation grant, Organization for Tropical Studies |
| 2015 | Post-course award, Organization for Tropical Studies |
| 2014 | Newkirk Center for Science & Society Graduate Student Grant |
| 2014 | Bloom-Hay Ecological Research Grant, Sea & Sage Audubon |
| 2013 | National Science Foundation Graduate Research Fellowship |

# ABSTRACT OF THE DISSERTATION

Between plant and predator: indirect interactions mediate plant resistance against herbivores

By

Colleen S. Nell

Doctor of Philosophy in Ecology and Evolutionary Biology

University of California, Irvine, 2018

Professor Kailen A. Mooney, Chair

Plant-herbivore interactions have traditionally been framed in terms of pairwise interactions, focusing on the direct effects of plant defensive traits on herbivores, herbivores on plant performance, and the resulting co-evolution between the two. However, a bi-trophic perspective is limited in that the ecological and evolutionary outcomes of species interactions are subject to indirect effects stemming from their surrounding communities. In particular, plant-herbivore interactions are shaped by predators, who through the consumption of plant herbivores can provide an indirect defense to plants by indirectly reducing plant damage and promoting plant performance. Likewise, plants can indirectly mediate predator-herbivore interactions with potential consequences for the magnitude of trophic cascades. I use a tri-trophic approach based upon plants, herbivores, and insectivorous bird predators to understand how plant traits influences interactions between herbivores and predators, and in turn how predators indirectly contribute to the plant defense at multiple scales of biological organization. Specifically I evaluate: (1) a trade-off in direct herbivore resistance and indirect defense from birds and underlying plant traits, (2) whether herbivore predation risk is mediated by

toxic host plants, and (3) the consequences of biodiversity loss on bird-herbivore interactions.

By assessing the relationships between interspecific variation in direct herbivore resistance and indirect defense from birds, I found that density-dependent foraging by bird predators shapes a trade-off in direct and indirect defense from birds. This relationship was underlain by the effects of plant structural complexity on both bird and arthropod communities (Chapter 1). Inversely, I found that toxic plants deter birds (Chapter 2). As a result, herbivores can gain enemy-free space by occurring in patches where toxic plants are more dominant. In contrast, bird diversity was positively affected by tree diversity which corresponded to stronger predation rates on herbivore models, suggesting a feedback between diversity and plant and predator trophic levels (Chapter 3). Collectively, this work highlights the importance of indirect effects across multiple trophic levels in shaping community structure and dynamics.

# INTRODUCTION

The selective impact of herbivores is a key factor in shaping the evolution of plant traits (Fritz & Simms 1992; Coley & Barone 1996; Howe & Jander 2008). To combat insect herbivory, plants have evolved an arsenal of defensive traits that directly mitigate herbivore feeding, including morphological traits that provide physical deterrence (e.g. spines), and chemical compounds that are toxic (e.g. alkaloids) or reduce nutrient value (e.g. tannins) to herbivores (Howe & Jander 2008; War *et al.* 2012). Through these traits, plants can influence the preference and performance of their herbivores and mitigate the negative effects of herbivory to plant fitness. In return, plant herbivores have evolved to combat these defenses: many herbivores are specialized to consume certain plant species or secondary metabolites and in doing so limit their diet breadth to fewer host plants (Ehrlich & Raven 1964; Feeny 1976; Opitz & Müller 2009).

But plants are not limited to these direct defensive strategies; there is a growing understanding that the ecological and evolutionary outcomes of plant-herbivore interactions are context dependent, and subject to indirect effects stemming from the complex communities in which they are embedded (Křivan & Schmitz 2004a; Hooper *et al.* 2005; Ohgushi 2005; Heil 2008; Barbosa *et al.* 2009). In particular, plant and predator trophic levels are linked through their shared interactions with plant herbivores. Predators have strong top-down effects on herbivorous insects that can cascade through trophic levels to indirectly reduce plant damage and promote plant performance (i.e. trophic cascade) (Heil 2008; Mooney *et al.* 2010a). Such indirect effects can have a large influence on the structure and dynamics of ecological communities and exert selective pressure on both herbivores and plants (Rudgers 2004; Griffin & Thaler 2006). Simultaneously, the bottom-up effects of plants can mediate predator-prey dynamics by implicating the density and traits of interacting species (Werner & Peacor 2003; Křivan & Schmitz 2004a). Thus, in order to develop a general theory of natural community structure and dynamics, we need to understand the mechanisms of both direct and indirect effects across multiple scales of biological organization.

Plants are central to structuring interactions with predators through their direct and indirect effects on higher trophic levels (Price *et al.* 1980). By shaping herbivore communities, plant defensive traits can indirectly mediate top-down predator effects (Ohgushi 2005; Griffin & Thaler 2006; Singer *et al.* 2012). Such effects may be density-mediated in which changes in herbivore density driven by plants implicates predation (Werner & Peacor 2003; Griffin & Thaler 2006; Bijleveld *et al.* 2016). For predators that forage with density dependence, it might be expected that plants hosting higher herbivore densities benefit from stronger top-down effects. Alternatively, indirect interactions may be trait-mediated in which plant traits modify herbivore or predator traits in a way that alters the per capita effect of predators on herbivores (Křivan & Schmitz 2004a). For example, low nutritional quality or plant defenses can inhibit herbivore growth rate, thus increasing their developmental time. By modifying the interaction between herbivore and predators – herbivores have increased vulnerability to predators – the slow-growth/high-mortality hypothesis predicts that herbivores on low quality hosts will have higher mortality i.e. greater predator effects (Williams 1999).

Predators may also be directly influenced by plant traits; in some cases, plants have evolved novel structures that directly attract predators by offering resources or refuge (e.g. extra-floral nectaries and domatia), increasing predator fidelity to the plant, and thus increasing the strength of indirect defense (Rudgers 2004). Upon herbivore damage, plants emit volatile signals that attract predators (Dicke & Baldwin 2010; Amo *et al.* 2013a). Moreover, any positive effects of predators to plant fitness may indirectly select for subtle plant morphological traits that either increase prey encounter rate or decrease handling time for predators, however this remains largely untested (Marquis & Whelan 1996).

Within a community context, individual tri-trophic food chains are embedded in a matrix of other plants (with their own tri-trophic food chains). Plant diversity and related associational effects may thus (i) influence the dynamics of focal food chains and (ii) have emergent properties that drive community patterns in a way not predictable from studying component food chains in isolation (Hooper *et al.* 2005; Barbosa *et al.* 2009; Hambäck *et al.* 2014). Intra- and inter-specific variation in plant traits, i.e. diversity, plays an important role in structuring herbivore communities and ecosystem functioning at a community scale (Balvanera *et al.* 2006; Crutsinger 2006). However, the effects of plant diversity have largely been studied from a mono-trophic perspective, and how diversity interacts across multiple trophic levels is not well understood.

I use a tri-trophic approach based upon plants, herbivores, and insectivorous bird predators to understand how plants influence interactions between herbivores and predators, and in turn, how the predators contribute to plant defense. Birds are formidable predators of arthropods whose consumptive effects suppress the biomass of arthropod predators (38%) and herbivores (39%), providing an important ecosystem service (Whelan *et al.* 2008; Mooney *et al.* 2010a). By feeding on herbivores, bird predators can have cascading effects that indirectly reduce plant damage (40%) and increase plant biomass (14%)(Mooney *et al.* 2010a). Further, insectivorous birds permeate terrestrial ecosystems, feeding as top predators within most ecological food webs, making them an integral link in ecosystem functioning globally. However, despite their significant ecological impact, birds are virtually unstudied in terms of multi-trophic interactions. Using this tri-trophic system I evaluate: (1) a trade-off in direct herbivore resistance and indirect defense from birds and underlying plant traits, (2) whether predation risk from insectivorous birds is mediated by toxic host plants on multiple spatial scales, and (3) the consequences of biodiversity loss on bird-herbivore interactions.

# CHAPTER 1

# Trade-off in direct and indirect defense plant defenses underlain by density-dependent bird foraging

## ABSTRACT

Density dependent foraging by predators for herbivores should result in a trade-off between plant direct defense and indirect defense, such that plants with low direct defense and high herbivore densities should receive greater protection by predators. We tested this hypothesis with a phylogenetic field experiment of nine sympatric shrub species to assess evolutionary convergent associations among direct defense, indirect defense from birds (via bird exclusion), and shrub structural complexity – a trait predicted to interfere with predation by birds. We found a trade-off between direct defense (herbivore density in the absence of birds) and indirect defense (the strength of bird predation), with direct defense explaining approximately half of the variation in indirect defense; indirect defense ranged from 59% reduction in herbivore density to no detectable effect between species with the lowest and highest direct resistance, respectively. Furthermore, high structural complexity weakened indirect defense, with the most complex species receiving no detectable benefit from bird predation. Correspondingly, structural complexity was associated with strong direct resistance and a higher ratio of arthropod predators to herbivores, suggesting that species with growth forms that inhibit indirect defense from birds in turn increase investment in direct defense or other predator functional groups. Accordingly, our results provide novel evidence for a potentially wide-spread mechanism underlying the evolution

of plant defense trade-offs driven by density dependence and access for foraging by birds and perhaps other larger insectivores.

## INTRODUCTION

Plants have evolved a myriad of strategies to protect themselves against herbivores, including both direct herbivore resistance and indirect defense incurred through trophic interactions (Heil 2008; War *et al.* 2012). Plant defenses 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 & Agrawal 2017). As such, redundant plant traits may be unfavorable and costly. In this sense, direct and indirect plant defenses have been predicted to trade-off (Janzen 1966), however the evidence of negative correlations between individual traits has been mixed (Heil *et al.* 2002; Koricheva *et al.* 2004; Ballhorn *et al.* 2008; Rasmann *et al.* 2011; Koricheva & Romero 2012; Moles *et al.* 2013; Kersch-Becker *et al.* 2017). This has contributed to the broader understanding that plant defense is multivariate, and under diffuse selection by complex interactions involving both predators and herbivores (Agrawal & Fishbein 2006; Agrawal 2011; Singer *et al.* 2012; Moles *et al.* 2013).

Despite fundamental differences in the foraging ecology of predator taxa, trade-offs in plant defense have mainly been studied with respect to arthropod predators and parasitoids (Koricheva *et al.* 2004; Kersch-Becker *et al.* 2017). Likewise, significant attention has been paid to whether predators have density-dependent effects on their prey, but the evolutionary implications for plant defense are unknown. In particular, insectivorous birds play a critical role in the top-down control of herbivorous insects and 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 comparatively larger spatial scales than their arthropod counterparts and exhibit prey-switching behaviors. Thus, due to the nature of their foraging behavior, indirect defense from birds should be negatively associated with direct herbivore resistance and with plant traits related to herbivore density.

Simultaneously, the top-down effects of predators should co-vary in predictable ways with plant traits that directly implicate predator foraging (Marquis & Whelan 1996; Křivan & Schmitz 2004b; Griffin & Thaler 2006). In addition to resistance traits that directly reduce herbivore performance, plants employ a variety of indirect defenses that increase predator attraction and retention and subsequently, promote plant fitness by mitigating herbivore pressure (Kessler André & Heil Martin 2010). This has been demonstrated primarily for novel traits that directly recruit and increase the retention of ant predators (e.g. domatia, extra-floral nectaries), however it is likely that this extends to a wider array of traits and predator taxa (Rudgers 2004; Kessler André & Heil Martin 2010; Trager *et al.* 2010). For instance, plant morphologies that make herbivores more accessible and influence the functional response of predators, could be under indirect selection by higher trophic levels (Marquis & Whelan 1996; Smout *et al.* 2010; Reynolds & Cuddington 2012). Specifically, we predict that complex branching morphologies can inhibit foraging by restricting predator movement and encounter rates. If this is the case, complexity should also increase the retention of invertebrate predators due to enemy free space from intraguild predators (Jeffries & Lawton 1984; Marquis & Whelan 1996).

Here, we examine whether density-dependent foraging by bird predators results in a trade-off between direct and indirect plant defenses, and plant morphology that mediates bird access is associated with this variation in herbivore defense strategy. To do so, we use 9 sympatric shrub species of the coastal sage scrub ecosystem of southern California and assess evolutionary convergent associations among direct defense, indirect defense from birds (via bird exclusion), and structural complexity. We use bird exclusion to measure the relative effects of bird predators on herbivores for each shrub species to assess the following questions: (1) Does interspecific variation in direct and indirect defense result in an evolutionary convergent trade-off among species? (2) Do host plant quality and structural complexity mediate herbivore resistance and the top-down effects of predators? In doing so, we test for a novel mechanism underlying potentially widespread trade-offs in defense.

## METHODS

### *Study system*

We assess herbivore resistance and indirect defense (via bird exclusion) for 9 plant species that co-occur in the Coastal Sage Scrub ecosystem (CSS); *Artemesia 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). This ecosystem 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 impacts (fire, invasive species, human recreation)(Davis *et al.* 1994; Talluto & Suding 2008). Among its inhabitants are several species of insectivorous birds, such as the threatened California Gnatcatcher (*Polioptila 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 some of the most common shrubs in CSS and exemplify the phenotypic range of species in this ecosystem.

### *Bird exclusion experiment*

At the Irvine Ranch Conservancy's native seed farm, located in Orange County, California (33°43'9.9624" N, 117°43'35.2452" W), we selected approximately 13 individuals of each plant species, to 8 of which we applied a bird exclusion treatment (1.9 cm mesh netting) with 5-6 individuals selected as control plants. At this site, plants of similar age (4 years) were grown in large mono-specific 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, and identified to Order, with the exception of Hemipterans, which were characterized by sub-order (Auchenorrhyncha, Heteroptera, Sternorrhyncha) to determine trophic groupings. Using the measured lengths of each arthropod, we estimate the total biomass of herbivorous and predatory arthropods (Hódar 1996).

### *Direct and indirect defense*

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. Cut branches were weighed after drying at 60°C for 120 hours. 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 the experimental plants. We measure direct defense for each species – herbivore resistance – as the mean herbivore density in bird exclusion (mg $kg^{-1}$), 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 on bird exclusion plants compared to control plants (=ln[exclusion/control]), where positive values indicate stronger indirect defense via reduced herbivore density when exposed to birds. In addition, the trophic composition of arthropod communities were characterized using the ratio of predatory arthropods to herbivores from bird exclusion plants.

### *Plant traits*

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. Accordingly, we performed a laboratory bioassay using a generalist herbivore, *Spodoptera exigua*, to assess host plant quality and test for an association between plant quality and resistance measured in the field*.* In this bioassay, 3 fresh leaves (or branches for small leaf morphologies) were collected from 3 separate plants of each species at the field site. In the lab, 1st instar larvae were placed on each leaf in petri dishes. Larvae fed on leaves for 10 days, after which their total weight gain was measured to reflect host plant quality. We use final size of larvae to quantify 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 & Leather 2002; Singer *et al.* 2012). For individuals that did not survive for 10 days, their final weight 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. In addition to raw correlations, 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; Qian & Jin 2016). This mega-phylogeny was resolved at the species-level for five of our nine experimental species, and at the genus-level for the remaining four species. The four species that were not a part of the mega-phylogeny were added within their respective parental lineages on the basis of genus, and for two congener species (*Artemisia*) by subgenera (Tridentatae, Artemisia) (Garcia *et al.* 2011)(Fig. S1). The resulting branch lengths were used to calculate independent contrasts, with Grafen's (1989) branch length transformation applied ($\rho = 0.5$) to meet test assumptions (Grafen 1989). All phylogenetic analyses were conducted using the 'ape' package in R (Grafen 1989; Paradis *et al.* 2004; R Core Team 2017). For significant correlations between contrasts, regression lines fit through the origin (0,0) (Garland *et al.* 1992).

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). Accordingly, we use a randomization test to determine the statistical significance of the raw correlation between direct and indirect defense. For 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 & 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 1-tailed statistical tests, although the 2-tailed P-values are simply double these values.

## RESULTS

Across our experimental plants, we collected and identified 2910 individual arthropods belonging to 16 different orders. On average, 79.9% ± 1.2% (mean ± 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* (0.0387 mg $kg^{-1}$ ± 0.009 SE) than to the most well-defended species, *E. palmeri* (0.009 mg $kg^{-1}$ ± 0.002 SE)(Fig. S2).

Across all shrub species, indirect defense from birds reduced herbivore densities by 48% (± 17.9% SE; mean LRR = 0.336 ± 0.122), with a mean herbivore density of 0.0218 mg $kg^{-1}$ (± 0.0018 SE) in bird exclusion compared to 0.0149 mg $kg^{-1}$ (± 0.0014 SE) 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 ± 0.242 SE) ranging to a 32% increase in herbivore density on *I. menziesii* (LRR = -0.28 ± 0.252 SE)(Fig. S2a). Of these species, *I. menziesii* was the most complex (8.51 ± 0.767) and *A. douglasiana* the lowest (2.39 ± 0.466) (Fig. S2c).

Interspecific variation in herbivore resistance traded-off (was negatively correlated) with indirect defense by birds ($R^2_{raw} = 0.52$, $P_{raw} = 0.032$; $R^2_{PIC} = 0.35$, $P_{PIC} = 0.048$) (Figs. 1a, S3a). In the randomization test, the observed correlation coefficient ($r = -0.72$) was significant by a one-tailed test (P = 0.032), indicating that the observed pattern was stronger than expected. Plant structural complexity was positively associated with herbivore resistance ($R^2_{raw} = 0.51$, $P_{raw} = 0.015$; $R^2_{PIC} = 0.42$, $P_{PIC} = 0.030$)(Fig. 1b, S3b) and showed a significant, negative association with indirect defense ($R^2_{raw} = 0.72$, $P_{raw} = 0.001$; $R^2_{PIC} = 0.71$, $P_{PIC} = 0.002$)(Fig. 1c, S3a). In contrast, the ratio of arthropod predators to herbivores increased with plant complexity ($P_{raw} = 0.039$, $R^2_{raw} = 0.38$; $P_{PIC} = 0.065$, $R^2_{PIC} = 0.29$). Further, there was a negative correlation between host plant quality and herbivore resistance, where low quality shrub species also tended to have lower herbivore densities ($R^2_{raw} = 0.46$, $P_{raw} = 0.022$; $R^2_{PIC} = 0.67$, $P_{PIC} = 0.003$) (Fig. S4).

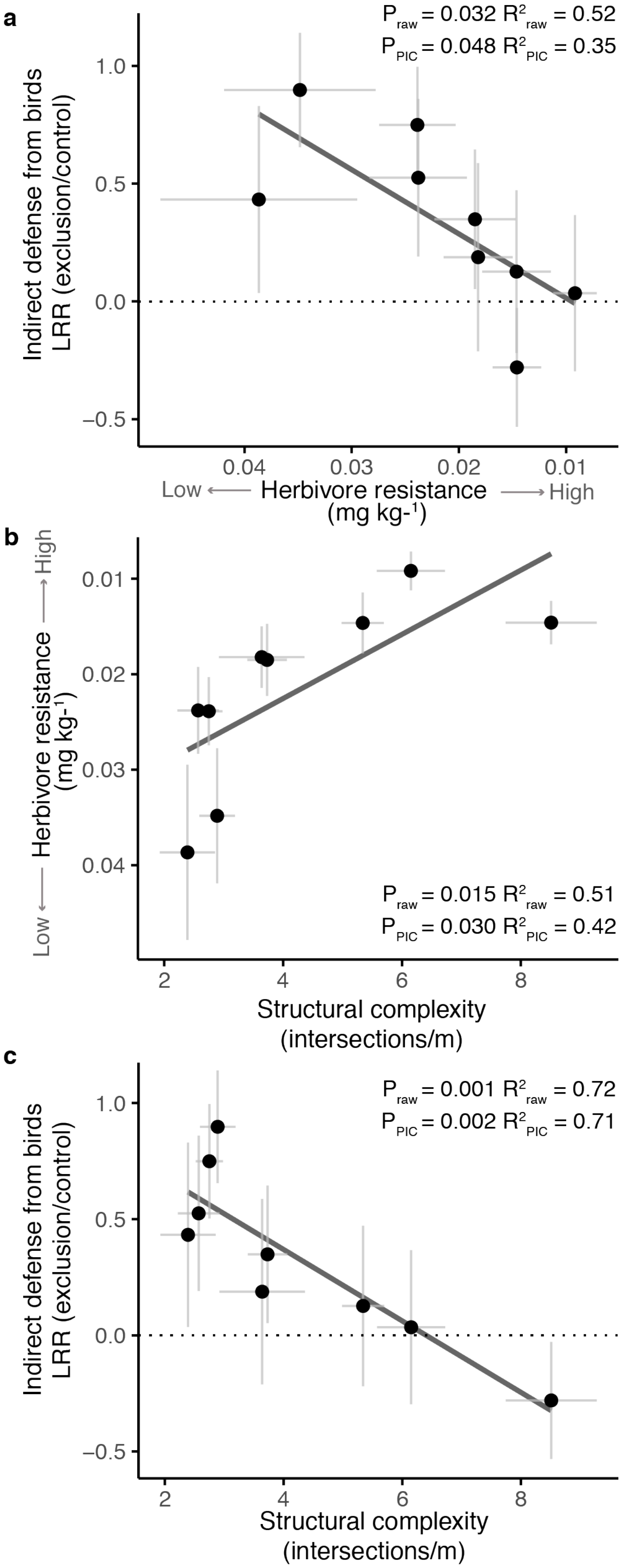

a
P_raw = 0.032 R²_raw = 0.52
P_PIC = 0.048 R²_PIC = 0.35
Indirect defense from birds
LRR (exclusion/control)
1.0
0.5
0.0
−0.5
0.04
0.03
0.02
0.01
Low ⟵ Herbivore resistance ⟶ High
(mg kg-1)
b
High
Low
Herbivore resistance
(mg kg-1)
0.01
0.02
0.03
0.04
P_raw = 0.015 R²_raw = 0.51
P_PIC = 0.030 R²_PIC = 0.42
2
4
6
8
Structural complexity
(intersections/m)
c
P_raw = 0.001 R²_raw = 0.72
P_PIC = 0.002 R²_PIC = 0.71
Indirect defense from birds
LRR (exclusion/control)
1.0
0.5
0.0
−0.5
2
4
6
8
Structural complexity
(intersections/m)

**Figure 1.1.** 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 $kg^{-1}$), such that high resistance is reflective of low herbivore density. Indirect defense from birds is the log response ratio of herbivore densities in bird exclusion compared to control plants (LRR=ln[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.

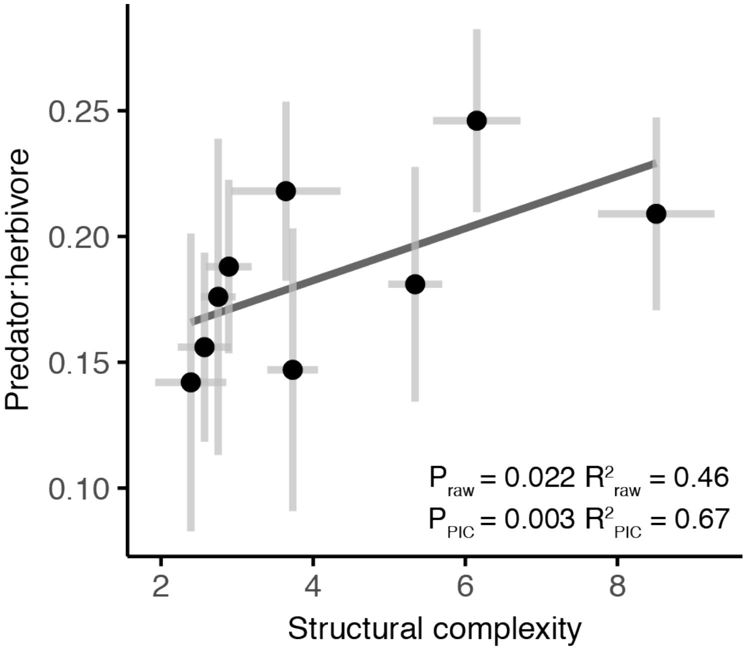


**Figure 1.2.** Relationship between shrub structural complexity and the trophic composition of arthropod communities ($P_{raw}$ = 0.039, $R^2_{raw}$ = 0.38; $P_{PIC}$ = 0.065, $R^2_{PIC}$ = 0.29), measured as the ratio of predatory arthropod density to herbivore density with bird exclusion.

## DISCUSSION

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 defense from bids – a 35% reduction in herbivore density – while the species with the highest direct resistance (*E. palmeri*) received no benefit. Accordingly, the plant's costs of reducing investment in direct resistance are at least partially mitigated by predator foraging behavior. Indirect defense from birds was further mediated by plant structural complexity which was associated with strong direct herbivore resistance and a higher ratio of arthropod predators to herbivores, suggesting that 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 wide-spread mechanism underlying the evolution of plant defense trade-offs driven by density dependence and access for foraging by birds.

Density-dependence leading to trade-off between direct and indirect defense is likely a common dynamic shaping indirect defense traits and community stability (Griffin & 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 positive relationships between herbivore density and plant signals that directly recruit predators to 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.* 2013a). 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). Thus in addition to a trade-off in direct and indirect defense, 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), while concurrently modifying the identity and efficacy of foraging birds (Robinson & 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 & Whelan 1996), and subsequently plant morphology may provide an axis by which the top-down effects of different predator taxa vary. 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 are 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 increasing complexity indicating that any benefit to foraging at the interior of dense shrubs does not enhance prey encounter rates or capture efficiency.

In conclusion, this work significantly advances plant defense theory, suggesting a fundamental trade-off between direct herbivore resistance and indirect defense by birds driven by 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.

## SUPPLEMENTAL FIGURES

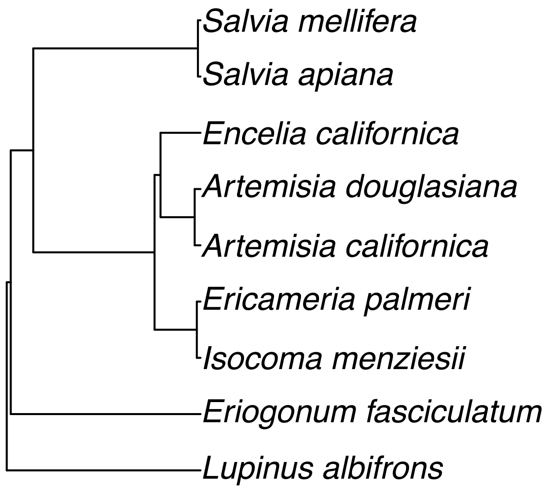


**Figure S1.1.** Phylogenetic relationships among study species with Grafen branch length transformation (ρ = 0.5).

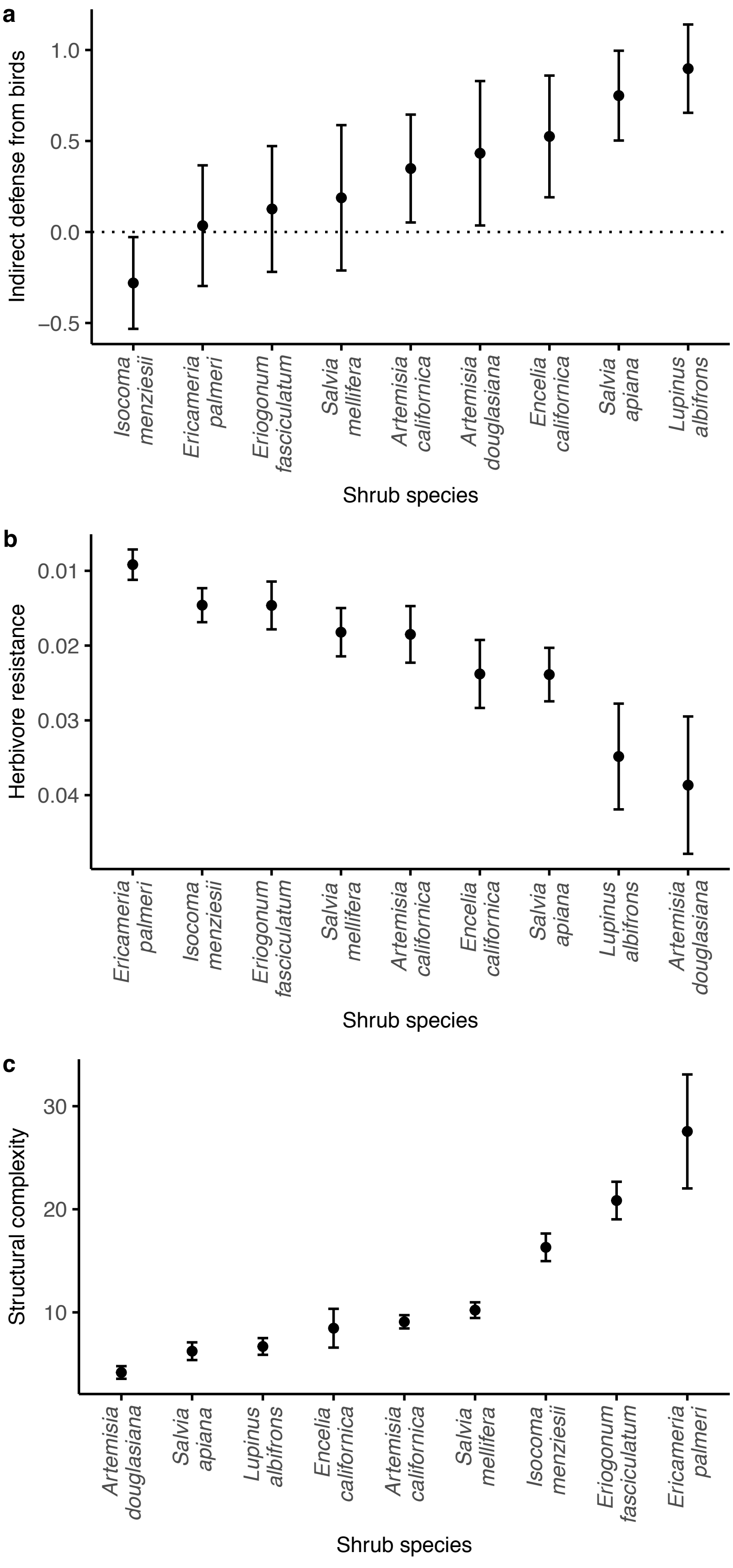

a
Indirect defense from birds
1.0
0.5
0.0
−0.5
Isocoma menziesii
Ericameria palmeri
Eriogonum fasciculatum
Salvia mellifera
Artemisia californica
Artemisia douglasiana
Encelia californica
Salvia apiana
Lupinus albifrons
Shrub species
b
Herbivore resistance
0.01
0.02
0.03
0.04
Ericameria palmeri
Isocoma menziesii
Eriogonum fasciculatum
Salvia mellifera
Artemisia californica
Encelia californica
Salvia apiana
Lupinus albifrons
Artemisia douglasiana
Shrub species
c
Structural complexity
30
20
10
Artemisia douglasiana
Salvia apiana
Lupinus albifrons
Encelia californica
Artemisia californica
Salvia mellifera
Isocoma menziesii
Eriogonum fasciculatum
Ericameria palmeri
Shrub species

**Figure S1.2.** Species means (± SE) for (a) indirect defense by birds, (b) herbivore resistance, and (c) structural complexity. Indirect defense is measured as the log response ratio of herbivore densities in bird exclusion compared to control plants (=ln[exclusion/control]). The dotted horizontal line at 0 reflects equal herbivore densities in control and bird exclusion treatments, or no indirect defense from birds. Direct herbivore resistance is measured as herbivore density in bird exclusion (mg $kg^{-1}$), such that high resistance is reflective of low herbivore density. Complexity is the density of branches along an axis through the plant.

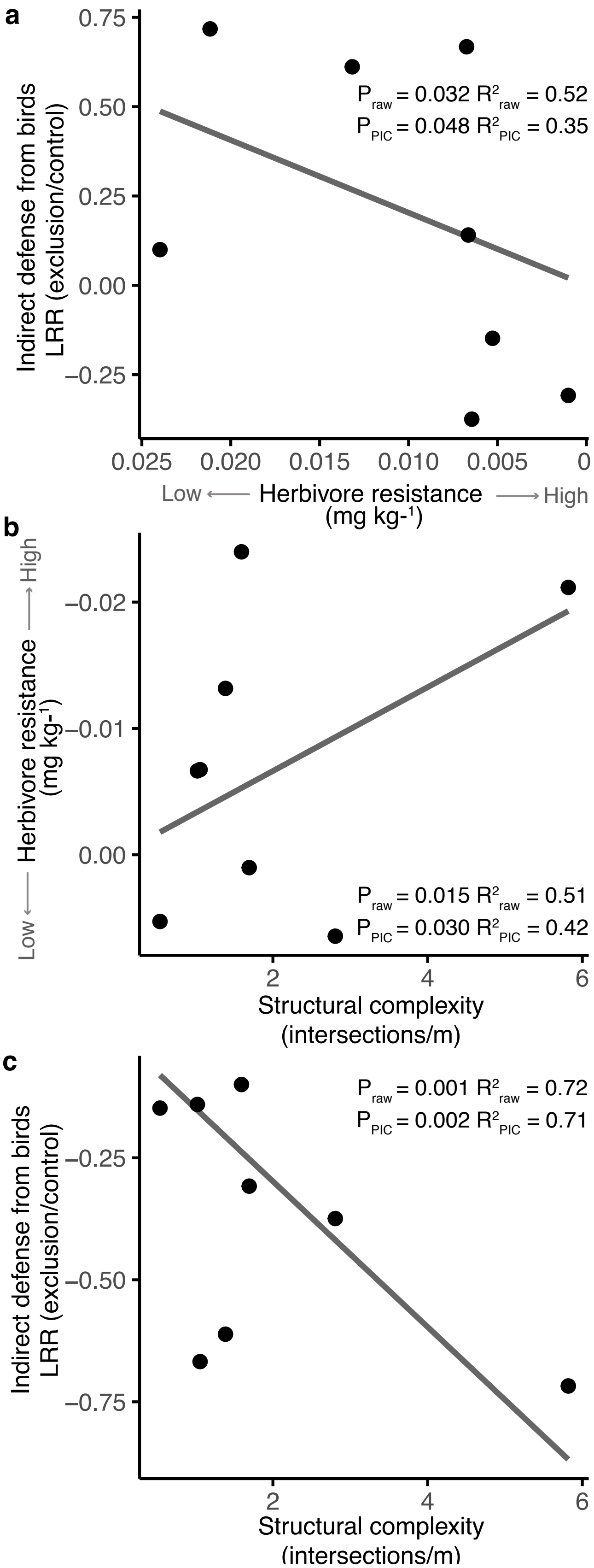

a
0.75
0.50
0.25
0.00
−0.25
Indirect defense from birds
LRR (exclusion/control)
P_raw = 0.032 R²_raw = 0.52
P_PIC = 0.048 R²_PIC = 0.35
0.025
0.020
0.015
0.010
0.005
0
Low ⟵ Herbivore resistance ⟶ High
(mg kg-¹)
b
−0.02
−0.01
0.00
Low ⟵ Herbivore resistance ⟶ High
(mg kg-¹)
P_raw = 0.015 R²_raw = 0.51
P_PIC = 0.030 R²_PIC = 0.42
2
4
6
Structural complexity
(intersections/m)
c
P_raw = 0.001 R²_raw = 0.72
P_PIC = 0.002 R²_PIC = 0.71
−0.25
−0.50
−0.75
Indirect defense from birds
LRR (exclusion/control)
2
4
6
Structural complexity
(intersections/m)

**Figure S1.3.** Pairwise phylogenetic independent contrast correlations between (a) direct herbivore resistance and indirect defense from birds, (b) structural complexity and herbivore resistance, and (c) structural complexity and indirect defense.

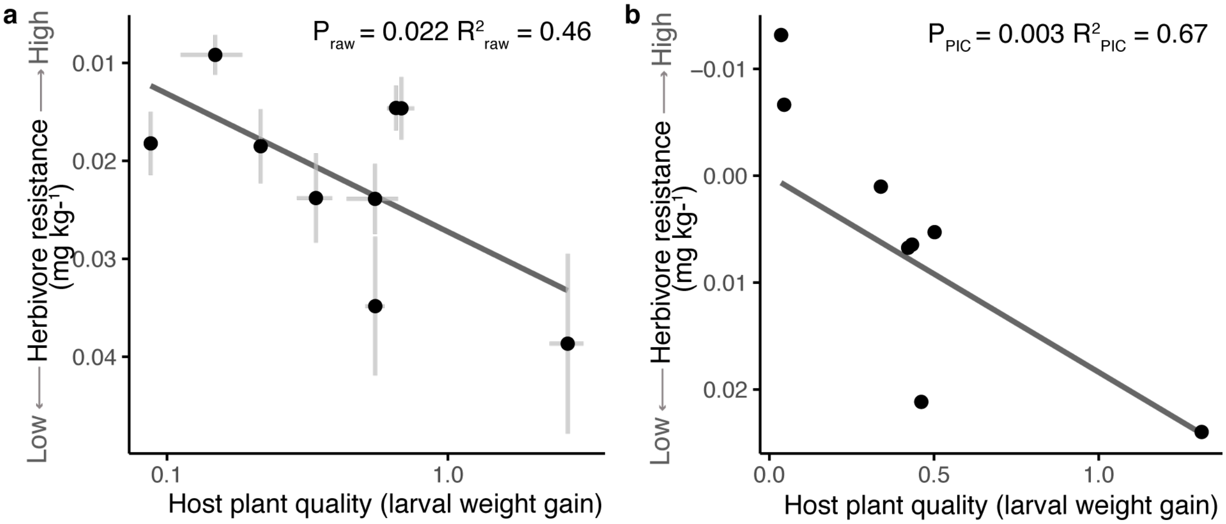


**Figure S1.4.** Raw (a) and PIC (b) correlations between host plant quality and herbivore resistance.

# CHAPTER 2

## Multiple mechanisms for herbivores achieve enemy-free space from bird predators associated with toxic host plants

### ABSTRACT

Birds are important predators of herbivorous insects, and herbivore traits conferring enemy free space (EFS) are well studied. In contrast, relatively little is known of the means by which host plants affect EFS by altering bird foraging. Using plasticine herbivore models to assay bird predation in a tropical forest understory, we uncovered novel evidence for multiple mechanisms by which host plants mediate bird-herbivore interactions. First, being located upon an exceptionally toxic plant (*Zamia* spp. Cycads) reduced the risk of model attack by 57% as compared to less toxic plants, including morphologically similar species (*Chamadorea* spp. Palms). Second, being located in association with (but not on) toxic host plants also provided EFS, with the risk of bird attack declining by 89% between understory patches with the lowest vs. highest toxic plant density. Third, visible plant damage by herbivores increased the risk of bird attack by 57% between plants with the lowest and highest rates of herbivory. These three plant-mediated effects on EFS were comparable to the 79% reduction in the risk of attack between aposematic (red clay) vs. cryptic (green clay) coloration. Our study highlights the importance of plant traits in mediating predator-prey interactions on multiple spatial scales, and that such effects can be comparable to, or exceed those affects associated with traits of the herbivores themselves.

## INTRODUCTION

Insectivorous birds are predators in most terrestrial ecosystems, and their top-down effects play an important role in the suppression of arthropods (Mooney *et al.* 2010a; Mäntylä *et al.* 2011). By consuming plant herbivores, bird predators can have cascading effects that indirectly reduce herbivore damage and promote plant productivity, however the magnitude of bird-mediated trophic cascades are highly variable within and between communities (Mooney *et al.* 2010a; Roslin *et al.* 2017). Understanding how predators forage is important to develop a mechanistic foundation to predict their top-down effects. Insectivorous birds are highly mobile, dietary generalists that track prey resources in time and space and exhibit specialized foraging tactics to exploit unique prey microhabitats (MacArthur & MacArthur 1961; Greenberg & Gradwohl 1980; Robinson & Holmes 1984; Whelan 2001). Bird predators tend to forage with density dependence, favoring larger bodied herbivores and greater herbivore densities (Naef-Daenzer *et al.* 2000; Gunnarsson 2007; Singer *et al.* 2012). Further, birds in general are recognized for their high visual acuity and cognitive abilities, that collectively promote optimal foraging behaviors (Bennett & Cuthill 1994; Honkavaara *et al.* 2002).

Herbivores employ a multitude of strategies to escape predation, and obtain enemy-free space (EFS), which in turn reflect the behaviors of the predators (Jeffries & Lawton 1984; Bowers 1993; Lee Dyer 1995; Ruxton *et al.* 2004; Greeney *et al.* 2012; Lichter-Marck *et al.* 2015). Herbivores can avoid predator detection through cryptic coloration or masquerading behaviors, in which they resemble their background or otherwise disguise themselves to evade predator search images (Skelhorn *et al.* 2010). Alternatively, some herbivores are armored against predator attack via spines and hair that provide physical defense (Lindstedt *et al.* 2008; Murphy *et al.* 2010), or chemical defenses sequestered from their host plants that render themselves toxic (Bowers & Larin 1989; Bowers 1993; Lee Dyer 1995; Opitz & Müller 2009). Well-defended herbivores frequently advertise their distastefulness with bright warning coloration (aposematism) which is thought to be effective for visual predators, like birds, because learned avoidance is enhanced with conspicuousness (Sillén-Tullberg 1985; Lindstedt *et al.* 2008; Skelhorn & Rowe 2010). Further, aposematic insects are commonly gregarious which serves to promote predator learning at lower cost to the prey (Gittleman & Harvey 1980; Gamberale & Tullberg 1998; Finkbeiner *et al.* 2012).

There is a growing recognition that plant species and the attributes of the surrounding plant community can mediate predator-herbivore interactions and, accordingly, be a major determinant of herbivore enemy-free space (Barbosa *et al.* 2009; Singer *et al.* 2012). Birds have strong capabilities for learning and memory, allowing them to develop associations between host plants with herbivore reward. For example, birds can use visible cues associated with herbivory as an indication of arthropod prey (Heinrich & Collins 1983; Mäntylä *et al.* 2008), thus plants that are more susceptible damage, leaf traits may be important in attracting predators to moderate herbivores. Similarly, it has been demonstrated that some insectivorous birds use olfaction to detect prey both directly, by honing in on pheromones (Saavedra & Amo 2018), and indirectly by responding to herbivore-induced plant volatiles associated with plant damage (Amo *et al.* 2013b; Mrazova & Sam 2018). There are other ways in which plants may act to inform predators about the resources they offer. In terms of prey avoidance, aposematic signals by chemically-defended herbivores effectively deter bird predators (Lichter-Marck *et al.*

2015), which has been largely attributed to learning associations between coloration signals and distastefulness (Gamberale-Stille & Tullberg 1999; Skelhorn & Rowe 2010), however nothing is known about whether predators use related plant cues to infer prey toxicity. Because the traits of herbivore communities are largely derived their host plants (Opitz & Müller 2009; Singer *et al.* 2012, 2014), a more common dynamic may be that birds learn certain plants are better places to forage. In this regard, birds should be expected to show preference for foraging habitats that are heterogenous, and offer diversity of foraging and nesting niches (MacArthur & MacArthur 1961), plant morphologies that are accessible and facilitate prey capture (Marquis & Whelan 1996), and plants that host abundant resources (Singer *et al.* 2012). Similarly, if birds learn that specific plants are not rewarding or are associated with toxic prey, herbivores could gain EFS by being on a toxic plant without being defended itself. For predators that forage with density dependence, using plant cues may be advantageous because they are apparent at larger spatial scales and can be used to make patch-level decisions. Further, variation in plant traits that render some species more predator-rich and others predator-deficient, which could affect bird-herbivore interactions on neighboring plants due by association (Barbosa *et al.* 2009), but the importance of such plant effects vs herbivore effects on predation by birds is unknown.

In this study, we document and qualitatively compare contrasting mechanisms by which plants may mediate herbivore EFS from bird predators. Specifically, we address the following questions: 1) Do highly toxic host plants reduce the risk of predation by insectivorous birds? 2) At the community-level, does being located in association with (but not on) toxic host plants reduce the risk of bird attack? 3) Is predation risk greater on plants with higher levels of visible leaf damage? In doing so, we compare the magnitude of plant-based cues to those arising from one of the best studied herbivore traits known to achieve EFS, aposematic coloration.

## METHODS

### *Study system*

Cycads (Order Cycadales) are an ancient plant lineage endemic to the Neotropics, whose potent chemical defenses are well known for their neurotoxic and fatal effects to consumers (Schneider *et al.* 2002; Castillo-Guevara & Rico-Gray 2003; Borenstein *et al.* 2007; Kisby *et al.* 2013). Combined with tough mechanical defenses, cycads are susceptible to relatively few herbivore taxa. However, the larvae of *Eumaeus* butterflies (Order Lepidoptera, Family Lycaenidae) feed exclusively on the tissues of *Zamia* cycads (Family Zamiaceae) and sequester compounds from their hosts for their own defense (Rothschild *et al.* 1986; Bowers & Larin 1989; Schneider *et al.* 2002). Both the larval and adult morphs are gregarious, use bright warning coloration (aposematism) to advertise their toxicity to potential predators, and have been demonstrated to be highly unpalatable to insectivorous birds (Bowers & Larin 1989; Bowers & Farley 1990). At the Las Cruces Biological Station of the Organization for Tropical Studies located in Coto Brus, San Vito, Costa Rica (8°47'7"N, 82°57'32"W; 1200 m.a.s.l.), *Zamia* cycads, and the herbivorous *Eumaeus* caterpillars, are common inhabitants of the tropical forest understory. Las Cruces is characterized as a premontane tropical wet forest in which cycads are typically found alongside plants from families Zingiberaceae, Heliconiaceae, Piperaceae, Rubiaceae, Melastomataceae, and *Chamadorea* palms (Family Arecaceae).

*Assessing predation risk*

We use artificial caterpillar models made from plasticine to measure the relative predation risk by insectivorous birds. To do so, we expose plasticine caterpillars to bird predators on the upper sides of the outermost, fully developed leaves on toxic hosts (*Zamia* cycads) and less toxic neighbors.  All caterpillar models were identical in size (4x25mm) and comparable to locally occurring herbivores. This method provides a highly consistent, unbiased assessment of predator effects (Low *et al.* 2014; Roslin *et al.* 2017) that can be easily manipulated to separate plant- and herbivore-driven effects from of natural variation in herbivore traits and behavior. Further, due to the malleable consistency of the plasticine, predator bite marks on caterpillar models are identifiable at a coarse taxonomic level allowing the separation of bird attack from other predator taxa (e.g. mammalian or arthropod)(Low *et al.* 2014). For every focal plant, any apparent herbivores were removed prior to the clay model experiments in order to control for herbivore density. Caterpillar models remained on their host plants for 2-3 consecutive days, during which they were examined for evidence of attack (bite marks) every 24 hours. In cases where artificial caterpillars were not recovered after 24 hours and their fate was uncertain (6.6% of all models) they were excluded from analyses. Models that were either attacked or missing after each 24 hour period were replaced with new models to maintain a constant density for the duration of the predator exposure.

*Effects of toxic host plants and herbivore aposematism*

In July 2015, we used identical caterpillar models made from red and green plasticine to compare the risk of predation for aposematic (red) and non-aposematic prey (green) on both toxic hosts (cycads) and less more palatable host plants (non-cycad neighbors). Across 4 sites approximately 400m apart from one another, we applied clay models to cycads and other co-occurring plants. Each focal cycad was paired with 2-3 non-cycad neighbors (within 3m) of a similar size. On each focal plant, one red and one green clay model were applied to opposite stems on the upper sides of fully developed leaves. Clay models were deployed synchronized within experimental sites, and sites were staggered such that predation data were collected concurrently for 2-3 sites at a time. Palms (*Chamadorea* spp.) comprised 35% of the experimental plants. Palms are very similar in appearance and morphology to *Zamia* cycads and are commonly found together at Las Cruces, however greatly differ in their defense and animal associations. Thus differences in the probability of attack between these two hosts could indicate that birds are influenced by factors other than broad visual appearance.

### *Associational effects of toxic neighbors*

In a second experiment, we examined whether cycad density had associational effects on the tri-trophic interactions of neighboring understory plants. To do so, we used clay models representing undefended prey (green color) to measure bird predation across on co-occurring plants across 11 plant "neighborhoods". Plant neighborhoods were spatially separated by a minimum of 300m and selected to capture variation in cycad density and plant community composition. Within each neighborhood, we randomly chose 30 individual plants along parallel transects (separated by 10m). Focal plants were selected as the nearest individual of a certain size (between 0.5m and 3m tall) every 2-3m along the transects. A single green model was applied to each focal plant and was checked for predation every 24 hours for 2 or 3 consecutive days. The total density of cycads in the surrounding 10m radius and leaf herbivory were measured in the same manner as the previous experiment.

### *Effects of herbivory*

To test whether herbivory mediates predation risk by birds, we measured the visible leaf damage due to chewing herbivores on each experimental plant. To do so, we visually assessed the amount of leaf area removed to the nearest 10% for the 3 outermost leaves of 3 separate stems or branches (9 leaves total), including the leaves corresponding to the location of the caterpillar models. In some cases, focal plants had fewer than 3 stems or 3 leaves per stem and herbivory was recorded as possible. For each plant, leaf damage was quantified as the mean percent leaf damage.

### *Statistical analyses*

The fates of the clay caterpillars were modelled using generalized linear mixed models (GLMM) fit by the Laplace approximation with a binomial error distribution and logit link function. Caterpillar predation was assessed across all predator exposure days as a binary outcome (0 = no attack, 1 = attack) and the total number of exposure days were included as a covariate. In comparing the effects of toxic plants and aposematism, we test for the main effects model color, host plant (cycad  or non-cycad), and their interaction on predation by birds. We include plant replicate nested within host plant and site as a random effects in the model. For the second experiment assessing the associational effects of toxic hosts, we use linear regression to evaluate the relationship between cycad density at the neighborhood-level and the mean proportion of models attacked by birds. In addition, we combined plant-level data on bird attack and herbivory from both experiments to test whether leaf damage mediates bird predation. We use a GLMM to test for the main effects of herbivore damage on bird attack with experiment as a fixed effect and site as a random effect.

## RESULTS

### *Effects of toxic host plants and herbivore aposematism*

A total of 338 plasticine models were deployed across 169 experimental plants (45 cycads). The survival of our herbivore models was contingent on model color ($P < 0.001$), host plant identity ($P = 0.015$), and their interaction ($P = 0.008$) (Table 1). Aposematism reduced the risk of bird predation by 79%, in which 40.2% of undefended green models were attacked versus 8.3% of red models attacked. The effect of aposematism was similar regardless of host plant, such that the probability of attack on cycads and their neighbors were 11.1% and 7.3%, respectively. However, for undefended green models, EFS was mediated by the host plant they occurred on; the risk of bird attack was reduced by 57% on toxic hosts compared to neighboring plants (20% attacked on cycads, 47.6% attacked on neighbors) (Fig. 1).

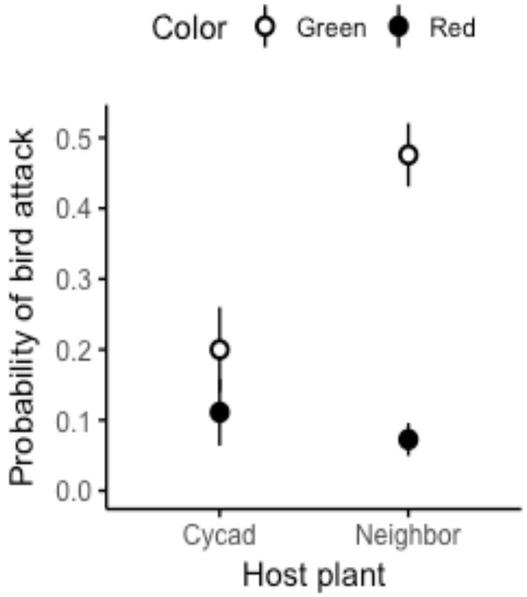


**Figure 2.1.** Effects of model color and host plant on the probability of bird attack (± SE). Green clay models are indicated with open circles and red clay models are filled.

**Table 2.1**

Summary of fixed effects from generalized linear mixed model (GLMM) predicting clay model predation by birds (N = 338). GLMM includes site and plant as random effects. Parameter significance is based on type III Wald $X^2$ tests.

| **Parameter** | **Est** | **SE** | **z** | **P** |
|---|---|---|---|---|
| (Intercept) | -0.127 | 0.343 | -0.372 | 0.710 |
| Model color | -3.334 | 0.682 | -4.891 | **< 0.001** |
| Host plant | -1.725 | 0.706 | -2.443 | **0.015** |
| Model color x host plant | 2.414 | 0.909 | 2.656 | **0.008** |

*Associational effects of toxic neighbors*

Green herbivore models were applied to a total of 330 non-cycad host plants across 11 sites in the second experiment. At the neighborhood-level, the mean proportion of models attacked within 24 hours was negatively related to mean cycad density ($P < 0.001$), corresponding to an 89% reduction in predation risk between understory patches with the lowest and highest toxic plant density (Fig. 2). Attack rates ranged from 42% (± 7.1% SE) in the understory patch with the lowest cycad density (0.43 ± 0.11 cycads within 10m of the focal plant) compared to 4.44% (± 2.6%) of models attacked in the highest cycad density (8.7 ± 0.48 cycads per focal plant).

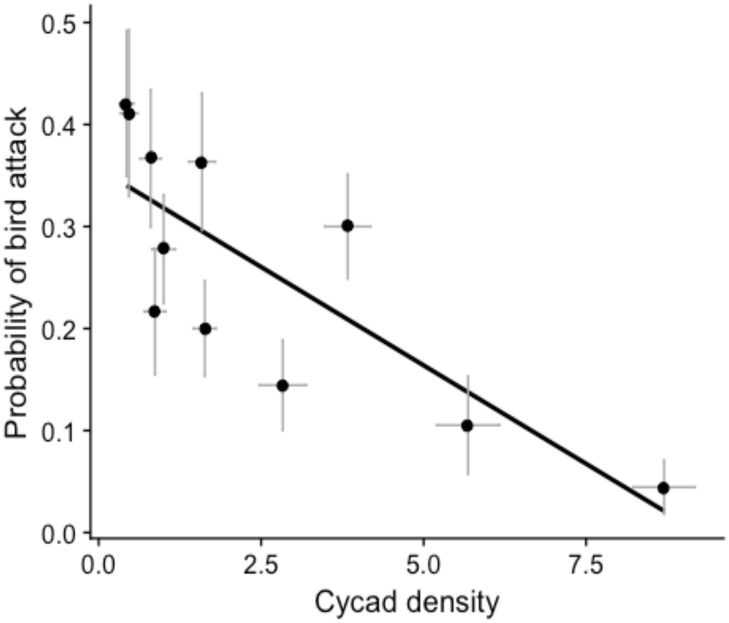


**Figure 2.2.** Relationship between neighborhood cycad density and the probability of bird attack (P = 0.0036, $R^2$ = 0.63). Neighborhood cycad density is the mean number of cycads within 10m of focal plants (± SE) per site (N = 11). The probability of bird attack at each site is the mean proportion of green models attacked per day (± SE).

### *Effects of herbivory*

Across both experiments, predation risk was higher for models that occurred on plants with greater levels of leaf damage (P = 0.039)(Fig. 3). The probability of bird attack ranged from 0.395 on plants with no visible leaf damage (herbivory = 0%) to 0.620 on plants with high levels of herbivory (herbivory = 40%), a 57% increase in predation risk attributed to visible leaf damage.

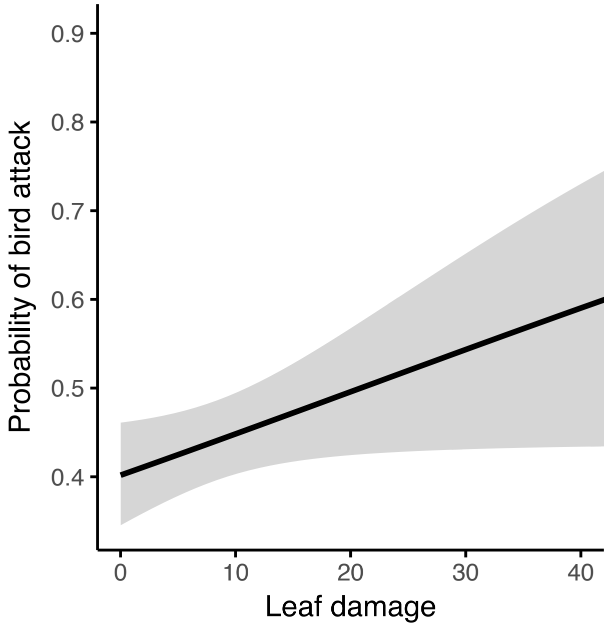


**Fig. 3.** Relationship between herbivore damage and the probability of bird attack (±SE) on clay models across all experimental plants (N = 471).

## DISCUSSION

We document evidence for multiple mechanisms by which host plants mediate enemy-free space from insectivorous bird predators. First, for undefended herbivore models, being located upon toxic plants (*Zamia* app. Cycads) reduced the risk of model attack by 57% as compared to less toxic plants. Second, EFS associated with toxic host plants extended to the neighboring plant community; predation risk declined by 89% between understory patches where cycads were rare vs. patches with the highest cycad density. Third, leaf damage due to herbivory increased the risk of bird attack by 57% between plants with the lowest and highest rates of herbivory. The magnitude of these three plant-mediated effects were comparable to aposematism, a widely appreciated anti-predator trait, which effectively reduced bird predation by 79% regardless of host plant. Collectively, these results provide novel support for the notion that plants mediate the top-down effects of bird predators and highlight the importance of multiple trophic levels in understanding community dynamics.

Although aposematism is widely recognized as an effective anti-predator signal, the direct contribution of toxic host plants to predator deterrence has been overlooked. From the herbivore perspective, the cost of consuming low quality plant tissues or spending time on suboptimal plants may be offset by gained EFS. The efficacy of such a strategy is likely contingent on the reliability of the plant in signaling toxicity shaped by the frequency and potency of toxic individuals. At larger spatial scales, herbivores may be more resource-limited in patches with higher densities of toxic plants but simultaneously benefit from reduced apparency to their predators and generally less attractive resources.

In our study, green models gained EFS on toxic plants and on neighboring plants when toxic plants were in higher density. In other studies it has been shown that prey avoidance can be learned where any ill effects follow the consumption of a novel food are associated with visual, olfactory, or gustatory cues (Ruxton *et al.* 2004), thus it is likely that predators can learn aversions to certain host plants due to prior negative experience with unprofitable herbivores or low prey reward. Because specialized herbivores spend the majority of their life cycle on their host plant, negative associations between aposematism and palatability could secondarily be associated with the plants on which they occur and other co-varying traits. These effects are likely more pronounced when prey toxicity is high due to the increased cost of ingestion (Skelhorn & Rowe 2010). Similarly, because negative stimuli from eating toxic prey are a product from the plant itself, the plant could be a larger cue and more effective deterrent. Just as the function of aposematic signals increases with the density of an aggregate signal (Gamberale & Tullberg 1998), the effect of toxic plants was stronger as their density increased. Patches with high densities of cycads should be more easily detectable and apparent at broader scales, promoting optimal foraging among microhabitats.

For undefended prey, visible leaf damage positively affected the probability of bird attack. This agrees with previous work that had documented increased bird recruitment and predation associated with higher levels of herbivory (Mäntylä *et al.* 2008). In addition to host plant identity, visual cues of leaf damage can provide information about habitat suitability at larger scales and be indicative of the density or size of feeding herbivores ) the consequences of biodiversity loss on bird-herbivore interactions. However while such cues may be useful to locate prey microhabitats, they should be secondary to other signals that are more indicative of quality, and more effective in conjunction with co-occurring signals like herbivore-induced volatiles or other time-relevant olfactory cues.

This study contributes to a larger body of work that demonstrates that plant traits and plant communities affect bird-herbivore interactions (Marquis & Whelan 1996; Mäntylä *et al.* 2008; Singer *et al.* 2012; Amo *et al.* 2013b; Muiruri *et al.* 2016; Mrazova & Sam 2018) and builds upon it by showing that in addition to attracting bird predators, plants play a role in predator deterrence at multiple spatial scales.

# CHAPTER 3

# Tropical tree diversity mediates foraging and predatory effects of insectivorous birds

## ABSTRACT

Biodiversity affects the structure of ecological communities, but little is known about the interactive effects of diversity across multiple trophic levels. We used a large-scale forest diversity experiment to investigate the effects of tropical tree diversity on insectivorous birds, and the subsequent indirect effect on predation rates by birds. Diverse plots (4 tree species) had higher bird abundance (61%), phylogenetic diversity (61%), and functional diversity (55%) than predicted based on single-species monocultures, which corresponded to higher attack rates on artificial caterpillars (65%). Tree diversity effects on attack rate were driven by complementarity among tree species, with increases in attack rate observed on all tree species in polycultures. Bird abundance and diversity were each strongly correlated with attack rate, but the indirect effect of tree diversity was mediated by bird diversity, providing evidence that diversity can interact across trophic levels with consequences tied to ecosystem services and function.

## INTRODUCTION

Biodiversity loss is one of the fundamental consequences of human-driven global change (Haddad *et al.* 2015; Newbold *et al.* 2015). These losses are problematic not only for species conservation, but also because of the emergent, higher order effects of biodiversity on ecosystem function (Hooper *et al.* 2012; Tilman *et al.* 2014) and associated services

(Balvanera *et al.* 2006; Cardinale *et al.* 2012). Studies of biodiversity-ecosystem function (BEF) have reported extensively on the bottom-up effects of plant diversity on primary productivity (Balvanera *et al.* 2006; Duffy *et al.* 2017) and, to a lesser extent, on the structure of associated animal communities (MacArthur & MacArthur 1961; Greenberg & Gradwohl 1980; Robinson & Holmes 1984; Naef-Daenzer *et al.* 2000)(Duffy *et al.* 2007; Haddad *et al.* 2009; Scherber *et al.* 2010; Dinnage *et al.* 2012). In parallel, a smaller number of BEF studies have addressed the top-down effects of predator diversity on lower trophic levels (Finke & Snyder 2008; Griffin *et al.* 2013), collectively demonstrating how diversity can promote ecosystem productivity, stability, and resilience to disturbance (Haddad *et al.* 2011; Tilman *et al.* 2014). However, most studies to date have approached these processes in terms of the top-down or bottom-up effects emanating from diversity within a single trophic level (i.e. plants or predators) without addressing the non-linear dynamics of diversity across multiple trophic levels. Accordingly, the linkages between plant diversity and consumer (particularly predator) diversity are poorly understood.

Originally proposed to explain high rates of herbivory in simplified (non-diverse) agricultural systems, the Enemies Hypothesis (EH) conceptually links diversity effects across trophic levels (Root 1973). According to Root (1973), plant diversity increases predator abundance, and this in turn strengthens top-down control of herbivorous insects (Root 1973; Letourneau *et al.* 2011). As such, the EH describes a compelling example of ecosystem services from biodiversity; high-diversity agricultural systems (i.e. polycultures) are on average associated with higher predator abundance (44%), herbivore mortality (54%) and reduced crop damage (30%) compared to low diversity (i.e. monoculture) systems (reviewed by [Letourneau *et al.* 2011]). Accordingly, the EH guides agricultural practices aimed at maximizing biological control (Crowder & Jabbour 2014; Isbell *et al.* 2017), however whether such feedbacks extend to natural systems is unclear. The paucity of tests with vertebrate predators is especially notable given their prevalence in terrestrial ecosystems, sensitivity to anthropogenic impacts, and strong top-down effects on herbivores (Halpern *et al.* 2005; Mooney *et al.* 2010a; Hallmann *et al.* 2014).

Despite the demonstrated importance of the EH, the underlying mechanisms driving plant mediation of predator effects are not well understood. The EH predicts plant diversity should increase predator abundance (Root 1973; Letourneau *et al.* 2011) through an increase in predator niche space (Hooper *et al.* 2005). While not formally proposed by the EH, this same mechanism can also increase predator diversity (Dinnage *et al.* 2012). Both predator abundance and diversity (Philpott *et al.* 2009; Griffin *et al.* 2013) have been demonstrated to enhance top-down control of herbivore populations, but past tests of the EH have focused nearly exclusively on measuring predator abundance (Letourneau *et al.* 2011; Lichtenberg *et al.* 2017). As a result, a fundamental aspect of the EH mechanism – how predator communities mediate the indirect effects of tree diversity on herbivore suppression– is unknown.

Here we quantitatively decompose the strength of EH effects operating via predator diversity vs. predator abundance. We do so within the context of tropical tree diversity and insectivorous bird predators, thus addressing these dynamics within a complex ecosystem as compared to the simplified agricultural systems that have been the focus of past EH studies (Root 1973; Matson *et al.* 1997; Letourneau *et al.* 2011). Working within a tropical forest diversity experiment, we test for the effects of tree diversity directly on insectivorous bird foraging. We use clay model caterpillars to assess the indirect effects of tree diversity on predation rates, and compare the extent to which these indirect effects of tree diversity were mediated by direct effects on bird abundance vs. diversity. This study thus provides a novel test of the mechanisms underlying the EH in a natural ecosystem and, in so doing, demonstrates the importance of biodiversity across multiple trophic levels.

## METHODS

### *Experimental design*

We tested for tree diversity effects within the context of a large-scale forest diversity experiment (7.2-ha) in the Yucatan Peninsula (20°24’44”N, 89°45’13”W), ca. 70 km southwest of Merida, Yucatan (Mexico) and found at the "Uxmal Experimental Site" of the Instituto Nacionalde Investigaciones Forestales, Agrícolas y Pecuarias (INIFAP). In 2011, we planted 74 replicate forest plots (21 x 21 m each) as polycultures of four tree species or single-species monocultures from a pool of six long-lived deciduous tree species (*Swietenia macrophylla* King (Meliaceae), *Tabebuia rosea* (Bertol.) DC. (Bignonaceae), *Ceiba pentandra* (L.) Gaertn. (Malvaceae), *Enterolobium cyclocarpum* (Jacq.) Griseb. (Fabaceae), *Piscidia piscipula* (L.) Sarg. (Fabaceae), and *Cordia dodecandra* A. DC. (Boraginaceae) (Fig. S1; as described in [Abdala-Roberts *et al.* 2015]). At the time of sampling, the site was composed of ca. 4600 trees (4780 originally planted) at a constant density of 64 plants per plot (3 m spacing between trees, 6 m aisles between plots). The average tree height was approximately 7-8 m during the time of the experiment.

### *Bird community metrics*

In July of 2015, we surveyed bird community composition within 32 of the total 74 plots (12 monocultures and 20 polycultures), totaling 40 minutes of observation per plot at peak bird activity (0600 and 0930 on rain-free days). We conducted visual surveys of birds, using 10x42 binoculars and field guides for identification (Howell & Webb 1995). Surveys were done by two observers experienced with these techniques and the local bird fauna. During these observations, birds were recorded only if they were actively foraging. In our analysis we focus on the subset of species reported to feed partially or entirely on insects (based on (Wilman *et al.* 2014); Table S1). The plot size (0.1 ha) and that of the larger experimental site are relatively small with respect to the territory sizes of some of the species observed. Accordingly, our data reflect the effects of tree diversity on the foraging movements of birds among plots rather than on the diversity of site overall.

We characterized the effects of tree diversity on three bird community metrics at the plot-level: abundance, functional trait diversity (FD), and phylogenetic diversity (PD). Insectivorous bird abundance was measured as the total number of individuals per plot. We use FD and PD to quantify the ecological and phylogenetic dissimilarity among species, respectively, measured as the sum of all branches (phylogenetic or trait-based dendrogram) connecting species observed across observations (Faith 1992; Petchey & Gaston 2002; Flynn *et al.* 2011). We calculate FD, the total trait diversity represented among observed species, based on available species-level traits hypothesized to be important for herbivore suppression: body mass, period of activity [diurnal or nocturnal], major diet type [vertebrate, invertebrate, fruit/nectar, plant/seed, omnivore], portion of diet by type [vertebrate, invertebrate, fruit, nectar, seeds, other plant], and relative time foraging in forest strata [ground, understory, mid-canopy, canopy, aerial]) (compiled from

(Wilman *et al.* 2014), Table S1). Body mass was log transformed to reduce the influence of a few uncommon and larger-bodied species. All functional traits were rescaled (mean = 0, SD = 1) and weighted equally to calculate Gower's pairwise dissimilarity among species (Gower 1971), from which we applied hierarchical clustering (UPGMA method) to construct a dendrogram reflecting bird species functional similarity. Here we report on the subset of birds that consume any insect prey in their diet and traits based on a priori hypotheses. While trait selection can have significant influence over measures of FD (Zhu *et al.* 2017), in exploratory analyses (not shown) our results were qualitatively the same using different subsets of the observed birds (e.g. all birds, strict insectivores only) and other similar trait combinations. In addition, we quantify PD, the total evolutionary history shared among species, which can be used as a proxy for FD. To calculate PD, phylogenetic branch lengths were inferred from a 95% consensus tree containing mean branch lengths. This phylogeny was derived from 200 time-calibrated phylogenies of the Hackett-backbone, pruned to the species observed (Hackett *et al.* 2008; Jetz *et al.* 2012). For each bird community metric (abundance, FD, and PD), we quantified the overall effect size of tree diversity as the grand mean of the log of the proportional difference (LR) between observed and expected bird communities for each polyculture plot, where the expected was calculated as the weighted mean of component tree species in monoculture. A positive LR where the 95% C.I. does not bracket zero indicates a significant positive effect of tree diversity, such that polyculture bird communities exceeded predictions under an additive scenario based on tree species monocultures.

### *Assessing bird predation*

Concurrent with bird surveys, we assessed bird predation in the same plots (all 12 monocultures and 17 of the 20 polycultures). Using established methods (Low *et al.* 2014; Roslin *et al.* 2017), we deployed and inspected artificial caterpillar models of green plasticine clay (4x25mm) to record bird attack (bite marks). Tree species- and plot-level predation rates were calculated as the proportion of caterpillar models attacked per 24-hour period. This method provides a highly consistent, unbiased assessment of predator effects (Low *et al.* 2014; Roslin *et al.* 2017) independent of variation in herbivore morphology, size, behavior and density that may occur among tree species and diversity treatments. Caterpillar models were exposed for two consecutive days on the upper side of leaves from two opposing branches of 12 trees per plot (three trees of each species in polyculture). Caterpillar models were placed between 2 and 4m in the canopy on interior trees, to exclude perimeter trees that bordered neighboring plots (and potentially different tree species). After a 24-hour period, caterpillar models were visually assessed for bird attack. Any attacked models were then replaced, and all models were again assessed after a second 24-hour period. Caterpillar models were similar in size to generalist leaf-chewing herbivores found at the experimental site, and were sufficiently malleable that attack marks could be used to distinguish predation by birds from that caused by other taxonomic groups such as arthropods and mammals (Low *et al.* 2014). Caterpillar models attacked or lost after 24 hours were replaced with intact models for a constant model density per plot (n = 24) in the following survey. Cases where the fate of the model was uncertain were excluded from predation rate calculations (n = 67; 4.05% of models). This experiment was repeated twice over a three-week period in which we used the same 12 monoculture plots (but different trees) across iterations, and different polyculture plots between the first and second iterations (11 and 7 polyculture plots respectively). Tree- and plot-level attack rates were calculated from these data as the proportion of models attacked by birds per 24-hour period. There was no effect of experiment iteration on model attack rates, thus predation rates in monoculture plots are calculated as the mean proportion attacked across all four exposure days.

We calculated plot-level tree diversity effect ($LR_{pred}$) in the same manner used to assess diversity effects on bird community metrics (Fig. 1). In addition, we also used tree-level predation data to compare attack rates between monoculture and polyculture separately for each tree species, and to decompose the net biodiversity effect on predation into selection effects and complementarity effects (following (Loreau & Hector 2001)). Selection effects are driven by the increased probability of polycultures including species that have particularly strong effects on attack rates (Huston 1997; Loreau & Hector 2001). In contrast, complementarity effects arise due to interactions among tree species leading to non-additive increases in attack rates (e.g. niche differentiation, facilitation), where polycultures differ from additive predictions from monocultures (Loreau & Hector 2001; Hooper *et al.* 2005).

### *Comparing bird community metrics*

We evaluate the pairwise relationships between bird community metrics and attack rate first using linear regression. We compare these models to all possible regression models (abundance, FD, and PD alone and in combination) using Akaike's information criterion. As bird abundance, FD and PD were all positively correlated with plot-level attack rates (Fig. 4), we used SEM to evaluate which of the observed bivariate relationships between the bird community metrics and attack rate mediated the indirect effects of tree diversity. Because of high covariance between bird abundance, PD, and FD (Fig. S3), we only included FD based upon its stronger bivariate relationship with attack rate (Table 1, Fig. 4), although all conclusions from our analyses were qualitatively identical when PD was used in place of FD (analyses not shown). Having dropped PD, we began with an initial SEM model that included indirect effects of tree diversity on attack rate via both FD and abundance; specifically, this model included the direct pathways from tree diversity to bird abundance and FD, the direct pathways from bird abundance and FD to attack rate, and the covariance between bird abundance and FD (Fig. 5a). Following the assessment of this initial hypothesized model, we then removed the non-significant pathways in a stepwise procedure. Both the initial model and this reduced model were then evaluated for their fit to the data using chi-square ($P > 0.05$ indicates valid model fit), and the significance of each pathway was evaluated with Z-statistics (Grace 2006). In addition, for both models we quantified the indirect effects of tree diversity as the product of the standardized regression coefficients of component direct pathways in the SEMs (Grace 2006). Indirect effects stemming from tree diversity were deemed significant when the two individual pathways making up the indirect effect were significant. The resulting indirect effects are visualized using curved grey arrows that encapsulate the underlying direct effects in the model, with nonsignificant pathways indicated by dashed lines (Fig. 5). SEM was conducted using the 'lavaan' package in R (Rosseel 2012; R Core Team 2017).

## RESULTS

A total of 44 bird species (5.4 ± 0.5 species per plot; mean ± SE) and 381 individuals (11.9 ± 1.3 individuals per plot) that consume insects were observed foraging in our surveys. Tree diversity had a positive effect on all bird community metrics, resulting in higher bird abundance (61%), phylogenetic diversity (61%), and functional trait diversity (55%) in polyculture plots relative to expected values in monocultures (Fig. 1; $LR_{abun}$ = 0.48, 95% C.I. = 0.23 to 0.73; $LR_{FD}$ = 0.44, 95% C.I. = 0.28 to 0.59; $LR_{PD}$ = 0.47, 95% C.I. = 0.35 to 0.61). Mean bird abundance per plot increased from 8.5 (± 1.99) to 13.9 individuals (± 1.64) and species richness from 3.8 (± 0.58) to 6.4 (± 0.64) in monoculture and polyculture, respectively. In polycultures, mean bird PD exceeded that of the highest tree species in monoculture (i.e. transgressive overyielding; (Schmid *et al.* 2008)) (Fig. 2). In contrast, polyculture mean abundance and FD were not significantly different than that observed in the highest tree species monoculture (Fig. 2).

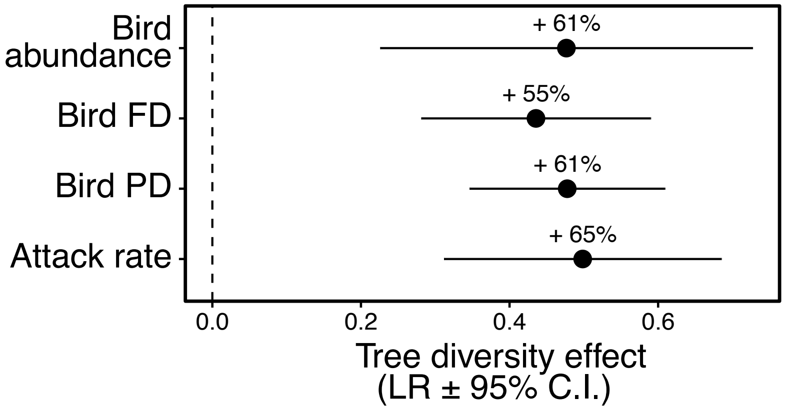


**Figure 3.1.** Tree diversity effect (LR ± 95% CI) on attack rate (n =17), bird abundance (n = 20), bird FD (n = 20), and bird PD (n = 20) at the plot-level.

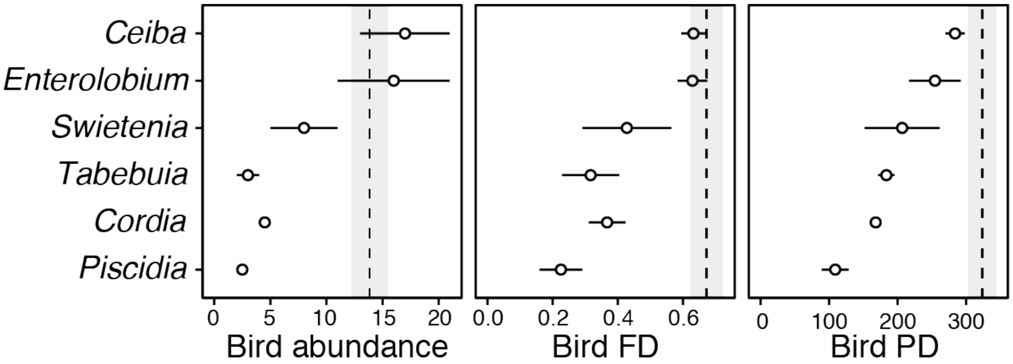


**Figure 3.2.** Monoculture plot-level means (± SE; n = 2) of bird abundance (individuals per plot), FD (total Gower distance), and PD (millions of years) for each tree species (indicated by genus name). Dashed lines indicate the mean values observed in polyculture (shading indicating ± SE; n = 17), respectively.

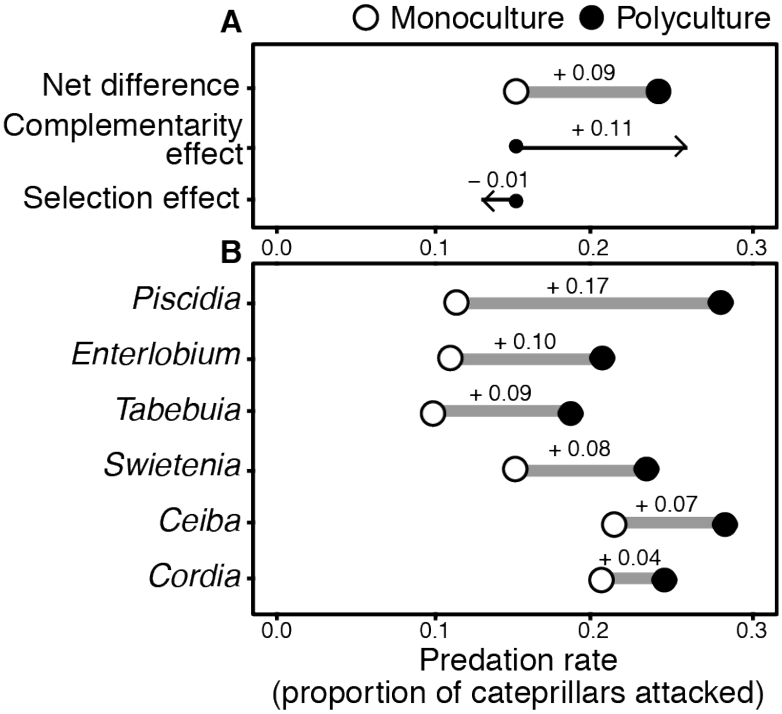


**Figure 3.3.** Differences in model attack rates between monoculture (open circles) and polyculture plots (filled circles). (A) Net plot-level effects depict mean expected polyculture values (weighted average of monocultures) and observed polycultures. This net effect is then decomposed into selection and complementarity effects. (B) Tree-level effects, comparing attack rate for each tree species when grown in monoculture vs. tree-level attack rates when the species is included in polyculture.

Across all experimental plots, we observed a mean attack rate (proportion of caterpillar models attacked per 24 hours) of 0.20 (± 0.016 SE). In support of the EH, tree diversity increased bird attack rate, with polyculture plots (0.24 ± 0.022) exhibiting a significantly (64%) greater mean value than expected values based upon monocultures (0.15 ± 0.004) (Fig. 1). This corresponded to a mean increase in attack rate of 0.09 (± 0.022) with tree diversity (Fig. 3), in which all but 3 polyculture plots had stronger attack rates than the highest monoculture (Fig. S3). Furthermore, the average attack rate across polyculture plots exceeded that of all tree species in monoculture plots (i.e. transgressive over yielding), due to increased attack rates for all tree species in polyculture plots compared to monoculture plots (Fig. 3). Accordingly, the net effect of tree diversity was attributed to a small, negative selection effect (-0.011 ± 0.004 SE; t.test, t(16) = -2.78, P = 0.011) and a larger, positive effect of tree complementarity (0.105 ± 0.023; t.test, t(16) = 4.52, P = 0.0003) (Fig. 2), indicating the positive effect of tree diversity on attack rate was driven by multi-species processes.

Differences in bird attack rate between monoculture and polyculture plots were mediated by the direct effects of tree diversity on bird communities; attack rate was positively correlated with bird abundance ($R^2 = 0.27$, F[1,27] = 10.37, P = 0.003), FD ($R^2 = 0.36$, F[1,27] = 15.55, P = 0.0005), and PD ($R^2 = 0.31$, F[1,27] = 12.36, P = 0.0016), with bird diversity (FD and PD) showing slightly stronger associations with attack rate than abundance (Fig. 4). When these bivariate models were compared with all possible multiple regression models using Akaike's information criteria, we found that models with bird FD and PD (alone) best explained variation in attack rate. Of the two top models ($\Delta AIC_c < 2$), the model containing FD had the highest weight (0.437 compared to 0.180) but the relative effects of PD and FD were similar (Table 1). In contrast, abundance was not included as a parameter in the top competing models and the bivariate model including abundance had weak support (weight = 0.053, $\Delta AIC_c = 4.21$) .

We used structural equation modelling to quantitatively compare the extent to which tree diversity indirectly affected attack rate via bird abundance vs. diversity. Preliminary analyses indicated the multicollinearity between bird PD and FD (Fig S3; $R^2 = 0.87$, $P < 0.001$) was too high to include both variables in our model, and suggested FD to be the superior to PD in predicting variable to represent variation in bird diversity driving attack rate (Table 1). Thus we compare bird FD and abundance as mediators of the indirect effect of tree diversity on attack rate (i.e. product of two partial beta coefficients for direct effects (Grace 2006)). In our initial hypothesized model, the indirect effect of tree diversity mediated by bird FD had a positive effect on attack rate (indirect effect = 0.32, $P = 0.043$) while the bivariate relationship between bird abundance and attack rate was not significant ($P = 0.82$), suggesting that the indirect effect of tree diversity on attack rate was mediated largely, or entirely by bird diversity (Fig. 5a; SEM, $X^2 = 3.25$, $P = 0.071$). When non-significant paths were removed from this initial model in a stepwise procedure, the resulting final model reflected a full mediation of tree diversity effects by bird FD (Fig 5b; SEM, $X^2 = 3.25$, $P= 0.072$). Using AIC model selection, this final model was deemed the best fit to our data compared to alternative models including bird abundance ($\Delta AIC = 206.85$).

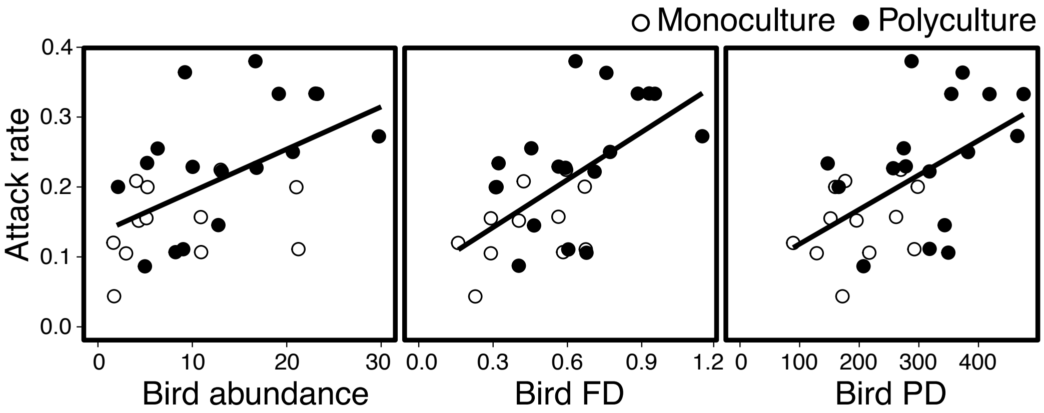


**Figure 3.4.** Bivariate relationships between plot-level attack rates and bird abundance ($R^2 = 0.27$, $P = 0.003$), FD ($R^2 = 0.36$, $P = 0.0005$) and PD ($R^2 = 0.31$, $P = 0.001$). Monoculture plots are indicated with open circles (n = 10) and polycultures are filled circles (n = 17). X-axis units are the same as in Fig. 2.

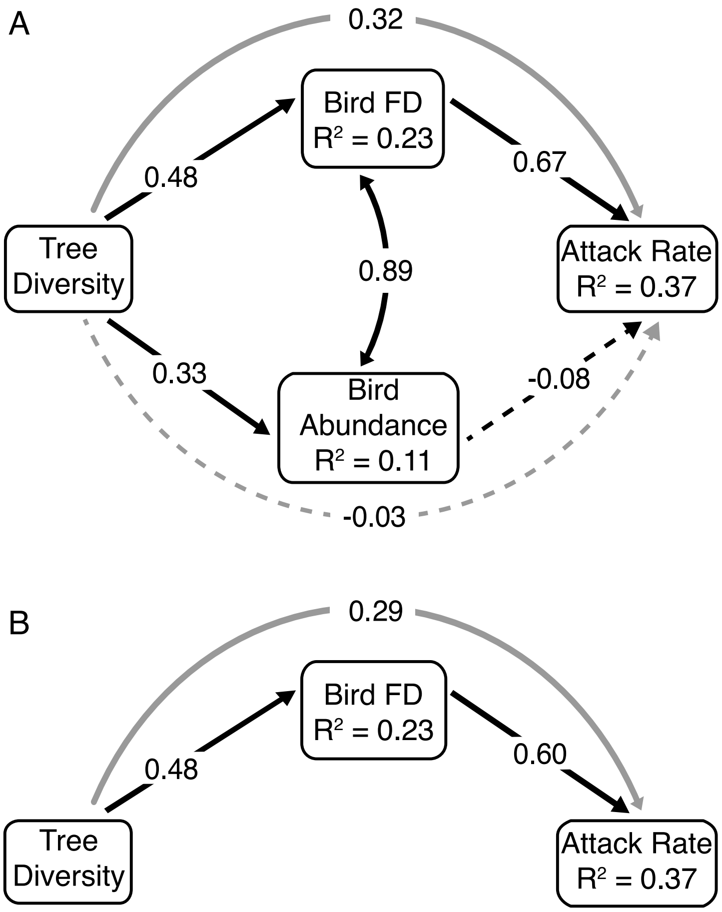


**Figure 3.5** Initial (a; X2 = 3.25, P= 0.071) and final (b; X2 = 3.25, P= 0.072) structural equation models comparing the indirect effects of tree diversity on model attack rate, mediated by the bird community (curved grey arrows). Arrows represent causal relationships among variables, with direct effects in black and indirect effects indicated with grey. Dashed arrows indicate a non-significant path (P ≥ 0.05). For each path the magnitude of effect is provided as the standardized regression coefficient for direct effects, and the product of component standardized coefficients for indirect effects. $R^2$ values of component models are provided in boxes with the response variable.

**Table 3.1**

Comparing bird community metrics as predictors of model attack rates.

| Model | Df | logLik | AICc | ΔAIC | weight | ABUN | FD | PD |
|---|---|---|---|---|---|---|---|---|
| FD | 3 | 35.68 | -64.41 | 0.00 | 0.437 | | 0.578 | |
| PD | 3 | 34.80 | -62.64 | 1.77 | 0.180 | | | 0.534 |
| ABUN + FD | 4 | 35.84 | -62.02 | 2.38 | 0.132 | -0.189 | 0.749 | |
| FD + PD | 4 | 35.68 | -61.71 | 2.70 | 0.113 | | 0.565 | 0.014 |
| ABUN | 3 | 33.58 | -60.20 | 4.21 | 0.053 | 0.474 | | |
| ABUN + PD | 4 | 34.86 | -60.06 | 4.35 | 0.050 | 0.099 | | 0.452 |
| ABUN + FD + PD | 5 | 35.84 | -59.08 | 5.33 | 0.030 | -0.189 | 0.742 | 0.007 |
| (none) | 2 | 29.78 | -55.11 | 9.30 | 0.004 | | | |
| | | | | **Top models:** | | | 0.578 | 0.534 |

AIC model selection results evaluating bird community metrics as predictors of model attack rates (n = 27), ranked by model weight. Parameter estimates for bird abundance (ABUN), functional diversity (FD), and phylogenetic diversity (PD) are z-transformed for comparison and used to calculate weighted averages across a subset of the top models in which $\Delta AIC_c < 2$.

## DISCUSSION

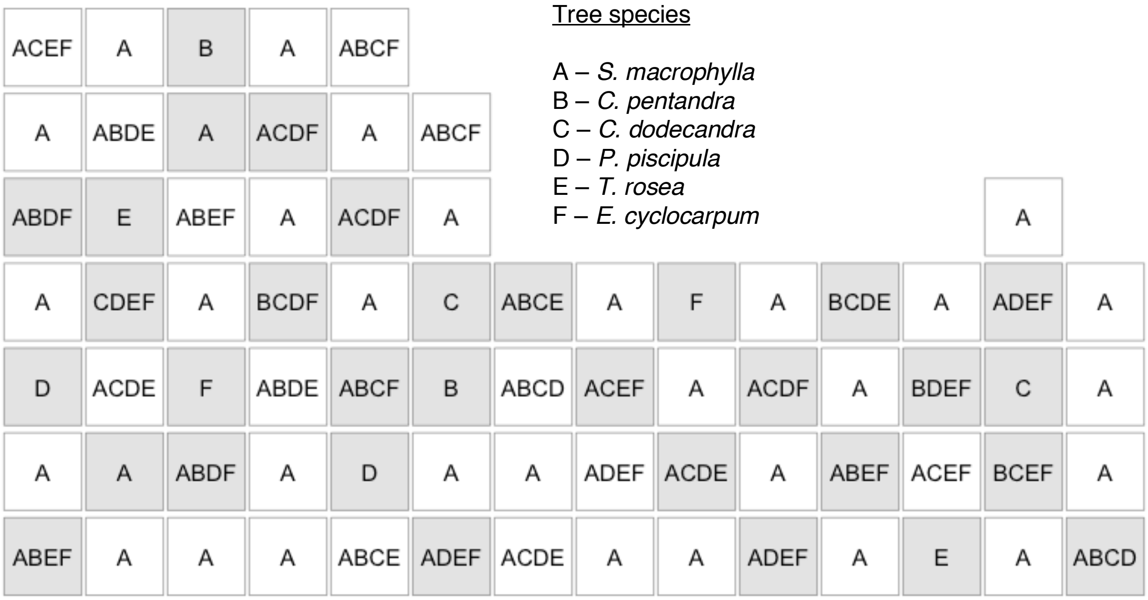
Where past tests of the EH have largely investigated the effects of plant diversity on predator abundance (Letourneau *et al.* 2011; Lichtenberg *et al.* 2017), our findings demonstrate that indirect effects of plant diversity on top-down control are mediated by predator diversity. We link the positive effects of tree diversity on attack rate (65% higher) to tree species complementarity and increases in the functional diversity of foraging birds (55%), indicating that multi-species processes are responsible for the observed effects at multiple trophic levels. This work is the first to decompose EH effects, demonstrating the importance of predator diversity over abundance.

Bird diversity may increase attack through several, non-mutually exclusive mechanisms. Predator diversity is most often presumed to increase prey attack due to predators foraging in separate microhabitats and thus eliminating enemy free space (Schmitz 2007). Our design likely underestimates such effects, as we placed caterpillar models in a uniform location across tree species (upper side of leaves on lower branches) and thus did not capture the breadth of foraging niches that span forest strata, microhabitats, and prey type. Alternatively, increased bird diversity may have reduced time spent on intra-specific interactions including territory defense or courtship (Morse 1970; Gómez *et al.* 2010), while abundance could increase competitive interactions. Consistent with our results, previous meta-analyses found that bird effects on arthropods in tropical agroforestry systems were correlated with bird diversity, but not abundance (Bael *et al.* 2008; Philpott *et al.* 2009). Together, these findings suggest a feedback linking diversity on multiple trophic levels to the top-down effects of predators.

Our work extends the mechanisms of the EH to forest ecosystems as vertebrate predators, both of which dominate terrestrial communities globally. While our focus is on plants and predators, it is likely that similar mechanisms influence other ecological processes contingent on species interactions. Birds in particular are a highly diverse group that are linked to ecosystem function in a variety of ways, such as pollination and seed dispersal (Sekercioglu *et al.* 2004; Whelan *et al.* 2008; Jetz *et al.* 2012). Accordingly, the consequences of biodiversity loss are likely more complex and far-reaching than is currently appreciated. This is exceedingly important given human dependence on forest services and products, and the rapid pace of environmental change (Newbold *et al.* 2015).

Biodiversity effects are commonly studied with regard to a single trophic level, but the interactive effects of diversity across multiple trophic levels may affect ecosystem processes synergistically. Consequently, biodiversity loss at one trophic level has not only direct implications, but also indirect effects through the disruption of such synergies, that could result in negative feedbacks across trophic levels. As such, conservation strategies that consider multi-trophic biodiversity may support an array of community dynamics that are critical to ecological function.

## SUPPLEMENTAL FIGURES



Tree species

A – *S. macrophylla*
B – *C. pentandra*
C – *C. dodecandra*
D – *P. piscipula*
E – *T. rosea*
F – *E. cyclocarpum*

| | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| ACEF | A | B | A | ABCF | | | | | | | | | |
| A | ABDE | A | ACDF | A | ABCF | | | | | | | | |
| ABDF | E | ABEF | A | ACDF | A | | | | | | | A | |
| A | CDEF | A | BCDF | A | C | ABCE | A | F | A | BCDE | A | ADEF | A |
| D | ACDE | F | ABDE | ABCF | B | ABCD | ACEF | A | ACDF | A | BDEF | C | A |
| A | A | ABDF | A | D | A | A | ADEF | ACDE | A | ABEF | ACEF | BCEF | A |
| ABEF | A | A | A | ABCE | ADEF | ACDE | A | A | ADEF | A | E | A | ABCD |

**Figure S3.1.** Map of the UADY Tree Diversity Experiment plot design. Letters indicate tree richness and composition in each plot; A = *S. macrophylla*, B = *C. pentandara*, C = *C. dodecandra*, D = *P. piscipula*, E = *T. rosea*, F = *E. cyclocarpum*. Experimental plots used for this study are shaded.

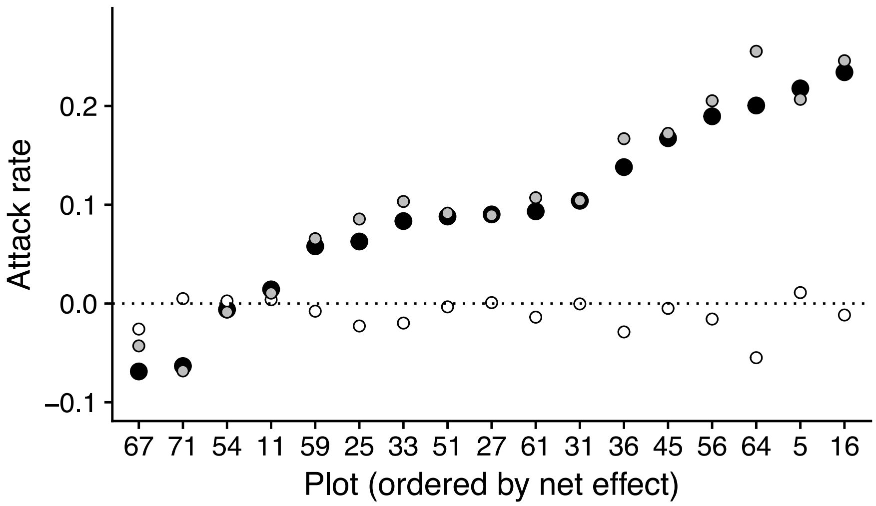


**Figure S3.2.** The net effect of tree diversity on model attack rate for each polyculture plot (n = 17, black fill) based upon tree-level attack rates. The net effect is the difference between attack rates in polyculture and the average attack rates for component tree species in monoculture. This net effect is decomposed into selection (white fill) and complementarity effects (grey fill) (Loreau & Hector 2001).

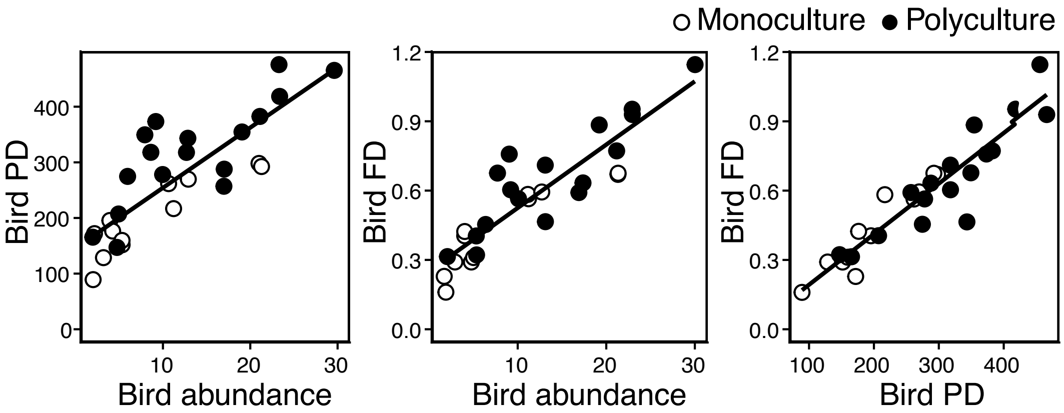


**Figure S3.3.** Bi-variate relationships between plot-level bird abundance and PD ($R^2 = 0.68$, $P < 0.001$), abundance and FD ($R^2 = 0.80$, $P < 0.001$) and PD and FD ($R^2 = 0.87$, $P < 0.001$). Monoculture plots are indicated with open circles (n = 10) and polycultures are filled circles (n = 17). Axis units are the same as in Fig. 2.

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