RECOVERY OF INSECTIVOROUS BIRD ECOLOGICAL FUNCTION IN TROPICAL FOREST RESTORATIONS

By

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ABSTRACT

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Recovery of animal-dependent ecosystem functions is a key component of ecological restoration on degraded tropical forest lands. One of these functions, regulation of herbivorous insects by birds, shapes tropical communities through trophic cascades that protect trees from insect damage. Understanding how bird-driven trophic cascades vary with environmental context, reforestation strategy, and management would guide restoration practitioners seeking to facilitate beneficial relationships between birds and plants. My dissertation examines the speed of bird community recovery following restoration action, the effects of climate dynamism on bird-driven trophic cascades, the mechanisms by which bird-driven trophic cascades occur, and insectivorous bird ecological function in forest restorations relative to other land cover types.

In Chapter 1, I studied temporal trends and spatial patterns in bird activity and diversity over a five-year period at a forest restoration in Panama. Four years after tree planting, bird activity had increased three-fold and species richness eleven-fold, compared to pre-planting. However, species richness differed strongly between experimental plots within the field site. Using a multi-species hierarchical occurrence model, I considered possible reasons for this variation. Features within plots, such as the number of tree species planted, did not explain differences in the number of species observed. However, neighborhood context did explain differences; there were more species in plots with more adjacent woodland and farther from pasture. My results demonstrate that native tree planting can generate rapid responses from tropical bird communities but the surrounding matrix will mediate bird responses to restoration.

In Chapter 2, I considered the ecological significance of insectivorous bird and bat activity in tropical forest restorations. I conducted bird and bat exclosure experiments in a Panamanian forest restoration during a typical wet season, dry season, and wet season with an El Niño drought. A trophic cascade was present on one of two tree species studied but only during a wet season with normal rainfall. These results highlight the importance of resident bird species for regulation of damaging insects in forest restorations and also point to the ability of regular seasonality and irregular El Niño events to alter trophic relationships in restoration ecosystems.

In Chapter 3, I more closely inspected the mechanisms that produced the trophic cascade described in Chapter 2. On the tree species featuring a trophic cascade, predation by birds and bats during the normal wet season reduced biomass for five folivorous insect orders and reduced numbers of individuals for four of the five orders. Birds and bat effects were especially noticeable for larger-bodied arthropods. These patterns were weaker or absent on the tree species where a trophic cascade was not observed.

In Chapter 4, I compared predation pressure by birds on artificial caterpillars in six land cover types, including the plantation-style forest restoration featured in Chapters 2 and 3. Bird predation pressure was lowest in intensively managed tree plantations and highest in land covers with structurally complex vegetation, such as successional forest and residential countryside. My results suggest insectivorous bird ecosystem function can be enhanced on reforestation lands by incorporating unmanaged areas and tolerating non-planted understory vegetation.

Facilitation of bird-driven trophic cascades is potentially a useful tool for tropical forest restoration but the presence of a substantial trophic cascade cannot be assumed or taken for granted. I recommend that land managers adopt a holistic approach to reforestation that restores bird habitat and encourages recovery of animal-dependent ecosystem functions.

This dissertation is dedicated to my parents,
who encouraged me to play in the dirt, catch bugs, and chase birds,
and to my wife, who still does.

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KEY TO ABBREVIATIONS

ASP	Agua Salud Project
cm	centimeter
hr	hour
m	meter
mg	milligram
min	minute
O.p.	*Ochroma pyramidale*
STRI	Smithsonian Tropical Research Institute
T.a.	*Terminalia amazonia*

CHAPTER 1:

Recovery of Bird Activity and Species Richness in an Early-stage Tropical Forest Restoration

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ABSTRACT

Creation of bird habitat is often a goal of tropical forest restoration because bird-driven ecosystem services can accelerate forest recovery. However, resident tropical bird responses are not well-characterized in the earliest years following restoration action. During a five-year study of the bird community in an experimental tropical forest restoration, we examined temporal trends in bird activity and diversity and the effects of habitat variables on the distribution of bird species within the site. Our site consisted of 16 replicate plots with 1, 2, 4, or 8 native tree species planted into former heavily-grazed pasture. Four years after tree planting, we observed a three-fold increase in bird activity and eleven-fold increase in species richness compared to pre-planting. We also found changes in proportions of habitat guilds, with marked declines in open country birds and increases in birds associated with brushy, early secondary growth, and forest edge habitats. Number of bird species observed differed strongly between experimental plots four years post-planting. Using a Bayesian multi-species hierarchical occurrence model, we considered possible reasons for these differences related to plot content and context. Content features within plots (‘content’), including number of tree species planted, canopy cover, tree species identity, and presence of legacy trees, did not explain differences in number of bird species observed, potentially because of small plot size relative to bird mobility. Neighborhood features (‘context’) of each plot did explain differences; more bird species were detected in plots with more adjacent woodland and farther from actively grazed pasture. Our results demonstrate that planting native tree species in highly degraded sites can generate rapid, positive responses from tropical bird communities. These responses are likely mediated by surrounding habitat matrix, which influences rates of bird community recovery. Considering site context can improve predictions of fine-scale distribution of bird activity and diversity within restoration sites.

INTRODUCTION

Interest in forest restoration is increasing in tropical regions because forests provide significant ecosystem services such as carbon sequestration, timber production, recreational opportunities, and wildlife habitat (Lamb et al. 2005, Chazdon 2008, Rodrigues et al. 2011, Suding et al. 2015). Although disturbed tropical forests can recover via natural regeneration (Aide et al. 2000), native tree planting may accelerate forest and ecosystem service recovery (Parrotta et al. 1997, Carnevale and Montagnini 2002, Fink et al. 2009, Holl et al. 2016). Recovery of wildlife habitat is often a rationale for forest restoration (Miller and Hobbs 2007) but how wildlife populations respond to different restoration techniques is often uncertain. Furthermore, wildlife-plant interactions can influence long-term restoration outcomes via mutualisms, herbivory, and trophic cascades so an improved understanding of wildlife activity during the early stages of forest restoration is important for restoration planning (Fraser et al. 2015, McAlpine et al. 2016).

Among wildlife taxa, birds are conspicuous early responders to forest restoration (Dunn 2004, MacGregor-Fors et al. 2010, Lindell et al. 2012, Rolo et al. 2017). Due to their diverse life history strategies including wide variation in diet, specialized foraging strategies, and micro-niche preferences, birds can act as an indicator taxon for recovering ecological complexity during forest restoration (Da Silva and Vickery 2002). In addition, birds provide ecosystem functions that facilitate forest recovery including seed dispersal, pollination, and herbivorous insect reduction (Sekercioglu 2006, Morrison and Lindell 2012, Lindell et al. 2013, Frick et al. 2014, Carlo and Morales 2016). Bird-driven ecosystem functions are tied to activity levels and composition of the local-scale bird community and should be closely related to habitat affiliations of species using restoration sites. For example, bird species that regularly use trees are more likely to carry seeds of woody species than open-country species (Lindell et al. 2013). Forest restoration sites experience rapid changes in the bird community during the early stages of forest recovery, potentially affecting bird ecosystem function (Gould and Mackey 2015, Lindenmayer et al. 2016).

The return of forest-associated birds to forest restorations is a metric of restoration progress (Twedt et al. 2002, Nichols and Nichols 2003, Rolo et al. 2017). Increasing compositional overlap with forest bird communities at less disturbed reference sites indicates progress towards biodiversity conservation goals (Catterall et al. 2012, Rolo et al. 2017). In restorations intended as wildlife corridors between forest fragments, forest-associated birds demonstrate restorations are functioning as planned (Jansen 2005). Finally, forest-associated species can carry seeds and pollen from forest plant species into restorations, encouraging the re-establishment of a diverse native plant community (Wunderle 1997, Frick et al. 2014, Carlo and Morales 2016). Prior studies of regenerating tropical forests have found bird activity and species richness rapidly increase in the first decade or two, although a return to compositional similarity with primary forest bird communities may take over a century (Dunn 2004, Catterall et al. 2012, Paxton et al. 2018).

Greater insight into bird responses to fine-scale habitat characteristics in forest restorations will aid restoration practitioners seeking to create wildlife habitat or harness bird ecosystem services to accelerate the restoration process. Choices made at project initiation, such as the identity and number of tree species planted, affect development of characteristics like vegetation density and canopy cover (Holl et al. 2013, Rolo et al. 2016). Such structural characteristics can, in turn, affect site attractiveness to birds several years after tree planting (Fink et al. 2009, Lindenmayer et al. 2010, Lindell et al. 2012, Lindell et al. 2013). Other fine-scale habitat characteristics may be less easy to alter, such as legacy features (e.g., old snags or land use history) or land use on adjacent parcels with different ownerships, but are also potentially relevant to birds and thus restoration planning.

Studies of bird recovery in forest restorations frequently substitute space for time, using chronosequences to assess trajectories in bird abundance and diversity (e.g., Catterall et al. 2012, Rolo et al. 2017). However, chronosequences with limited temporal resolution may not provide insights into the pace of bird recovery during earliest years, when change should be most dynamic (Jansen 2005, Paxton et al. 2018). Setting expectations for the earliest years, such as when the first forest-associated birds will appear, is especially important for restoration projects that plan to use an adaptive management framework with ongoing monitoring (Murray and Marmorek 2003). As such, longitudinal data on bird responses to restoration, starting at project initiation, are useful.

We conducted a five-year study of the bird community in a plantation-style forest restoration in Panama, beginning at the initiation of restoration efforts. Prior research in bird responses to forest restoration strategies has examined effects of planting configuration (Fink et al. 2009, Lindenmayer et al. 2016), understory enrichment plantings (MacGregor-Fors et al. 2010), and fast-growing nurse trees (Hamel 2003). Our study site featured replicate plots to compare bird responses to restoration planting regimes with different numbers and mixes of tree species. Tropical forest restoration efforts are challenged by extremely high diversity of tree species present in natural forests. In central Panama, a single wet lowland forest site can harbor over 300 tree species (Condit et al. 1992). Restoration with a large component of the native tree diversity (e.g. Rodrigues et al. 2009) is ideal but practical considerations, such as seed collection, tree nursery space, and labor costs, mean that plantation-style tropical forest restorations typically occur with far less than a full complement of old-growth forest species. Nevertheless, we hypothesized that planting a few tree species would still be sufficient to quickly induce a strong response from the bird community. A previous restoration study in Central America showed that only 2–4 years of growth by four planted tree species was enough to attract a diverse bird community to heavily degraded areas (Fink et al. 2009; Lindell et al. 2012).

At the scale of our entire site (all plots aggregated), we predicted bird activity and species richness would increase quickly after restoration initiation because high plant productivity in the tropics supports rapid development of vegetative structure, long known to be a determinant of bird diversity (MacArthur and MacArthur 1961, Karr 1968). We also anticipated vegetative development would result in species turnover as species associated with earlier seral stages abandoned the site (Twedt et al. 2002, Gould and Mackey 2015).

At the scale of individual plots, we hypothesized that plot planting regime would influence the number of bird species recorded. Specifically, we expected the number of bird species in a plot to be positively associated with greater canopy cover, more planted tree species, and the presence of a particular planted tree genus, *Inga*. Canopy cover and number of tree species have previously been associated with greater bird species diversity in neotropical coffee plantations (Van Bael et al. 2007, Philpott et al. 2008). Many tropical bird species rely on the canopy layer as foraging, resting, and breeding habitat. Higher tree species diversity could affect bird diversity by providing complementary resources, such as variable foraging substrates, host-specific arthropod prey, open branch structures for foraging, and dense branch structures for nesting and predator protection. However, the original authors who emphasized the importance of vegetative structure to bird also regarded plant species diversity *per se* as having little effect on bird diversity (MacArthur and MacArthur 1961, Karr 1968). The tree genus, *Inga* (Family: Fabaceae), has a bushy growth form and tends to produce canopy cover more rapidly than other kinds of trees planted at our site. *Inga* trees have previously been shown to be an attractive habitat feature for birds (Fink et al. 2009). In addition to aspects of our planting regimes, we expected a positive response of bird diversity to the presence of legacy trees that remained in the former pasture; such trees can draw a variety of woodland species into otherwise open country (Fischer and Lindenmayer 2002).

During our study, we noticed strong spatial patterns in the distribution of bird activity and number of species observed within plots that appeared unrelated to planting regime or legacy trees. We collected data on the distance to nearest pasture and amount of woodland adjacent to our plots to examine the hypothesis that habitat features external to plots influenced number of species observed. Understanding the relative importance of restoration “content” (i.e. habitat features within restoration sites) and restoration “context” (i.e. features of the surrounding neighborhood) is key to effective restoration planning for faunal recovery (Lindenmayer et al. 2010, Reid et al. 2014, Gould and Mackey 2015).

METHODS

Study site

We conducted our study at a forest restoration site in the Mamoní Valley, Panama (9°18.6’ N, 79°7.8’ W, 185 m a.s.l.). The valley was historically forested but is now a mosaic of pasture, small agricultural plots, secondary growth of various ages, tree plantations, and primary forest fragments. In July 2010, sixteen 50 m x 50 m forest restoration plots were established on 4 ha of recently abandoned heavily-grazed pasture featuring only a few, scattered trees. Plots were arranged in a loose grid with 12-m minimum buffers between plots, avoiding steep slopes and excessively wet soils that could negatively affect the survival and performance of planted trees.

Each plot was manually cleared of herbaceous vegetation and planted with seedlings of native trees grown from locally collected seed. Seedlings were planted in a grid with 3 m between rows, resulting in 256 seedlings per plot. Plots were planted with 1, 2, 4, or 8 species with equal shares in multi-species plots (see Appendix, Table 1.1 for planting mixes). Tree species were selected based on a variety of characters including ease of seed germination, ability to act as a wildlife resource (e.g. nectar producing flowers, edible fruits), potential for eventual timber harvest, and performance in plantation contexts. Planting mixes were chosen based on seedling availability and also to include at least one nitrogen-fixing legume (Family Fabaceae). One tree type, *Inga*, was discovered post-planting to be a mix of several *Inga* species. The majority were *I. thibaudiana*, but *I. stenophylla*, *I. ruiziana*, and *I. sapindoides* were also planted (Rolando Perez, personal communication). Because these *Inga* species have similar growth forms, we grouped them as “*Inga* spp.” for our analyses. The seedlings of one species (*Minquartia guianensis*) in the plots planted with 8 species died and were replaced in 2011, primarily with a new species

(*Hieronyma alchorneoides*) and secondarily with other species already present in those plots. To reduce competition for the young trees, non-planted vegetation in plots and buffers was manually cleared multiple times in the first two years and again in the fifth year. Although we did not measure tree growth, we observed that canopy height four years after planting was typically 3–5 m, with some tall trees exceeding 6 m.

Bird surveys

We define bird “Activity” as the cumulative number of birds recorded during surveys. Thus, Activity can increase due to 1) more individuals using a survey location; 2) more time by the same individuals at a survey location; or 3) a combination of 1 and 2. We did not attempt to distinguish between these possibilities because our objectives were to characterize general habitat suitability for birds and potential changes in bird ecological function. To distinguish between numbers of species in individual plots (“plot-scale”) and the site as a whole (“site-scale”) within a year, we call the number of species in a single plot across all replicate counts “Species Use” and the number of unique species across all counts for all plots “Species Richness.” We attempted to correct for detection bias when measuring Species Use and Species Richness four years post-planting (see Analyses) but did not do so for Activity due to data limitations.

Multi-year survey protocol

To measure changes in Activity and Species Richness through time, we conducted annual bird surveys mid-rainy season (July-August) for five years (“Multi-year survey”), beginning with a baseline survey prior to tree planting in 2010. In each plot, we conducted 12-min area counts, recording all birds present by sight and sound while taking care to avoid double-counting of individuals within counts. We used two to four vantage points in each plot to limit the effect of obstructive vegetation and terrain on bird detection. Counts were conducted four times in each plot within a single day each year, with a minimum of 15 min between counts. All counts were conducted between 0630–1100 hr. Daily temperatures were fairly consistent (low: ~23°C, high: ~32°C) but morning fog, cloud cover, and scattered rain showers were highly variable. To reduce detection bias, counts were not conducted during rain, fog, or high winds. However, other weather variables such as cloud cover may have affected detection. Birds flying overhead or flying through plots without landing or foraging were not included in the final data set.

2014 Single-year survey protocol and mist netting

In July–August 2014, a single observer (S. Roels) conducted replicated surveys ("Single-year survey") to evaluate hypotheses regarding plot content and context effects on Species Use. Repeated 10-min area counts were made in each plot except Plot 16, which was excluded due to difficult access. The change from 12-min (multi-year survey protocol) to 10-min counts was due to the need to accommodate travel time between plots while still completing surveys in the morning hours. All plots were surveyed once each day and visited in a set sequence with a randomized starting plot. Count protocol was otherwise similar to the annual protocol. Ten surveys were conducted over a 20-day period, resulting in a Single-year data set containing 10 replicates for each plot. As a supplement to our surveys in 2014, we operated mist nets at ten locations across the site for total of 180 net hours from May–July 2014. Mist net sampling is a complementary approach to point counts that can effectively detect taxa often undersampled by point counts in tropical forests (e.g. Blake and Loiselle 2001). Net operations were conducted under fair weather conditions between 0600–1130 hr and nets were checked every half hour. Captures were identified to species and were banded or had a tail feather trimmed to identify re-captures.

2014 plot content and context measurements

In 2014, we collected data for six variables that described the plot (content variables) or surrounding neighborhood (context variables). Content variables were: 1) Percent canopy – amount of canopy cover in a plot; 2) Tree species – the number of tree species planted in a plot; 3) Inga – whether *Inga spp.* were planted in a plot; and 4) Residual trees – whether legacy trees greater than 5 m tall were present in a plot prior to planting. Context variables were: 5) Adjacent woodland – percentage of land adjacent to plot that was forest restoration or forest fragment; and 6) Pasture distance – distance from plot center to nearest actively grazed pasture.

To quantify canopy cover, we divided each plot into quadrants and took canopy measurements with a spherical densiometer at 3 random points per quadrant (12 points per plot). Measurement points were between rows of planted trees to avoid inflating canopy cover values by standing directly next to tree trunks. Densiometer readings were taken in the four cardinal directions and then averaged to create the percent canopy estimate for an individual point. The mean of all points within a plot is our estimate of percent canopy cover for a plot. Variables "Tree species" and "Inga" were known aspects of the original plot design and were confirmed with tree survivorship surveys in 2014. Residual trees, either alive or dead, were noted as "present" or "absent" in each plot.

We calculated “Adjacent woodland” by visually estimating percentage of wooded land cover at a set distance of 25 m from each of the four plot edges. We defined woodland as any area of forest restoration or secondary forest. Forest restoration included an adjacent restoration planting with a similar tree species mix initiated one year prior to our study. Non-woodland vegetation included active pasture, weedy fields, marsh, and brushy areas. To create a single value for each plot, we averaged the percentage of wooded land cover from the four plot edges. The variable “Pasture distance” was calculated in QGIS 2.18 (QGIS Development Team 2017) using the straight-line distance between plot center points and the nearest pasture.

Bird guild assignment

We assigned all recorded bird species to habitat guilds based on published natural history descriptions (Ridgely 1981, Stiles and Skutch 1989, Angehr and Dean 2010, Neotropical Birds 2018) and personal experience (Appendix, Table 1.2). We placed species into one of four guilds: Open Country, Brushy, Early Secondary, and Forest Edge. Open Country habitats are characterized by a lack of woody vegetation, although perches such as isolated tall trees may be present. Brushy habitats are weedy and have woody growth less than 2 m tall. Early Secondary habitats feature dense, woody growth greater than 2 m tall. Forest Edge habitats are established woodland/forest adjacent to other, less heavily wooded areas. Individual birds not identified to species level were assigned to guilds based on partial identifications if possible (e.g. all members of the genus were in the same guild).

Statistical analyses

Changes in Activity and Species Richness through time

All analyses were conducted in R (version 3.4.3; R Development Core Team, 2017). Activity and Species Use were low in individual plots during the first three years of the study (many plots with 1 or 0 species recorded) so we investigated trends in the Multi-year data for the restoration site as a whole, rather than conduct plot-scale analyses. To facilitate analyses of Multi-year data, we pooled all plot-scale surveys within a year into a single site-scale data set. Thus, annual site-scale Activity was the total number of birds recorded each year. Annual site-scale observed Species Richness was the total of unique species recorded each year. To estimate actual Species Richness (including hypothetical species present but unobserved) for a given year, we used the first-order jackknife estimator (Walther and Moore 2005; function “specpool” in package “vegan”, Oksanen et al. 2018). The first-order jackknife is a resampling technique that estimates undersampling bias using the number of ‘singletons’, that is, observations that were recorded only once in the data set. As applied to species richness estimation, the first-order jackknife is calculated as: $S_{\mathrm{actual}} = S_{\mathrm{observed}} + (n\text{-}1)f_1/n$, where S is the number of species, n is the sample size, and f_1 is the number of singletons. To compare survey methods (Multi-year vs. Single-year) and richness estimation techniques, we also produced Species Richness estimates for 2014 from the Single-year data set using the first-order jackknife and our occurrence model (see below).

Species Use responses to plot content and context variables

To examine effects of content and context variables on use of plots by birds, we analyzed the Single-year (2014) data set collected by SR in a multi-species hierarchical occurrence model (Dorazio et al. 2006, Zipkin et al. 2010). This class of models uses aggregate occurrence data for all species and survey replicates to improve parameter estimates for rare and unobserved species and also accounts for imperfect detection of individuals inherent in avian surveys. In our context, with plot sizes smaller than the typical home range of most bird species, we interpret the model as estimating the effect of variables on probability that a given species will use habitat in a plot rather than site occupancy *per se*.

Our full model had two components: an occurrence model and a detection model. The occurrence model assesses effects of six plot variables on plot use by birds, which is assumed to be the outcome of a Bernoulli random variable for each species. This distribution is specified as: z_(*i*,*j*)~Bern(*ψ*;_(*i*,*j*), where z is the actual use, *i* is the species, and *j* is the plot. Continuous variables (Percent canopy, Tree species, Adjacent woodland, and Pasture distance) were standardized by subtracting the mean and dividing by one standard deviation. Categorical variables (Inga and Residual trees) were treated as binary (0 or 1). To guard against problems with collinearity, we confirmed all pairwise correlations of variables had $r < |0.7|$ (Dormann et al. 2013). The occurrence model for species *i* at plot *j* is represented as:

$$\mathrm{logit}(\psi_{i,j}) = \alpha0_i + \alpha1_i\mathrm{PercentCanopy}_j + \alpha2_i\mathrm{TreeSpecies}_j + \alpha3_i\mathrm{Inga}_j + \alpha4_i\mathrm{ResidualTrees}_j + \alpha5_i\mathrm{AdjacentWoodland}_j + \alpha6_i\mathrm{PastureDistance}_j$$

The term $\alpha0_i$ represents the probability of plot use (on a logit scale) by species *i* given mean values for continuous variables and zero values for binary variables (i.e. *Inga* and Residual trees absent). Coefficients α1–α6 represent the effects of predictor variables on plot use by species *i*. Effects are either linear (continuous variables) or the effect of changing states (binary variables).

The detection model assesses the effect of survey Date and Time on the detection of birds. Like species occurrence, species detection is assumed to be the outcome of a Bernoulli random variable for each species. This distribution is specified as: y_(*i*,*j*,*k*)~Bern(p_(*i*,*j*,*k*)*z_(*i*,*j*)), where y is the observed use, p is the probability of detection, *i* is the species, *j* is the plot, and *k* is the replicate. Thus, our observed use is the product of the probability of detection (p) and actual use (z). Both predictor variables were standardized by subtracting the mean and dividing by one standard deviation. The detection model for species *i* at plot *j* in replicate *k* is represented as:

$$\text{logit}(p_{i,j,k}) = \beta 0_i + \beta 1_i \text{Date}_j + \beta 2_i \text{Time}_j$$

The term $\beta 0_i$ represents the probability of detection (on a logit scale) for species *i* given mean values for variables. Coefficients $\beta 1_i$ and $\beta 2_i$ represent the linear effects of each survey variable on detection of species *i*.

We analyzed our model in a Bayesian framework in R and JAGS (function “jags” in package “jagsUI”, Kellner 2017). To represent unobserved species, we augmented our species occurrence data with 40 additional “species,” all having encounter histories of zero (Royle et al. 2007). We assessed effects of model variables on plot use by the bird community as a whole by examining posterior estimates for parameters at the community level of the hierarchical model. We used uninformed priors for these “hyper-parameters”, each having normal distributions with mean=0 and variance=2.70, as proposed by Lunn et al. (2012). The shape and scale parameters of the gamma priors for the variance parameters were set to 0.1. The hyper-parameters govern estimation of species-level occurrence and detection parameters, which we assume are drawn from the corresponding community-level distributions (Zipkin et al. 2010). We ran three MCMC (Markov chain Monte Carlo) chains for 275,000 iterations with a burn-in of 225,000 (10,000 in the adaptive phase). Posterior chains were thinned by 5, yielding a total of 30,000 estimates for each model parameter. We used the R-hat statistic to confirm model convergence (Gelman and Hill 2007).

RESULTS

Over the Multi-year survey (five years), we recorded 40 bird species with 607 occurrence records (Appendix, Table 1.2). In the Single-year survey of 2014, four years post-planting, we recorded 525 birds representing 41 species (Appendix, Table 1.2). That same year, our mist nets captured 252 birds representing 47 species (Appendix, Table 1.2).

Multi-year trends in site-scale Activity and Species Richness

Site-scale Activity and observed Species Richness were strongly correlated post-planting (Multi-year data: 2011–2014, r = 0.988). Activity prior to tree planting was moderate and initially declined after planting before a sustained three-year increase (Fig. 1.1). Four years after tree planting, our Multi-year survey protocol recorded over three times as much Activity as before planting (Fig. 1.1). Open Country Activity decreased rapidly following tree planting and remained at low levels throughout the study. One Open Country species, Eastern Meadowlark (*Sturnella magna*), represented 89.9% of Activity (62 of 69 birds identified) pre-planting and was not recorded after one year post-planting. All other habitat guilds showed year-to-year gains in Activity.

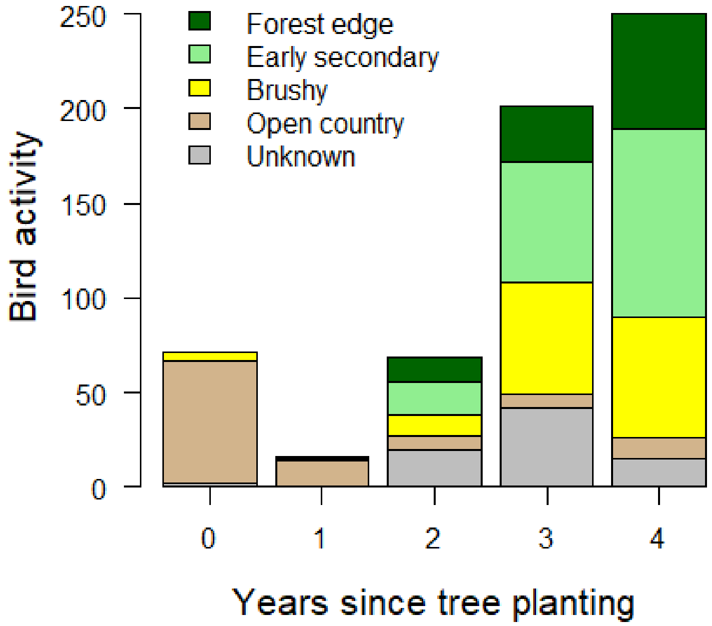

Figure 1.1. Multi-year trends in site-scale Activity for four habitat guilds following tree planting in a forest restoration in the Mamoní Valley, Panama. Some birds could not be assigned to a guild because of insufficient taxonomic identification during field surveys.

Site-scale Species Richness was low prior to tree planting and did not significantly change until two years post-planting (Fig. 1.2). Four years after tree planting, we observed eleven times as many species as before planting (Fig. 1.2). The actual difference in richness may be even greater than directly observed; estimates of true richness (total observed and unobserved species) increased at a faster rate than observed species. First-order jackknife estimates of Species Richness four years after planting were similar between Multi-year (46.1 species, 95% confidence interval: 34.9-57.4) and Single-year data sets (51.3 species, 95% confidence interval: 41.6–61.0) (Fig. 1.2). The Single-year occurrence model estimate (56.1 species, 95% credible interval: 46.0–74.0) was also similar to the Single-year jackknife estimate (Fig. 1.2). All habitat guilds except Open Country demonstrated a general pattern of increasing Species Richness from two years after planting onward (Appendix, Table 1.2).

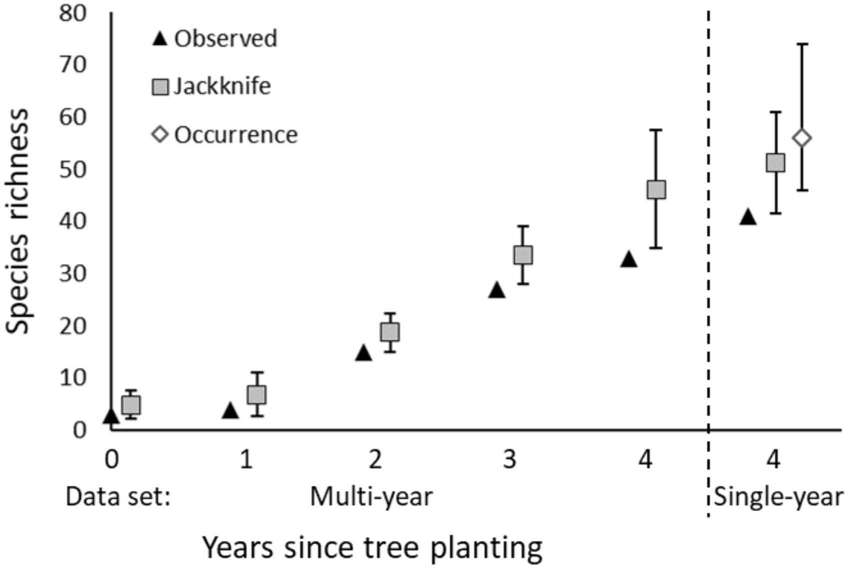

Figure 1.2. Estimates of site-scale bird Species Richness following tree planting. For the Multi-year survey data set, we present observed species and the first-order jackknife estimate. For the Single-year data set (2014), we present observed species, the first-order jackknife estimate, and the occurrence model estimate. Error bars are 95% confidence or credible intervals for the jackknife and occurrence estimates, respectively.

Plot-scale Activity and Species Use four years after planting

In the Single-year survey of 2014, plot-scale Activity and Species Use were strongly correlated (r = 0.935), with a tendency toward higher values in southeastern plots and lower values in northern plots (Fig. 1.3). At the community level (i.e. hyper-parameters) of our occurrence model, the context variables Adjacent woodland and Pasture distance were significant (95% credible intervals did not overlap 0) while all content variables were not (Fig. 1.4). Accounting for unobserved species in our model made the univariate relationships between context variables and plot-scale Species Use more evident (Fig. 1.5). The regression slope for the relationship between estimated Species Use and Adjacent woodland predicts one additional species for every ~2.8% increase in Adjacent woodland (Species = 16.67 + 0.359*Adjacent woodland, $r^2 = 0.431$). For the relationship between the estimated Species Use and Pasture distance, the model predicts one additional species for each additional ~10.8 m from the nearest pasture (Species = 15.72 + 0.0929*Pasture distance, $r^2 = 0.745$). In the detection component of our model, Date was a significant variable, with higher detection on later dates (mean: 0.35, 95% credible interval: 0.14–0.56), while Time was not significant (mean: -0.04, 95% credible interval: -0.19–0.11).

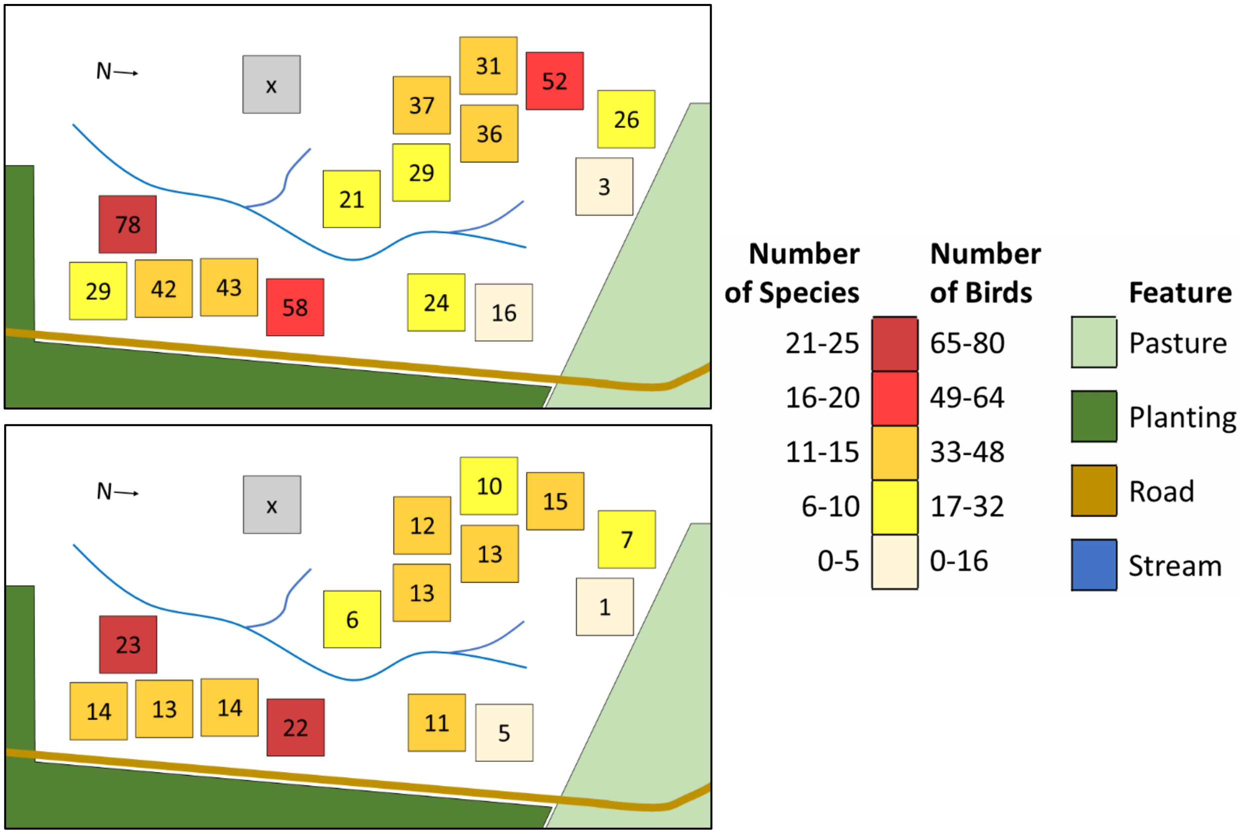

Figure 1.3. Plot-scale bird Activity (upper panel) and observed Species Use (lower) by plot in 2014 Single-year survey. Numbers in plot are total individual birds (upper) and species (lower) observed in ten surveys. One plot (“x”) was not surveyed.

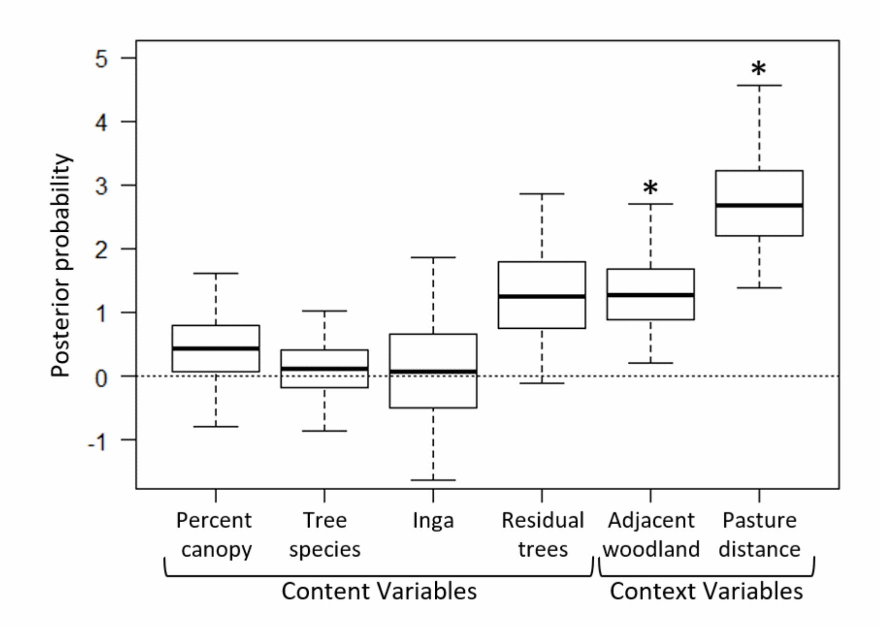

Figure 1.4. Effects of plot variables on Species Use. 95% credible intervals are presented for posterior distributions of six plot variables. Variables are: 1) Percent canopy – amount of canopy cover in plot; 2) Tree species – the number of tree species planted in plot; 3) Inga – Inga spp. were planted in plot; 4) Residual trees – legacy trees (alive or dead) were present in plot; 5) Adjacent woodland – percentage of land adjacent to plot that was forest restoration or forest fragment (see text for explanation); and 6) Pasture distance – distance from plot center to nearest actively grazed pasture. Credible intervals not overlapping zero are deemed significant variables and are denoted with a *.

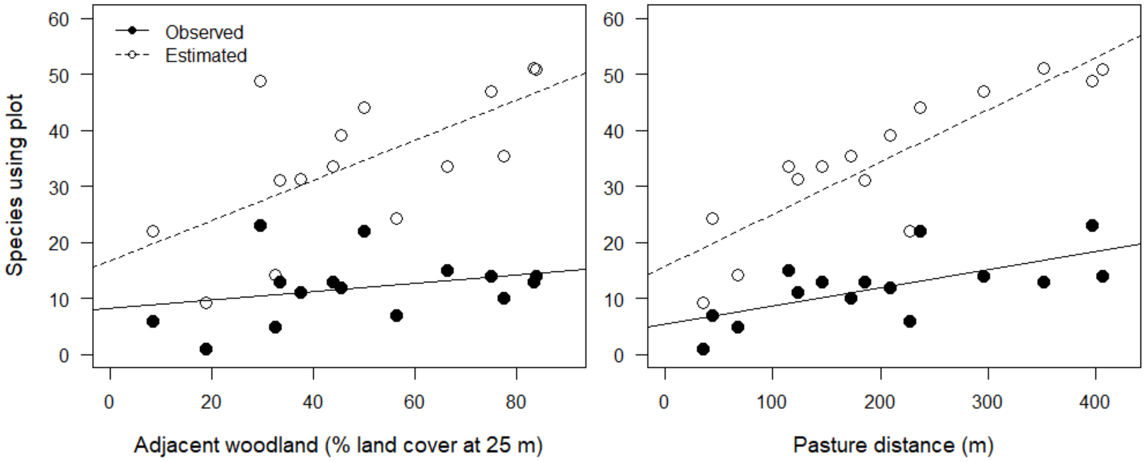

Figure 1.5. Relationships between plot context variables, Adjacent woodland and Pasture distance, and plot use by bird species. The bird community at the restoration site contained many species that irregularly used plots, leading to low estimates of detection. Accounting for detection with a multi-species occurrence model, yields estimates for the true number of species using each plot higher than was actually observed. Estimating true use may more effectively recover relationships between plot variables and use by birds.

At the species level, our occurrence model produced posterior distributions with wide credible intervals and point estimates that rarely deviated significantly from those of community-level hyper-parameters (Appendix, Fig. 1.6). Low detection of Species Use, likely due to single plots being smaller than typical home range sizes, limited our ability to recover evidence of species-specific responses to plot variables. For example, several species demonstrated use of a plot (i.e. at least one record) but were only recorded once out of ten replicate surveys making it difficult to infer those species' willingness to use plots where they were not recorded. We were also unable to discern any patterns in responses to plot variables when species were grouped by guild (Appendix, Fig. 1.6).

DISCUSSION

Trends and turnover

Over four years, we documented an increase in Activity and Species Richness at the restoration site, supporting our hypothesis that planting even a limited number of tree species can elicit a strong, rapid response from a tropical bird community. However, there was also an unexpected two-year time lag post-planting before increases in Activity and Species Richness were realized, which included a temporary drop in Activity one year post-planting. The few studies that have conducted annual monitoring starting with restoration initiation show varying results for the speed of avian response, possibly due to landscape context. Paxton et al. (2018) reported low bird densities in a Hawaiian montane forest region during the first five years post-planting, with more substantial gains occurring in the following twenty years. Jansen (2005) observed a strong response by birds in the first three years, including forest-associated species, to tree planting in an Australian rainforest region. Such differences are likely in part due to variable distance to large blocks of existing forest, with Paxton et al.'s (2018) surveys up to approximately 800 m from forest and Jansen's (2005) surveys no more than approximately 200 m. Our site was approximately 500 m from extensive forest but with smaller fragments at shorter distances. Different survey methodologies and community sizes make comparisons between studies difficult, but we regard the speed of bird response in our study to be intermediate to rates observed by Paxton et al. (2018) and Jansen (2005).

A meta-analysis of tropical forest bird community recovery found that species richness, standardized to that of mature forest, typically recovers after 20 years of forest regeneration (Dunn 2004). Exhaustive sampling of wet lowland forest in central Panama by Robinson et al. (2000) yielded average species densities of 111 resident species per 2 ha plot. Although our study site was slightly larger (4 ha), this suggests that species richness at our site had returned to approximately half of what would be expected in mature forest only four years after native tree planting.

The decline in Open Country guild dominance presents a case of rapid faunal turnover during the transition from pasture to young restored forest. This shift was essentially due to disappearance of Eastern Meadowlark, the most abundant species prior to restoration. Unlike continued substantial increases in Activity by Early Secondary and Forest Edge guilds, Brushy guild Activity leveled off from three to four years post-planting (Fig. 1.1). This may indicate a peak for this guild, which we expect will eventually decline as the site matures. In an Australian tropical forest, turnover of non-woodland species occurred in the first 10–15 years while woodland-associated species demonstrated a steady accumulation of species richness for at least the first 20 years after revegetation (Gould and Mackey 2015). If our site follows similar patterns, and eventually reaches a species density similar to mature forest as predicted by the model of Dunn (2004), then species accumulation rather than species turnover will be the primary driver of community changes at the site in the coming decade or two.

Site-scale Species Richness estimates four years post-planting

Regardless of the survey data set or estimation technique, we calculated actual Species Richness considerably higher than observed (Fig. 1.2), underscoring the difficulty of exhaustively sampling tropical bird communities and the importance of accounting for undetected species. Combining all observations from formal plot surveys, mist netting, and incidental encounters in 2014 yields a total of 67 species (Appendix, Table 1.2). This total is beyond the 95% confidence interval limits given by the jackknife estimates but within the 95% credible interval given by the occurrence model. Half of the species not recorded on formal plot surveys were hummingbirds, a group that is difficult to effectively survey with area counts because their behavior and size reduce surveyor ability to make species-level identifications. Forest birds with only mist net records may have been flying through the site but not using it for foraging or other activities. Even so, this would indicate the site is becoming a functional corridor between nearby forest fragments.

Effects of content and context variables on birds

Contrary to our hypothesis that plot planting regime would influence the number of bird species recorded, none of our content variables showed a significant relationship with plot-scale Species Use, suggesting these variables do not strongly differentiate plot attractiveness within a single year. From an avian perspective, differences between plot content may not have been as great as we perceived; most of the species using our site have fairly broad habitat tolerances and may only respond to coarser habitat differences. However, the site-scale multi-year trends of increasing Activity and Species Richness demonstrate vegetation structure (which developed substantially over the study) does matter. The significance of vegetation structure and unimportance of number of tree species planted are consistent with previous research (MacArthur and MacArthur 1961, Karr 1968). Many species using our site have home ranges larger than our plots, or even our entire study area, so within-year content effects may only become apparent at a larger scale. Finally, content effects may have been obscured by the overwhelming influence of context effects on Species Use. We caution our results only indicate content variables did not strongly affect Species Use of plots during our study, in an early stage of restoration. Effects of plot planting design may become more important over time as differences in tree growth habits manifest more strongly and trees become reproductively mature. *Inga*, for example, will not grow as tall as other species but will produce large amounts of flowers and fruit attractive to birds (Johnson 2000).

Like previous studies, we found restoration site context significantly influenced plot-scale Species Use (Lindenmayer et al. 2010, Reid et al. 2014). At our site, there were more species using plots near other woodland habitat and farther from pasture. Increasing Species Use with distance to pasture could be aversion to pasture or because plots nearest pasture represented poorly connected habitat not part of efficient foraging routes. We find the second interpretation more likely because we commonly observed substantial bird activity at forest-pasture interfaces in the Mamoní Valley, provided the forest area was large. Other adjacent land cover types also may have influenced Species Use but could not be included in our model because of small sample size. For example, birds were rarely observed in a dense fern-covered wetland that was within 25 m of some of the northernmost plots. The plot with highest Activity and observed Species Use was adjacent to a small fragment of riparian woodland. Riparian woodland was pooled inside the Adjacent woodland category but may have unique characteristics that make it especially attractive to birds.

Occurrence model potential and limitations

For tropical communities, where species richness is high and many species are rare, acquiring sufficient sample sizes for individual species is challenging (Gotelli and Colwell 2001; Herzog et al. 2002). In this context, multi-species occurrence modeling, which can assess both community- and species-level responses to environmental variables, may be particularly useful. The results of our model need to be interpreted in light of characteristics of our field site and the plot variables we included in the model. The proximity of our plots to each other means that plot-scale Species Use is likely not independent as birds move about the site. It is unclear why survey date was a significant detection model variable over the brief period when our Single-year survey was conducted (3 weeks). Possibilities include acclimation of birds to observer presence, changes in bird space use due to breeding cycle, or changes in local food resources.

Implications for bird conservation, ecological function, and forest restoration

Most species we recorded are typical of disturbed areas and not commonly found in primary or old secondary forest. Of nearly 300 resident species our research group has recorded in the Mamoní Valley, almost 200 occur in intact forest and only a few typical forest species, such as

Blue Dacnis (*Dacnis cayana*) and Red-legged Honeycreeper (*Cyanerpes cyaneus*), occurred at our restoration site (S. Roels, unpublished data). This lack of overlap is unsurprising given many studies have found bird species richness recovers more quickly than community composition (Dunn 2004, Catterall et al. 2012, Gould and Mackey 2015). Major groups characteristic of wet lowland forest in central Panama that were absent or nearly absent from our restoration site include antbirds (Thamnophilidae), woodcreepers (Dendrocolaptinae), trogons (Trogonidae), toucans (Ramphastidae), and parrots (Psittacidae). These groups correspond to foraging guilds that are often absent in young restorations and successional areas: understory insectivores (antbirds and woodcreepers) and large frugivores (trogons, toucans, and parrots) (Powell et al. 2015, Rolo et al. 2017). Many species within these groups are of conservation concern (Powell et al. 2015, Strahl and Grajal 1991). Presence of large frugivores in forest restorations is especially important for ecological function because they disperse large-seeded trees that are otherwise unlikely to colonize restoration areas (Wunderle 1997). Restoration of habitat for these groups and return of unique ecosystem services associated with them is a long-term prospect, even when native trees are planted in an effort to accelerate forest recovery.

At finer scales, within restoration sites, we should not expect uniform spatial distribution of bird-driven ecological functions. This is true despite early users of restored tropical forest habitat frequently being highly mobile species (e.g., tanager species in our study). Our study suggests that fine-scale patterns of habitat use, and thus ecological functioning, within a restoration site are influenced by neighborhood-scale features like adjacent habitat and connectivity. Relationships between neighborhood-scale habitat features and fine-scale spatial variation in tropical bird ecological function have been documented for seed dispersal and herbivorous insect control (Wenny and Levey 1998, Karp et al. 2013, Maas et al. 2015, Roels et al. 2018). Our study implies that recovery of bird-driven ecosystem functions may be reduced near pastures, even if vegetative structure is no different than areas farther from pasture that are heavily used by birds. For forest restoration projects that rely on bird-driven ecosystem functions like seed dispersal, areas near pasture and other matrix land covers unfriendly to birds may warrant additional monitoring and investment to ensure restoration goals are met. A complementary strategy would be encouraging silvopastoral techniques in pasture areas adjacent to forest restorations (Murgueitio et al. 2011). Adding native trees and shrubs to active pasture would encourage bird use of habitat at the edges of forest restorations by creating additional foraging habitat and facilitating bird movement along restoration-pasture interfaces.

ACKNOWLEDGEMENTS

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APPENDIX

APPENDIX

		Plot Number															
Tree Species	Family	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Inga spp.	Fabaceae		X	X	X	X	X				X	X	X	X		X	X
Dipteryx panamensis	Fabaceae	X	X	X	X	X		X	X	X	X	X	X	X	X		X
Manilkara bidentata	Sapotaceae			X		X		X		X	X		X	X	X		X
Anacardium excelsum	Anacardiaceae			X		X		X		X	X		X	X	X		X
Minquartia guianensis	Olacaceae					*		*		*	*			*	*		
Swietenia macrophylla	Meliaceae					X		X		X	X			X	X		
Calophyllum longifolium	Calophyllaceae					X		X		X	X			X	X		
Terminalia amazonia	Combretaceae					X		X		X	X			X	X		
Hyeronima alchorneoides	Euphorbiaceae					X		X		X	X			X	X		
Tabebuia guayacan	Bignoniaceae							X		X					X		
Total Species		**1**	**2**	**4**	**2**	**8**	**1**	**8**	**1**	**8**	**8**	**2**	**4**	**8**	**8**	**1**	**4**

Table 1.1. Tree species planted by experimental plot. Sixteen experimental plots (50 m x 50 m) were planted with 1, 2, 4, or 8 native tree species. Seedlings of *Minquartia guianensis* died and were replaced by other species, primarily *Hyeronima alchorneoides*.

		Multi-year survey					Single-year survey	Mist net
***Guild* (Common Name)**	**Latin Name**	**2010**	**2011**	**2012**	**2013**	**2014**	**2014**	**2014**
Open Country								
Ruddy Ground-Dove	*Columbina talpacoti*	-	-	-	-	-	-	1
Black-throated Mango	*Anthracothorax nigricollis*	-	1	-	-	-	-	5
American Kestrel	*Falco sparverius*	-	-	-	-	-	1	-
Tropical Kingbird	*Tyrannus melancholicus*	-	-	4	6	7	6	-
Fork-tailed Flycatcher*	*Tyrannus savana*	-	-	-	-	-	-	-
Tropical Mockingbird	*Mimus gilvus*	3	-	2	1	1	2	1
Eastern Meadowlark	*Sturnella magna*	62	13	-	-	-	-	-
Shiny Cowbird	*Molothrus bonariensis*	-	-	-	-	3	3	-
Yellow-faced Grassquit*	*Tiaris olivaceus*	-	-	1	-	-	-	-
Yellow-bellied Seedeater	*Sporophila nigricollis*	-	-	-	-	-	-	2
Open Country sub-total		65	14	7	7	11	12	9
Brushy								
Smooth-billed Ani	*Crotophaga ani*	4	1	-	8	18	23	5
Pale-breasted Spinetail	*Synallaxis albescens*	-	-	5	13	5	9	4
Cantorchilus sp. 1	*Cantorchilus* sp.	-	-	2	5	2	8	2
Blue-black Grassquit	*Volatinia jacarina*	-	-	-	7	-	12	4
Thick-billed Seedfinch	*Sporophila funerea*	-	-	-	8	13	42	22
Variable Seedeater	*Sporophila corvina*	-	-	3	18	25	39	10
Seedeater/Seedfinch 2	*Sporophila* sp.	-	-	1	-	1	16	-
Brushy sub-total		4	1	11	59	64	149	47
Early Secondary								
White-tipped Dove	*Leptotila verreauxi*	-	-	-	1	1	22	1
Striped Cuckoo	*Tapera naevia*	-	-	-	2	2	5	1
Common Pauraque	*Nyctidromus albicollis*	-	-	-	-	-	1	-
Long-billed Starthroat	*Heliomaster longirostris*	-	-	-	-	-	-	2
Garden Emerald	*Chlorostilbon assimilis*	-	-	-	3	6	2	17
Scaly-breasted Hummingbird	*Phaeochroa cuvierii*	-	-	-	-	-	-	7
Snowy-bellied Hummingbird	*Amazilia edward*	-	1	-	-	-	1	15
Rufous-tailed Hummingbird	*Amazilia tzacatl*	-	-	-	4	1	13	26
Striped Owl	*Asio clamator*	-	-	-	-	-	1	-
Barred Antshrike	*Thamnophilus doliatus*	-	-	-	1	-	2	1
Southern Beardless Tyrannulet	*Camptostoma obsoletum*	-	-	-	-	-	-	2
Yellow Tyrannulet	*Capsiempis flaveola*	-	-	-	3	11	33	6
Yellow-bellied Elaenia	*Elaenia flavogaster*	-	-	3	2	7	20	13
Lesser Elaenia	*Elaenia chiriquensis*	-	-	3	9	4	5	20
Elaenia sp. 3	*Elaenia* sp.	-	-	-	-	2	1	-
Bran-colored Flycatcher	*Myiophobus fasciatus*	-	-	-	-	-	1	-
Black-striped Sparrow	*Arremenops conirostris*	-	-	4	9	10	12	1
Palm Tanager	*Thraupis palmarum*	-	-	-	-	-	-	2
White-lined Tanager	*Tachyphonus rufus*	-	-	-	6	16	22	7
Flame-rumped Tanager	*Ramphocelus flammigerus*	-	-	2	7	5	6	-
Crimson-backed Tanager	*Ramphocelus dimidiatus*	-	-	6	17	34	49	10
Early Secondary sub-total		0	1	18	64	99	196	131

Table 1.2. Results from five years of bird surveys at a forest restoration in the Mamoní Valley, Panama. Counts should not be directly compared across survey types because of different methodologies (see text) and sampling effort. The Single-year survey was approximately double the effort (total observation time) of the annual effort in the Multi-year survey.

Table 1.2 (cont'd)

		Multi-year survey					Single-year survey	Mist net
***Guild* (Species)**		**2010**	**2011**	**2012**	**2013**	**2014**	**2014**	**2014**
Forest Edge								
Scaled Pigeon	*Patagioenas speciosa*	-	-	-	1	2	5	-
White-necked Jacobin	*Florisuga mellivora*	-	-	-	-	-	-	2
Rufous-breasted Hermit	*Glaucis hirsutus*	-	-	-	-	-	-	2
Long-billed Hermit*	*Phaethornis longirostris*	-	-	-	-	-	-	-
Stripe-throated Hermit	*Phaethornis striigularis*	-	-	-	-	-	-	2
Violet-headed Hummingbird	*Klais guimeti*	-	-	-	-	-	-	1
Rufous-crested Coquette	*Lophornis delattrei*	-	-	-	-	-	-	1
Crowned Woodnymph	*Thalurania colombica*	-	-	-	-	-	-	1
Olivaceous Piculet	*Picumnus olivaceus*	-	-	-	-	-	-	2
Red-crowned Woodpecker	*Melanerpes rubricapillus*	-	-	-	-	-	5	-
Lineated Woodpecker	*Dryocopus lineatus*	-	-	-	-	1	-	1
Yellow-crowned Tyrannulet	*Tyrannulus elatus*	-	-	-	-	10	10	9
Ochre-bellied Flycatcher	*Mionectes oleagineus*	-	-	1	-	-	-	-
Paltry Tyrannulet	*Zimmerius vilissimus*	-	-	-	-	-	-	1
Common Tody-Flycatcher	*Todirostrum cinereum*	-	-	-	10	7	32	8
Great Kiskadee	*Pitangus sulphuratus*	-	-	-	-	1	-	-
Panama Flycatcher	*Myiarchus panamensis*	-	-	-	-	1	-	1
Rusty-margined Flycatcher	*Myiozetetes cayanensis*	-	-	-	-	-	2	-
Lesser Greenlet	*Pachysylvia decurtata*	-	-	-	-	-	-	1
Yellow-green Vireo	*Vireo flavoviridis*	-	-	-	-	1	3	7
Tropical Gnatcatcher	*Polioptila plumbea*	-	-	-	-	-	1	-
Clay-colored Thrush	*Turdus grayi*	-	-	-	1	5	2	7
Thick-billed Euphonia	*Euphonia laniirostris*	-	-	-	-	1	-	-
Blue-gray Tanager	*Thraupis episcopus*	-	-	8	9	8	15	9
Golden-hooded Tanager	*Tangara larvata*	-	-	-	-	21	-	-
Plain-colored Tanager	*Tangara inornata*	-	-	3	3	1	6	-
Red-legged Honeycreeper	*Cyanerpes cyaneus*	-	-	-	-	-	2	-
Blue Dacnis	*Dacnis cayana*	-	-	-	-	-	2	-
Bananaquit	*Coereba flaveola*	-	-	-	-	-	1	2
Buff-throated Saltator	*Saltator maximus*	-	-	-	2	1	4	2
Streaked Saltator	*Saltator striatipectus*	-	-	1	3	1	8	4
Forest Edge sub-total		0	0	13	29	61	98	63
Forest Interior								
Black-crowned Antshrike	*Thamnophilus atrinucha*	-	-	-	-	-	-	1
Olivaceous Flatbill	*Rhynchocyclus olivaceus*	-	-	-	-	-	-	1
Forest Interior sub-total		0	0	0	0	0	0	2
No Habitat Guild								
Hummingbird sp.		-	-	4	12	1	20	-
Unidentified bird		2	-	16	30	14	50	-
Total Bird Activity		71	16	69	201	250	525	252

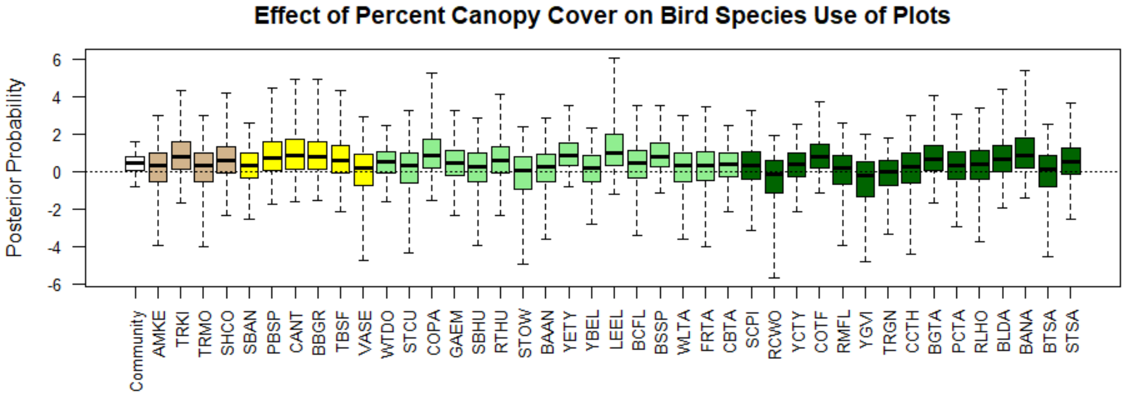
* Not recorded during formal surveys or mist netting in 2014 but observed during other field work

1 - Isthmian Wren (*Cantorchilus elutus*)/Buff-breasted Wren (*Cantorchilus leucotis*)

2 - Variable Seedeater/Thick-billed Seedfinch

3 - Lesser Elaenia/Yellow-bellied Elaenia

Code	Species	Code	Species	Code	Species
AMKE	American Kestrel	FRTA	Flame-rumped Tanager	STOW	Striped Owl
BAAN	Barred Antshrike	GAEM	Garden Emerald	STSA	Striped Saltator
BANA	Bananaquit	LEEL	Lesser Elaenia	TBSF	Thick-billed Seedfinch
BBGR	Blue-black Grassquit	PBSP	Pale-breasted Spinetail	TRGN	Tropical Gnatcatcher
BCFL	Bran-colored Flycatcher	PCTA	Plain-colored Tanager	TRKI	Tropical Kingbird
BGTA	Blue-gray Tanager	RCWO	Red-crowned Woodpecker	TRMO	Tropical Mockingbird
BLDA	Blue Dacnis	RLHO	Red-legged Honeycreeper	VASE	Variable Seedeater
BSSP	Black-striped Sparrow	RMFL	Rusty-margined Flycatcher	WLTA	White-lined Tanager
BTSA	Buff-throated Saltator	RTHU	Rufous-tailed Hummingbird	WTDO	White-tipped Dove
CANT	Cantorchilus wren sp.	SBAN	Smooth-billed Ani	YBEL	Yellow-bellied Elaenia
CBTA	Crimson-backed Tanager	SBHU	Snowy-bellied Hummingbird	YCTY	Yellow-crowned Tyrannulet
CCTH	Clay-colored Thrush	SCPI	Scaled Pigeon	YETY	Yellow Tyrannulet
COPA	Common Paraque	SHCO	Shiny Cowbird	YGVI	Yellow-green Vireo
COTF	Common Tody-Flycatcher	STCU	Striped Cuckoo		



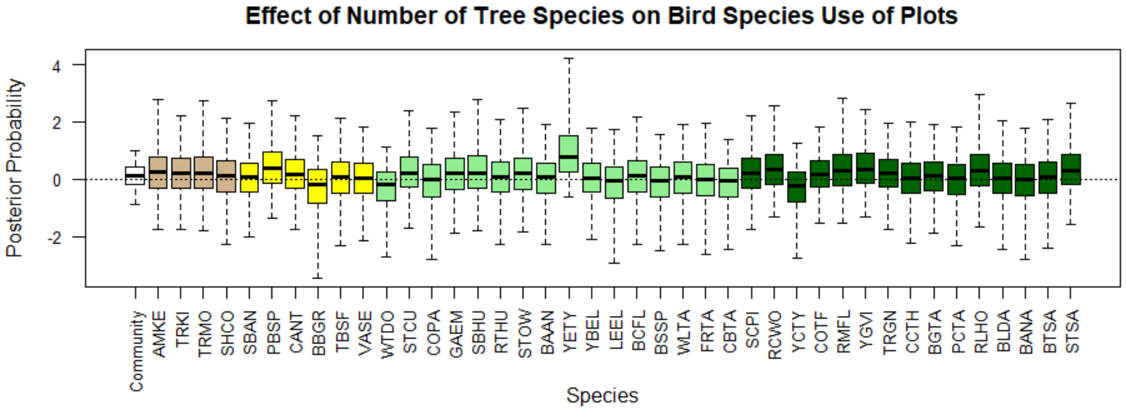
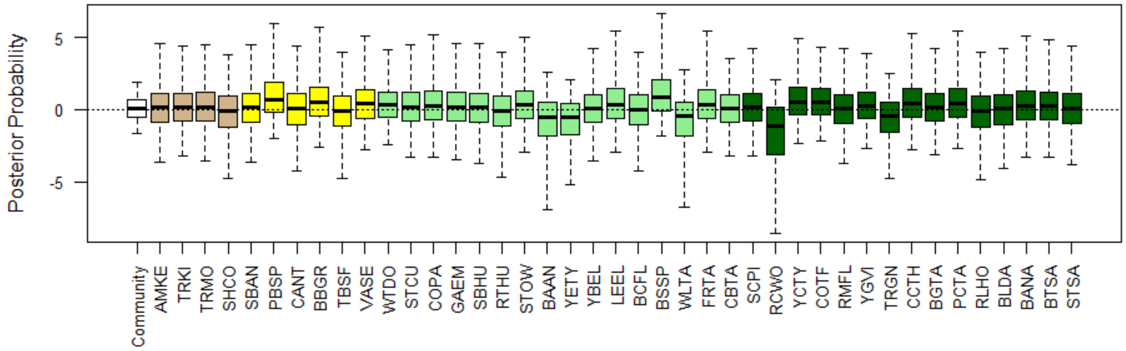


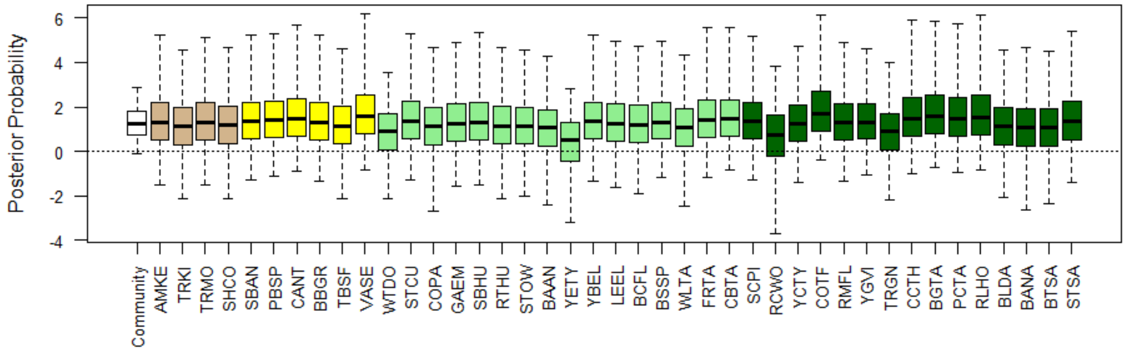
Figure 1.6. Posterior probabilities for effects of plot variables for individual species, sorted by habitat guild. The community-level estimates (hyper-parameters) are in white, Open Country species in tan, Brushy species in yellow, Early Secondary in light green, and Forest Edge in dark green. Species abbreviations in alphabetical order are in the first panel.

Figure 1.6 (cont'd)

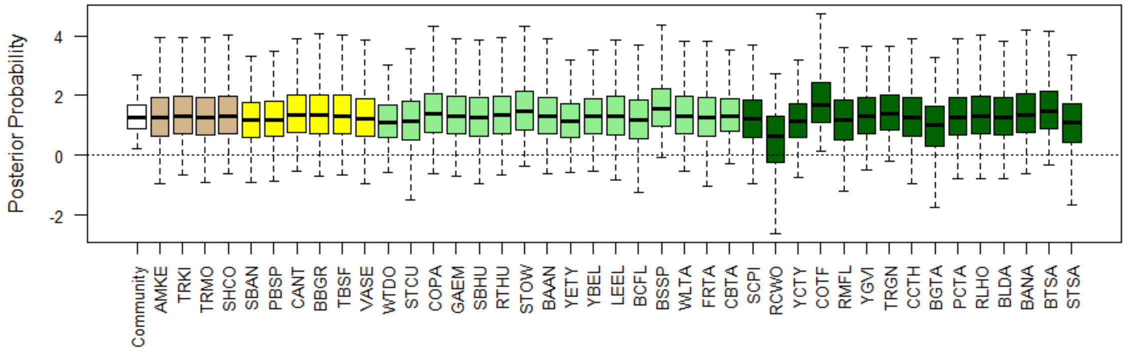
Effect of Planting Inga on Bird Species Use of Plots



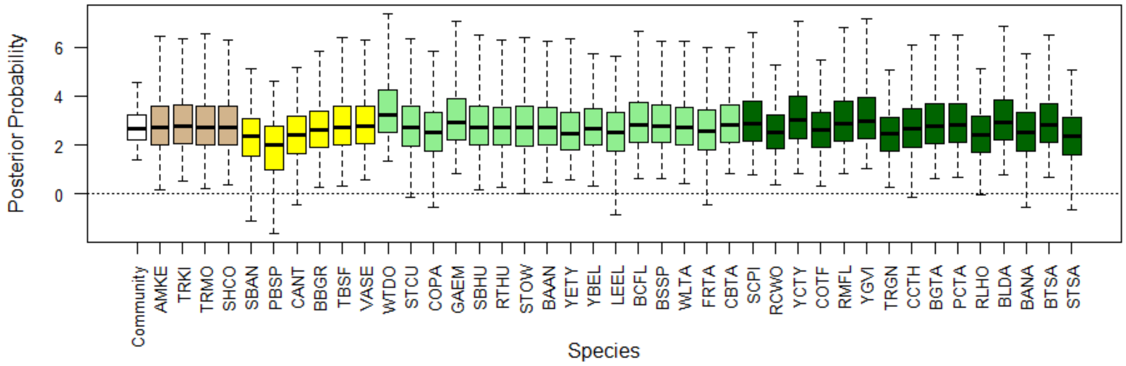
Effect of Residual Trees on Bird Species Use of Plots



Effect of Adjacent Woodland on Bird Species Use of Plots



Effect of Distance to Pasture on Bird Species Use of Plots



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CHAPTER 2:

El Niño Disrupts Bird- and Bat-Driven Trophic Cascade in a Tropical Forest Restoration

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ABSTRACT

Terrestrial trophic cascades are widespread but their interactions with other dynamic ecological processes, including seasonal variation in precipitation, migration of predators, and irregular global climate cycles, have uncertain effects on trophic cascade strength. In tropical ecosystems, bird- and bat-driven cascades influence ecological function, agricultural production, and ecosystem restoration. Ecological theory predicts that top-down forces on food webs increase with higher ecosystem productivity. In Neotropical regions with highly seasonal rainfall, productivity peaks in the wet season, suggesting cascades will be most evident then. However, insectivorous birds, key contributors to tropical cascades, are often most abundant during the dry season when migrants are overwintering. This misalignment between peaks in plant productivity and predator abundance generates competing predictions regarding when cascades should be strongest in tropical systems. We conducted bird and bat exclosure experiments on two tree species in a plantation-style forest restoration in Panama. We measured leaf production, herbivory rates, and abundance of arthropods and insect-eating birds during a typical wet season, a dry season, and an aberrant wet season featuring a severe El Niño-induced drought. Leaf production rates were lower during the dry season than either the typical or aberrant wet season, which were similar. Herbivory and folivorous insect biomass were higher during a typical wet season than in the dry season or aberrant wet season. Insect-eating bird abundance was highest during the dry season, when overwintering migrants augmented the resident bird population. During the typical wet season, exclosures impeding bird and bat foraging increased folivorous insect biomass on one of the two focal tree species, causing 38.0–58.2% more herbivory. No exclosure effects were detectable during the dry season or the aberrant wet season. Our results from the typical wet and dry seasons are consistent with the hypothesis that trophic cascade strength increases with ecosystem productivity. However, the El Niño-induced drought apparently disrupted the cascade in the aberrant wet season by uncoupling the correlation between plant productivity and herbivorous insect abundance; productivity was similar to the typical wet season but insect abundance was more like the dry season. Predicted climate change in the Neotropics has comparable effects to El Niño events, so the shift in trophic relationships we observed may preview consequences of planetary warming.

INTRODUCTION

Bird- and bat-driven trophic cascades, where predators indirectly benefit plants through reductions in herbivorous insects, are now recognized to be widespread in a variety of tropical ecosystems (Van Bael et al. 2008; Mäntylä et al. 2011; Maas et al. 2016). However, we have limited understanding of how trophic cascade strength varies within dynamic ecological contexts, such as intra-annual precipitation cycles, multi-year global climate cycles, or long-distance migration of predators (Pace et al. 1999; Meserve et al. 2003; Van Bael et al. 2008). Insights into mechanisms underlying variations in trophic cascade strength have implications for agricultural production (Van Bael et al. 2008; Maas et al. 2016) and ecosystem functioning and restoration (Holmgren et al. 2001; Morrison and Lindell 2012).

Theoretical ecologists suggest that top-down forces in food webs should be strongest where plant productivity is high because high productivity ecosystems feature sufficiently large herbivore populations to support stable carnivore populations (Oksanen et al. 1981). Consequently, population sizes of herbivores in high productivity systems will be regulated by predators, instead of by limited plant resources as in low productivity systems (Dyer and Coley 2008).

Maintenance of herbivore populations at levels lower than could be supported by available plant productivity results in lower herbivory in the presence of predators. In this manner, top-down predators indirectly reduce herbivory via cascading effects through the food web.

Several studies of bird-driven trophic cascades in both tropical and temperate ecosystems support the idea that top-down forces are more evident with higher productivity (Van Bael et al. 2003; Van Bael and Brawn 2005; Bridgeland et al. 2010; Garibaldi et al. 2010). Plant productivity in tropical regions often features significant seasonal variation, with major leaf flushing events typically occurring just before or at the onset of wet seasons (van Schaik et al. 1993). Wet and dry seasons also cause arthropod abundances to vary, with abundance generally higher during wet seasons (Robinson and Robinson 1970; Buskirk and Buskirk 1976; Wolda 1978). Similarly, insectivorous bird and bat breeding activity in many tropical locations coincides with wet seasons (Fleming et al. 1972; Karr 1976; Poulin et al. 1992); the increased metabolic demand of insectivore breeding activity may increase predation pressure on herbivorous insects. These seasonal patterns at three trophic levels (producer, herbivore, predator) may strengthen trophic cascades during wet seasons.

However, during the dry season many tropical regions receive an influx of insectivorous migratory birds escaping temperate winters, potentially increasing strength of top-down forces. In tropical Central America, abundance of insectivorous birds in some land cover types, such as shade coffee plantations, more than doubles with the arrival of overwintering migrants (Greenberg et al. 2000). Species richness of wintering migratory birds is positively associated with reductions in insect abundance in tropical agroforests (Van Bael et al. 2008), and wintering migratory birds have been credited with economically significant crop protection (Kellermann et al. 2008; Johnson et al. 2010). Migratory bird-friendly vegetation management is recommended to maximize this ecosystem service provided by wintering insectivorous birds (e.g. Van Bael et al. 2007a,b; Kellermann et al. 2008; Karp et al. 2013).

Similarly, tropical forest restoration goals may be advanced through encouragement of foraging activity by insectivorous birds and bats. The science and practice of forest restoration in tropical regions has progressed rapidly in recent decades but more research is needed on ecosystem functions of animals in restorations (Lindell 2008; Fraser et al. 2015; McAlpine et al. 2016). In Central America, resident bird species can rapidly recolonize forest restorations (Roels et al. unpublished manuscript) and wintering migratory birds also readily use habitat created by forest restoration activities (Lindell et al. 2012). Morrison and Lindell (2012) found birds and bats reduced insect damage to trees in a Costa Rican forest restoration but strength of the effect varied by tree planting strategy. Their study was conducted during the wet season and no comparable study has yet investigated trophic cascades in forest restorations over multiple seasons.

A seasonal comparison of bird-driven trophic cascades in a mature Panamanian forest found significant cascade effects during the wet season but not the dry season (Van Bael and Brawn 2005). Whether this pattern would hold in a forest restoration is uncertain. Although plantation-style forest restorations in Central America often include tree species representative of mature forests, they have vegetation structure and dry season bird communities more similar to those of agroforests. Canopy height and vegetation density in young plantation restorations and agroforests is comparable. In both land cover types, overwintering migrants are a substantial proportion of birds present in the dry season (S. Roels, personal observations). In contrast, in the mature forest where Van Bael and Brawn (2005) did not find a dry season trophic cascade, overwintering migrants comprised only 3% of foliage-gleaning birds in the dry season (Van Bael 2003). Thus, strength of top-down forces during the dry season in young forest restorations may be greater than those observed in mature forests.

Interpretation of ecological experiments is often challenged by interannual variability. We began our study during the 2015 wet season, during what became one of the strongest El Niño events ever recorded (Paek et al. 2017). El Niño events in the Neotropics are in some ways analogous to current climate change patterns (Meehl and Washington 1996) and may be considered a preview of biological responses in the tropics to ongoing planetary warming (Condit 1998). Climate records for central Panama, where our study was conducted, indicate a long-term drying trend and also show that strong El Niño events are associated with major droughts, as was the case during the 2015 wet season (Condit 1998; Condit et al. 2004). We responded to the aberrant conditions of the 2015 wet season (hereafter “2015 drought”) by extending our study to the 2016 wet season, when El Niño-Southern Oscillation (ENSO) conditions had returned to neutral and wet season rainfall was more typical (NOAA 2018; STRI 2018).

Prior studies have demonstrated how ENSO-caused shifts in precipitation and temperature regimes can dramatically alter trophic interactions via both bottom-up and top-down effects (Holmgren et al. 2001). For example, in a semi-arid ecosystem in Chile, low precipitation normally limits the strength of trophic interactions, as primary productivity is insufficient to support large populations at higher trophic levels. However, El Niño years bring above-average rainfall, boosting plant productivity and also intensifying top-down forces as populations of herbivorous small mammals and their predators increase dramatically in response to the pulse of resources (Meserve et al. 2003). In a tropical forest in Panama, the return of rainfall following an El Niño-induced drought caused an outbreak of folivorous insects and a more than three-fold increase in herbivory (Van Bael et al. 2004). If trophic cascade strength is regulated by productivity, itself regulated by precipitation, cascades should become stronger in locations where El Niño events increase rainfall and weaker where El Niño events cause droughts.

Studies to date in tropical ecosystems have produced inconsistent results regarding seasonal differences in arthropod abundance and the relationship between trophic cascade strength and ecosystem productivity (Maas et al. 2016). Despite the general presumption that arthropods are more abundant in the wet season, some studies in coffee plantations have found equal (Jedlicka et al. 2006) or higher (Williams-Guillén et al. 2008) arthropod abundance during the dry season. These observations may be related to coffee phenology, which can influence arthropod population cycles (Karp et al. 2013). Although numerous studies comparing two contexts have demonstrated stronger trophic cascades in the higher productivity context (Van Bael et al. 2003; Van Bael and Brawn 2005; Bridgeland et al. 2010; Garibaldi et al. 2010), some found either no productivity-based differences (Philpott et al. 2009; Mooney et al. 2010) or stronger cascades in what was presumed to be the lower productivity context (Greenberg and Ortiz 1994; Williams-Guillén et al. 2008).

We conducted a predator exclosure experiment on two native tree species during a typical wet season (2016), a dry season (2016), and a drought (2015) in a tropical forest restoration in central

Panama. Following other studies, we expected higher insect biomass associated with increased rainfall and plant productivity during the wet season would amplify top-down forces of birds and bats relative to the dry season. We anticipated a greater absolute decrease in leaf damage in the presence of birds and bats during the wet season than the dry season. However, we also predicted that birds and bats would cause a greater proportional reduction in insect biomass and leaf damage during the dry season, due to the addition of wintering migratory birds to the insectivore community (Fig. 2.1). We expected lower biomass of insects during the dry season would result in less total leaf damage, such that the absolute change in leaf damage between exclosure and control treatments would be less than during the wet season. Following the drought in 2015, we also predicted that trophic interactions during a wet season with an El Niño-induced drought would be more similar to a dry season than to a typical wet season because of reduced plant productivity during the drought.

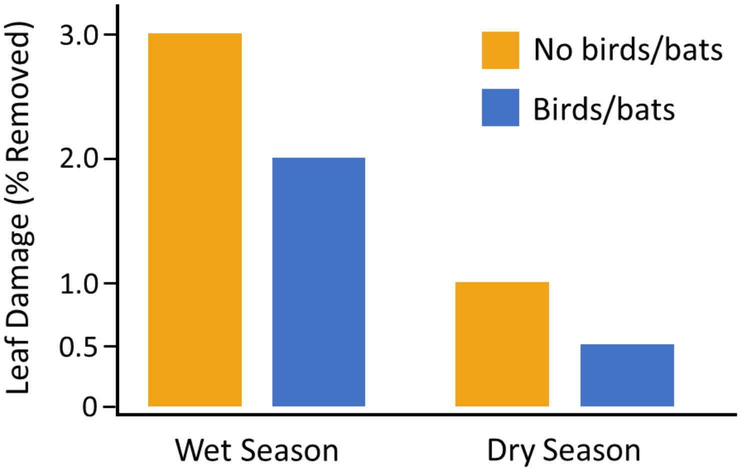

Figure 2.1. Illustration of trophic cascade predictions. We predicted the absolute decrease in leaf damage associated with bird and bat predation would be greater in the wet season than the dry season (illustrated difference of 1.0% damage in wet season and 0.5% damage in dry season). However, we also predicted the proportional decrease would be greater in the dry season (damaged reduced by one-half in the dry season and one-third in the wet season).

METHODS

Study site and species

We conducted our study at the Agua Salud Project (ASP), Colón Province, Panamá (9°12’52’’ N, 79°43’25’’ W, elevation: 200–300 m a.s.l., Fig. 2.2). The ASP contains a variety of experimental land covers, including a plantation-style native species forest restoration. The plantation was established in 2008 and contains replicate plots with native species monocultures or polycultures (Mayoral et al. 2017).

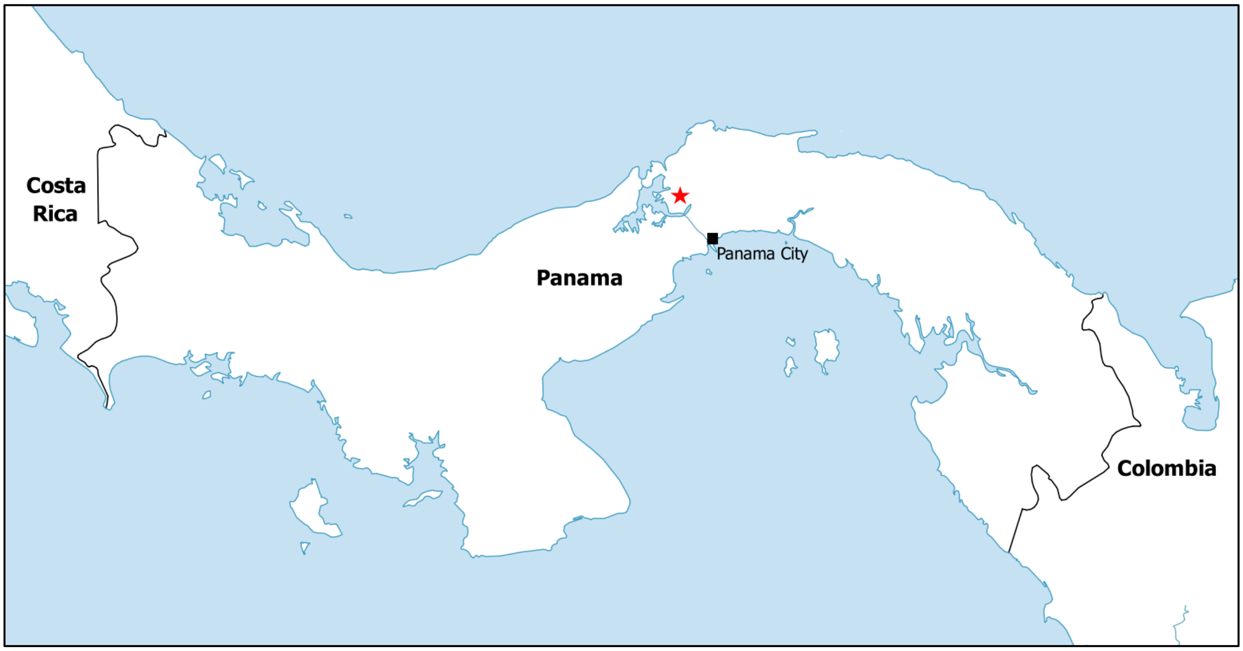

Figure 2.2. Location of the Agua Salud Project (star), Colón Province, Panamá (9°12’52’’ N, 79°43’25’’ W).

Non-planted understory vegetation is cleared approximately quarterly. We selected two plantation tree species for our experiments that are photosynthetically active year-round in central Panama (so we were able to conduct experiments in both the wet and dry seasons). The first species, *Ochroma pyramidale* (Cav. ex Lam.) Urb. (Family: Malvaceae), is a short-lived pioneer species common in recently disturbed areas (Condit et al. 2011). There is a commercial market for the timber of this species, with large plantations in the Neotropics (Stilwell et al. 2014). The second, *Terminalia amazonia* (J.F.Gmel.) Exell (Family: Combretaceae), is common in secondary forests and regularly planted in native species plantations in Central America due its reliable performance and quality timber (Condit et al. 2011; Carpenter et al. 2004).

Field seasons

Central Panama has pronounced seasonality with a wet season from approximately May–December and a dry season from approximately January–April. We conducted our experiments during three field seasons, corresponding to portions of the 2015 drought (9 July–17 August), 2016 dry season (24 January–4 March), and 2016 wet season (11 June–27 July). In 2015, June–August rainfall recorded at the ASP meteorological station was 426 mm; typical June–August rainfall at this station is 818 mm (average of 2009–2017, STRI 2018). In the 2016 wet season, ENSO conditions had returned to neutral and rainfall at the ASP station was 743 mm (STRI 2018). In addition to lower rainfall, the June–August period in 2015 featured higher mean temperatures and wind speeds and lower relative humidity than the same period in 2016 (STRI 2018). A longer term data set from the weather station on nearby Barro Colorado Island provides greater context for severity of the drought; year-to-date rainfall through August 2015 ranked as the lowest ever recorded in 90 years (Steve Paton, personal communication). Notably, the ASP received no rainfall during a two-week period in late June 2015, just prior to the start of our experiment. In 2016, January–March rainfall at the ASP was 32.3 mm; typical January–March rainfall is 103 mm (average of 2009–2018, STRI 2018).

Experimental protocol

Exclosure material and design

We constructed predator exclosures out of light-weight plastic netting (Standard BirdNet; Bird-X, Chicago, IL, USA), with mesh large enough (2 x 2 cm) to permit passage of large arthropods but not foraging birds or bats. Netting was cut into 80 x 160 cm pieces that were folded in half around branches, creating bubble-shaped exclosures with maximum dimensions approximately 70 x 70 x 35 cm. Exclosures were closed with either twist ties (*O. pyramidale*) or binder clips (*T. amazonia*) but a small gap (~10 cm) was left around the proximal end of the branch, allowing passage of large arthropods crawling along the branch toward the tip. The terminal end (~50 cm length) of a single branch was placed in each exclosure (Fig. 2.3).

Figure 2.3. Exclosures on *O. pyramidale* (left) and *T. amazonia* (right).

Branches of *T. amazonia* were assigned to one of three treatments: control, 24-hr exclosures, and daytime exclosures. The daytime exclosure (with no exclosure overnight) was intended to separate effects of diurnally foraging birds from nocturnally foraging bats. For exclosure treatments on *T. amazonia*, netting was stretched over a frame of wooden dowels that was supported by a plastic pole staked into the ground (Fig. 2.3). In this manner, the netting formed a bubble that limited contact with the branch contained inside (Fig. 2.3). For 24-hr exclosures, this netting was left in place for the duration of the experiment in each season. For daytime exclosures, netting was removed at dusk and replaced at dawn each day of the experiment. The dowel frame facilitated net opening and closing by reducing tangling of netting in branch tips. The daytime exclosure treatment was dropped from the experimental design during the 2016 wet season because of time constraints. Control branches had dummy frames with a pole and dowels but no netting.

Branches of *O. pyramidale* were assigned to one of two treatments: control or 24-hr exclosure. Logistical constraints prevented a daytime exclosure treatment for *O. pyramidale*. For the 24-hr exclosure treatment on *O. pyramidale*, netting was placed directly on branches (Fig. 2.3). We did not use dowel frames with support poles for exclosures on *O. pyramidale* because most branches were too far above the ground for poles and branch architecture did not allow for attaching frames directly onto branches. However, branch architecture naturally limited contact between the net and the actively flushing leaves at the branch tip. Control branches were left unaltered.

For each tree species, we created pairs or groups of neighboring trees within plantation plots and randomly assigned treatments within pairs or groups. The majority of trees selected during the first field season were used in subsequent field seasons although some replacements were necessary due to tree death and light competition from neighboring trees. For *O. pyramidale* there were 38, 37, and 36 pairs of trees in the 2015 drought, 2016 dry season, and 2016 wet season, respectively. For *T. amazonia* there were 40, 38, and 41 groups in the 2015 drought, 2016 dry season, and 2016 wet season, respectively. On each tree, we selected a single branch that showed evidence of active growth (newly flushed leaves). Branches ranged in height above the ground from 1.0–4.0 m for *O. pyramidale* and 0.5–2.0 m for *T. amazonia*. Exclosures remained in place on *O. pyramidale* for 28–32 days in the 2015 drought, 31–32 days in the 2016 dry season, and 30–31 days in the 2016 wet season. Exclosures remained in place on *T. amazonia* for 34–35 days in all field seasons.

Arthropod abundance surveys

A single observer, S. Roels, surveyed arthropod abundance just prior to the placement of exclosures and again at the end of the experiment. During each survey, S. Roels visually searched for arthropods on all leaves of focal branches, inspecting both upper and lower leaf surfaces. All arthropods were identified to order and categorized into the following size classes: ≤2 mm, >2–4 mm, >4–6 mm, >6 mm. Arthropods greater than 6 mm were measured with a hand ruler. For *O. pyramidale*, we recorded the length of each leaf searched and converted leaf length to leaf area using season-specific leaf length:area power functions fit to leaf area data produced with ImageJ (see below). For *T. amazonia*, measurements of every leaf were not feasible (often over 100 leaves per branch). We timed arthropod surveys, using time needed to search the entire branch as a proxy for leaf area. To convert search time into estimated leaf area, we conducted time trials where we surveyed test branches, harvested all the leaves, estimated total leaf area with ImageJ, and calculated the mean leaf area surveyed per second. The duration of each experimental branch survey was then multiplied by this rate to give a leaf area estimate.

We converted arthropod lengths into total dry arthropod biomass per branch using previously published length:mass regression relationships specific to taxonomic order (Schoener 1980;

Sample et al. 1993; Johnson and Strong 2000; Wardhaugh 2013; Appendix, Table 2.3). Because length:mass relationships vary by latitude and climate, we used equations from Schoener (1980) if they were available for an order. Schoener (1980) produced separate equations for dry and wet forests in Costa Rica, the location with published allometric equations nearest our study site. Our study site receives annual rainfall intermediate to the two forest types in Schoener (1980) so we calculated biomass estimates for individual arthropods by averaging Schoener's (1980) dry forest and wet forest equations. For larval Lepidoptera, we took the average of biomass estimates produced from equations in Sample et al. (1993) and Wardhaugh (2013). For both tree species, we report arthropod biomass per m^2 of leaf area. The biomass of arthropods placed into body length classes was calculated using the midpoint of the range (e.g. "2–4 mm" was treated as 3 mm for biomass calculations). Arthropods in the < 2 mm class were treated as having a body length of 1.5 mm because arthropods smaller than 1 mm were unlikely to be counted on visual surveys. We conducted analyses using only orders with folivorous (i.e. chewing) species that could be responsible for removal of leaf area (Blattodea, Coleoptera, Lepidoptera, Orthoptera, and Phasmida).

Productivity and herbivory measurements

All leaves flushed during the experimental period were harvested and either digitally photographed on a white background (*O. pyramidale*) or scanned with a flatbed scanner (*T. amazonia*). We distinguished new leaves from pre-existing leaves by marking leaves near the branch tip with a permanent marker at the start of the experiment. Leaves of *O. pyramidale* still in the leaf expansion phase (youngest of all new leaves) were distinguishable from fully flushed leaves by color and texture. We recorded leaf age (still expanding or fully flushed) for *O.*

pyramidale during the photography phase. Leaf age distinctions were not made for leaves of *T. amazonia* as differences in leaf age were less clear in this species. We calculated branch productivity and herbivory by processing leaf photos in ImageJ (version 1.50; Schneider et al. 2012) to measure total leaf area produced and leaf area removed.

Insect-eating bird surveys

To measure relative bird abundance during each field season, S. Roels conducted fixed-radius point counts throughout the native tree plantation. Fifteen points were arranged to maximize coverage of plots containing experimental trees while minimizing overlap between points. There was a minimum distance of 85 m between points (mean distance-to-nearest-neighboring point = 121 m, max = 176 m). Each point was surveyed four times while the exclosure experiments were active, with counts at a given point separated by at least 3 days. Count duration was 10 min and all birds detected by sight and sound within 25 m were recorded. We pruned the data by removing birds that flew overhead or through the count area without stopping and birds that do not eat insects. To characterize bird species diets, we reviewed published diet descriptions (Ridgely 1981; Stiles and Skutch 1989). Surveys occurred during the following times: 2015 drought, 0800–1030 hrs; 2016 dry season, 0800–1100 hrs; 2016 wet season, 0630–0900 hrs. Earlier survey times were possible in the 2016 wet season because we were no longer managing a daytime exclosure treatment for *T. amazonia*. We tested for effects of these different time periods on results.

Statistical analyses

Plant productivity

All statistical analyses were conducted in R (version 3.4.4; R Development Core Team, 2018). We used $\alpha = 0.05$ for all hypothesis testing. We calculated productivity on a per branch basis using the summed area of all leaves flushed by the branch during the experiment. Branch productivity was approximately normally distributed so we used a standard ANOVA to test for differences in mean branch productivity between seasons.

Herbivory models

We evaluated effects of our exclosure treatments on herbivory using mixed-effects regression models with a logit link created using the glmmTMB package (Brooks et al. 2017). Our herbivory data best fit a beta distribution, a continuous probability distribution appropriate for overdispersed proportion data where $0 < y < 1$. To include leaves with no herbivory (a zero value), we used the transformation recommended by Smithson and Verkuilen (2006): $y'' = [y'(N - 1) + 0.5]/N$ where N is the sample size.

For *O. pyramidale*, each beta regression model contained treatment, season, and their interaction as fixed effects and experimental branch within season as a random effect. During the exploratory phase of data analysis, we noticed that herbivory on still-expanding *O. pyramidale* leaves was substantially lower than on fully flushed leaves. This is not surprising given that still-expanding leaves would be younger than fully flushed leaves and, thus, exposed to herbivores for less time. We collected few still-expanding leaves in the 2015 drought, possibly because trees were becoming water stressed near the end of the experiment. Because of differences in herbivory between still-expanding and fully flushed leaves and variable ratios of still-expanding:fully flushed leaves across seasons, we decided to model fully flushed and still-expanding leaves separately. The 2015 drought is not included in the model for still-expanding leaves.

For *T. amazonia*, each beta regression model contained treatment as a fixed effect and experimental branch as a random effect. We were unable to collect sufficient herbivory data for *T. amazonia* during the 2016 dry season due to lack of leaf growth. It is likely that the 2015 drought compounded the normal water stress trees experience during the dry season and caused *T. amazonia* to stop flushing leaves in the 2016 dry season. During pilot studies the previous year, *T. amazonia* was flushing leaves during the dry season, so dry season herbivory measurements would be possible in a more typical year. We analyzed *T. amazonia* data from the 2015 drought and 2016 wet season in separate models because they had different treatment groups (the daytime exclosure treatment was dropped in the 2016 wet season).

Analysis of model residuals for *O. pyramidale* revealed some extreme data points associated with exceptionally high herbivory; these values represent less than two percent of leaves in either *O. pyramidale* data set. There was little difference between model results with and without these apparent outliers. Thus, we present models without the extreme values. Some *T. amazonia* leaves had similarly high herbivory but model residuals were more uniformly distributed than for *O. pyramidale* so no leaves were removed from the *T. amazonia* data set. To translate herbivory model coefficients into biologically interpretable values, we calculated the antilogit of model coefficients.

Folivorous insect biomass models

To evaluate the effect of our exclosure treatments on folivorous insect biomass, we created mixed-effect models for each tree species and season with treatment and survey period (pre- and post-experiment) as fixed effects and experimental branch as a random effect. The interaction term in these models characterizes differences in responses of experimental groups to treatment. The model reference group was control branches during the pre-experiment survey. Since our insect biomass data were derived from count-based surveys, models assumed a negative binomial distribution with a log link. Data were transformed to integers by rounding to nearest whole number to meet assumptions of a negative binomial distribution. To estimate seasonal differences in folivorous insect biomass, we pooled data from all treatments within seasons and created mixed-effect models with a fixed effect of season and random effect of experimental branch within season. For *T. amazonia*, the daytime exclosure treatment data was not used for this analysis because it did not occur in all seasons.

Bird abundance models

The average survey time of day was different between field seasons. We created linear regression models for each field season to estimate time of day effects on bird counts at survey points. While this effect would best be modeled over an entire day with a non-linear function, we believe a linear approximation is sufficient when modeling within our three-hour survey windows and avoiding extrapolation beyond the limits of the data. Models were used to predict the number of birds on a hypothetical count occurring at 0800 hrs, a time of day within the range of survey data for each field season.

RESULTS

Leaf production

Leaf production by both tree species was significantly higher during the 2016 wet season than the 2016 dry season (Fig. 2.4). Total leaf area flushed by *O. pyramidale* during the 2016 wet season was over double the leaf area flushed during the 2016 dry season. Total leaf area flushed by *T. amazonia* was much greater than area flushed during the 2016 dry season, when growth was almost zero (Fig. 2.4). Unexpectedly, leaf production for both tree species during the 2015 drought was not significantly different from the 2016 wet season (Fig. 2.4).

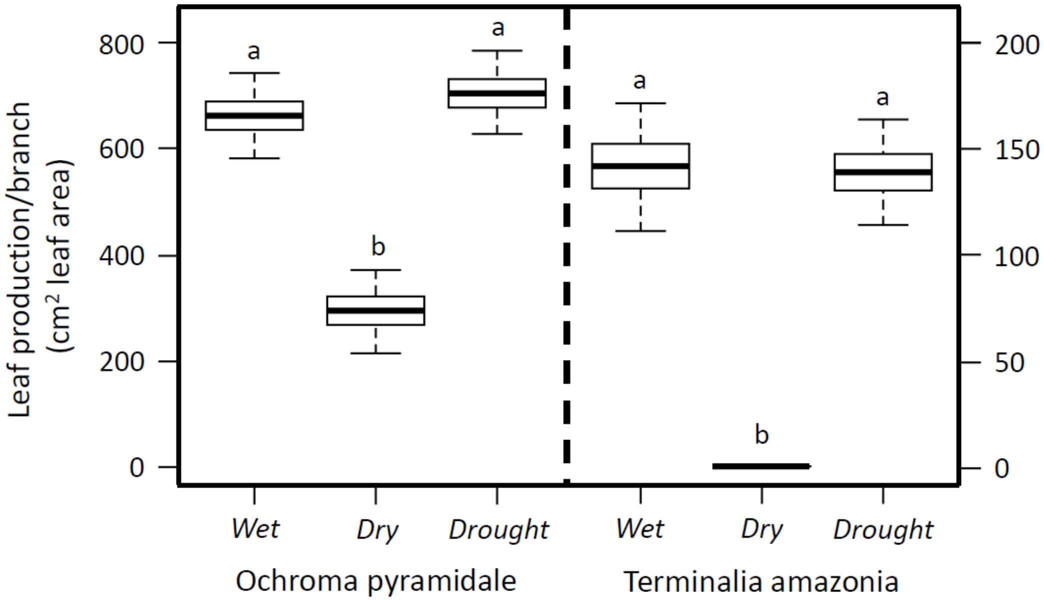

Figure 2.4. Leaf productivity by tree species and season. Plot depicts mean leaf production per branch with 50% (boxes) and 95% (whiskers) confidence intervals. Data from experimental treatment groups (control and exclosure branches) were pooled within seasons. *Terminalia amazonia* leaf production during the 2016 dry season was negligible.

Herbivory

Relative to the 2016 wet season, herbivory on fully flushed *O. pyramidale* leaves was significantly lower in both the 2016 dry season and 2015 drought, with estimated reductions in herbivory at 34.9% and 26.1%, respectively (Fig. 2.5). During the 2016 wet season, herbivory on fully flushed *O. pyramidale* leaves was significantly higher (38%) in exclosures that restricted bird and bat access, compared to leaves on control branches (Fig. 2.5; Appendix, Table 2.4). However, this effect was absent during the 2016 dry season and 2015 drought (Fig. 2.5).

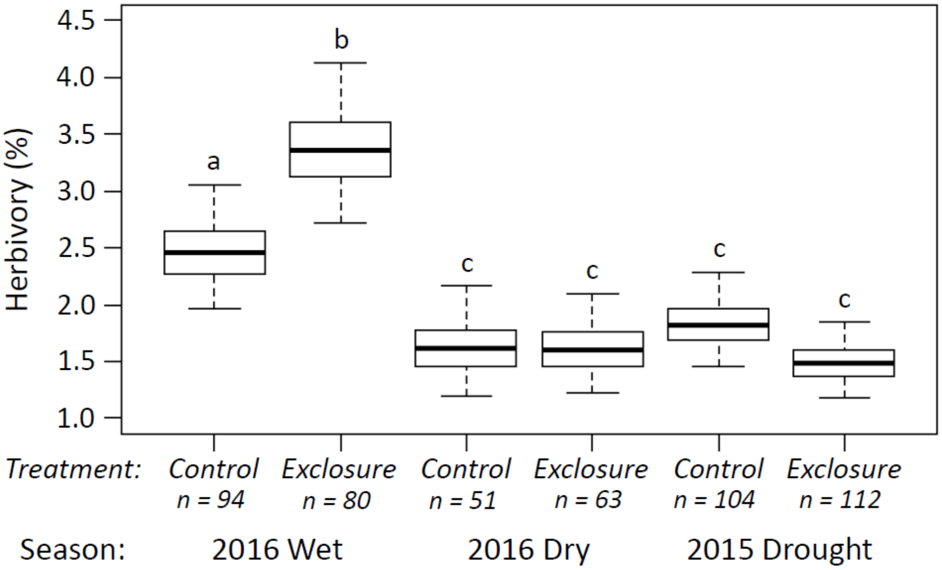

Figure 2.5. Herbivory on fully flushed leaves of *O. pyramidale* by season and treatment. Plot depicts herbivory estimates with 50% (boxes) and 95% (whiskers) confidence intervals. Sample size (number of leaves) is stated below each group. Letters denote statistically significant groups ($p < 0.05$).

Herbivory on still-expanding *O. pyramidale* leaves was not significantly different between the 2016 wet and 2016 dry seasons (Fig. 2.6). As was the case for fully flushed leaves, exclosures significantly increased herbivory on still-expanding leaves during the 2016 wet season, but not during the 2016 dry season (Fig. 2.6; Appendix, Table 2.5). Our model estimates that herbivory on still-expanding *O. pyramidale* was 58.2% higher when bird and bat access was restricted during the 2016 wet season.

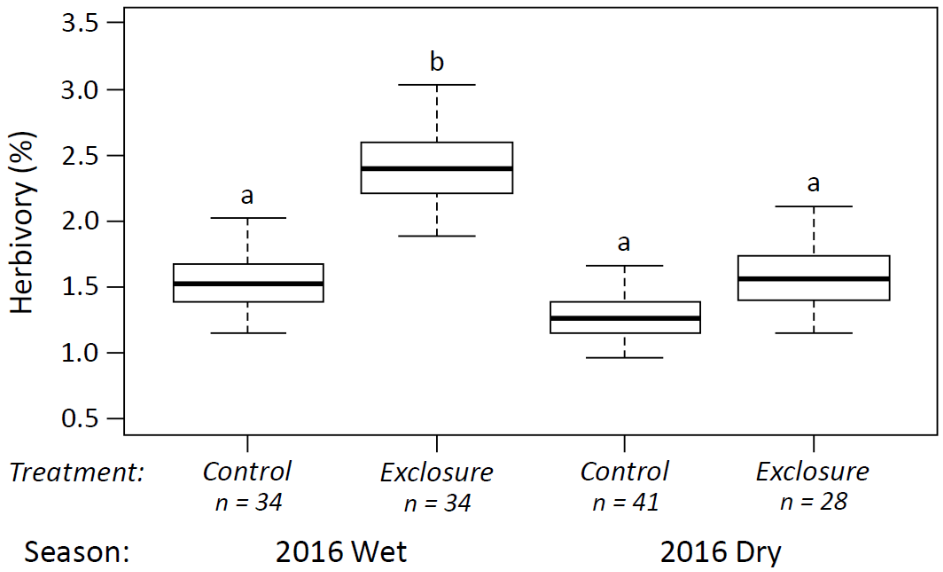

Figure 2.6. Herbivory on still-expanding leaves of *O. pyramidale* by season and treatment. Plot depicts herbivory estimates with 50% (boxes) and 95% (whiskers) confidence intervals. Sample size (number of leaves) is stated below each group. Letters denote statistically significant groups ($p < 0.05$).

Relative to the 2016 wet season, herbivory on *T. amazonia* was significantly lower in the 2015 drought, with an estimated reduction of approximately 56% (Fig. 2.7). Herbivory on *T. amazonia* during the 2015 drought was not significantly different between control, daytime exclosure, and 24-hr exclosure treatments (Fig. 2.7; Appendix, Table 2.6). During the 2016 wet season, herbivory on *T. amazonia* leaves was not significantly different between control and 24-hr exclosure treatments (Fig. 2.7; Appendix, Table 2.7).

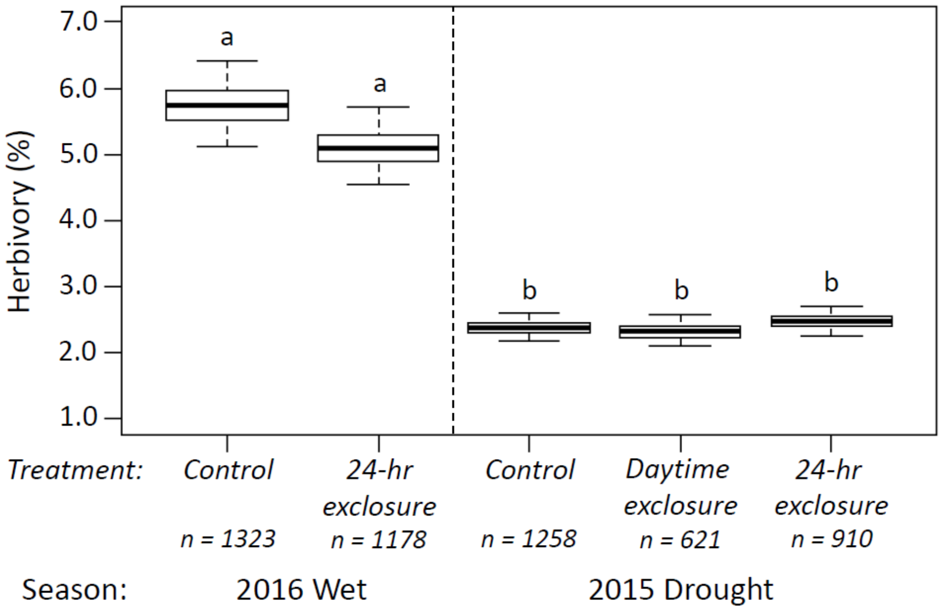

Figure 2.7. Herbivory on *T. amazonia* by season and treatment. Plot depicts herbivory estimates with 50% (boxes) and 95% (whiskers) confidence intervals. Sample size (number of leaves) is stated below each group. Herbivory estimates for each season were generated from separate models. Letters denote statistically significant groups ($p < 0.05$).

Folivorous insect biomass

Biomass of folivorous insects on *O. pyramidale* was not significantly different between seasons (Fig. 2.8; Appendix, Table 2.8). On *T. amazonia*, folivorous insect biomass was significantly lower in both the 2015 drought and 2016 dry season compared to the 2016 wet season (Fig. 2.9; Appendix, Table 2.9). Predator exclosures on *O. pyramidale* significantly increased folivorous insect biomass in the 2016 wet season but not in the 2016 dry season or 2015 drought (Fig. 2.10; Appendix, Tables 2.10–2.12). On *T. amazonia*, neither exclosure treatment (24-hr or daytime exclosure) significantly changed folivorous insect biomass in any season, compared to control treatments (Appendix, Tables 2.13–2.15).

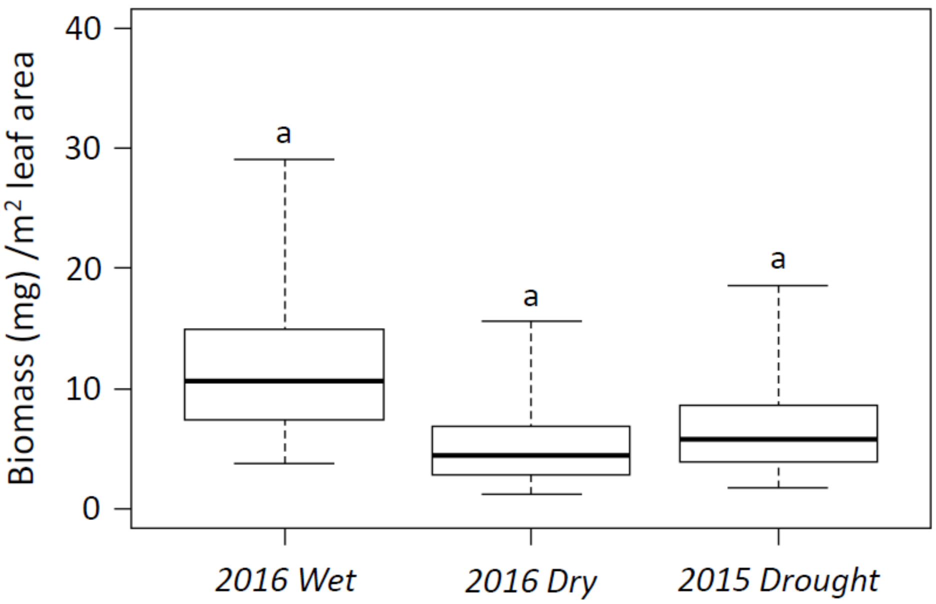

Figure 2.8. Total biomass of folivorous insect orders by season on *O. pyramidale*. Data from all treatment groups were used. Plot depicts biomass estimates with 50% (boxes) and 95% (whiskers) confidence intervals. Letters denote statistically significant groups ($p < 0.05$).

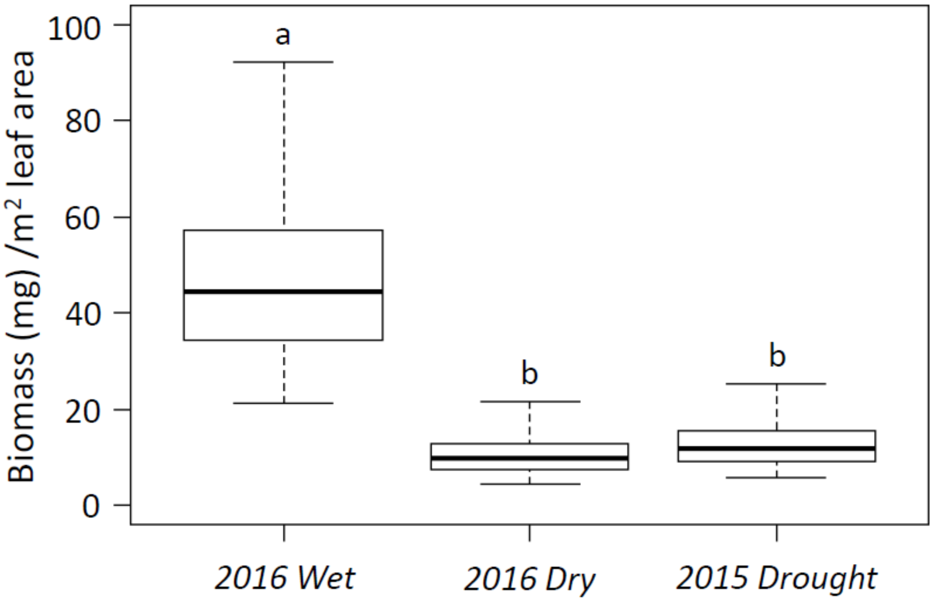

Figure 2.9. Total biomass of folivorous insect orders by season on *T. amazonia*. Data from all treatment groups were used. Plot depicts biomass estimates with 50% (boxes) and 95% (whiskers) confidence intervals. Letters denote statistically significant groups ($p < 0.05$).

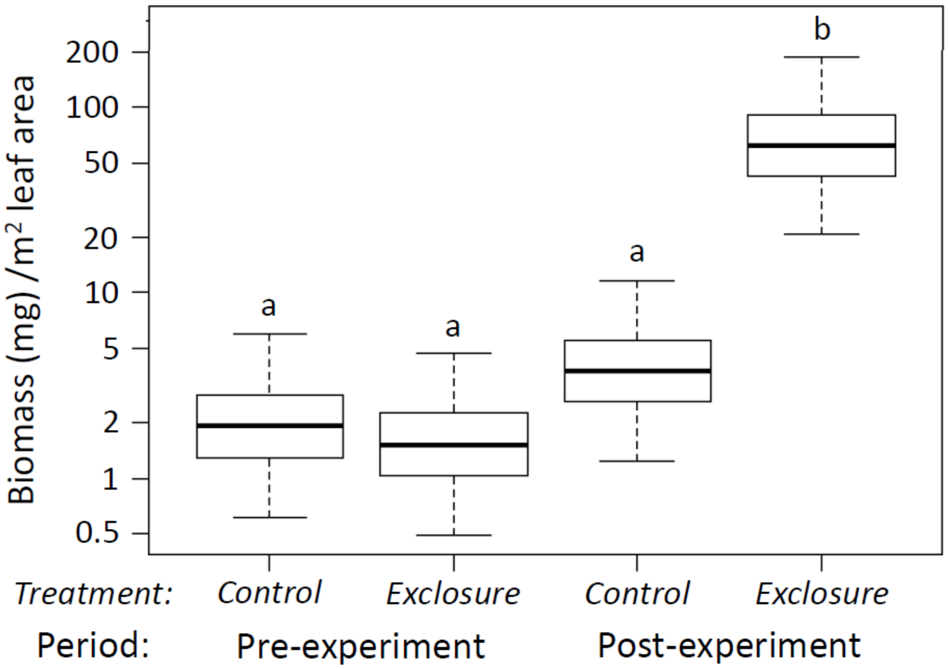

Figure 2.10. Biomass of folivorous insects on *O. pyramidale* in the 2016 wet season. Plot depicts biomass estimates with 50% (boxes) and 95% (whiskers) confidence intervals. Letters denote statistically significant groups ($p < 0.05$). Y-axis on log scale.

Insect-eating bird surveys

Insect-eating bird abundance in the native tree plantation was low, with only one or two birds recorded at a typical point (Table 2.1). Abundance of resident insect-eating birds was stable between seasons; regression models (Appendix, Fig. 2.11) estimated that a point surveyed at 0800 hrs in all seasons would yield between 1.15–1.26 resident birds. However, overwintering migrants boosted the population of insect-eating birds during the 2016 dry season by an estimated 42.3%, according to the models adjusting for count time.

Season	Total Birds		Total Insect-eating Birds		Predicted (0800 hrs)	
	Individuals	Species	Individuals	Species	Individuals	Per count
2016 Wet	87	27	71	21	70.2	1.17
2016 Dry	80	26	52 (68)	15 (22)	75.4 (107.4)	1.26 (1.79)
2015 Drought	55	20	48	18	69.2	1.15

Table 2.1. Bird survey results by field season. Fifteen points were surveyed four times per season, yielding 60 point counts. Dry season numbers in parentheses are results including overwintering migrant birds. Predicted survey results derive from season-specific linear regression models (Appendix, Fig. 2.11).

DISCUSSION

Our results show that bird- and bat-driven trophic cascades in the tropics are mediated not only by seasonality but also by irregular climatic fluctuations of the ENSO cycle (see Table 2.2 for summary of results). Predator exclosures increased biomass of folivorous insects and herbivory on *O. pyramidale* during a typical wet season, when leaf production was high, but not during the dry season, when leaf production was low.

	Rainfall	Leaf Production		Herbivory		Folivorous Insects		Insect-eating Birds	Trophic Cascade?	
Tree Species	**-**	***O.p.***	***T.a.***	***O.p.***	***T.a.***	***O.p.***	***T.a.***	**-**	***O.p.***	***T.a.***
2016 Wet Season	High	High	High	High	High	No difference	High	Very low	Yes	No
2016 Dry Season	Low	Low	Neglible	Low	No data	No difference	Low	Low	No	No
2015 Drought	Moderate	High	High	Low	Low	No difference	Low	Very low	No	No

Table 2.2. Qualitative summary of environmental conditions and results for *Ochroma pyramidale* (O.p.) and *Terminalia amazonia* (T.a.) across three seasons. Rainfall values are compared across seasons; rainfall totals in the 2016 wet season and 2016 dry season were near historical averages. Leaf production, herbivory, and folivorous insects (unmanipulated branches) are compared across seasons within tree species and should not be directly compared across species. Insect-eating bird abundance is compared across seasons but also to a priori knowledge of bird abundance in the broader landscape.

This result supports our prediction that the absolute trophic effect of birds and bats on herbivory is greater during the wet season than the dry season and is also consistent with ecological theory and prior empirical evidence that trophic cascade strength increases with higher ecosystem productivity (Oksanen et al. 1981; Van Bael and Brawn 2005). We did not find evidence for our second prediction that increased abundance of insectivorous birds during the dry season would lead to a greater proportional trophic effect compared to the wet season. Although we documented the expected increase in insectivorous bird abundance during the dry season, exclosures did not affect folivorous insect biomass or herbivory on either *O. pyramidale* or *T. amazonia* during this season.

Our third prediction was that trophic interactions in an aberrant wet season with drought conditions would be more similar to a dry season than to a typical wet season because of similarly low productivity. We found some support for the first part of our prediction. First, herbivory on fully flushed *O. pyramidale* and on *T. amazonia* was significantly lower during the 2015 drought compared to the 2016 wet season. For fully flushed *O. pyramidale*, herbivory during the 2015 drought was comparable to the 2016 dry season. Second, on *T. amazonia*, folivorous insect biomass was higher in the 2016 wet season than either the 2016 dry season or 2015 drought, which were not different from each other. Third, the trophic cascade effect on *O. pyramidale* present during the 2016 wet season was not evident during the 2016 dry season or 2015 drought.

However, patterns observed in herbivory and folivorous insect biomass did not closely align with our measure of plant productivity. Leaf production rates for both species during the 2015 drought were not distinguishable from the 2016 wet season and much higher than during the 2016 dry season. This suggests that low folivorous insect biomass during the 2015 drought was the result of unfavorable abiotic conditions for arthropods (lower precipitation and humidity, higher temperatures and winds), rather than being regulated by plant productivity. Why leaf production did not decline on either tree species during the 2015 drought relative to the 2016 wet season is unclear, given that physiological responses by many tropical trees to El Niño mirror their dry season responses (Detto et al. 2018). It may be the case that water is not a limiting resource for *O. pyramidale* and *T. amazonia* in typical wet seasons and that rainfall during the 2015 drought was still sufficient for these species to avoid water stress. Alternatively, trees could have been depleting water stored in their root systems to compensate for the lack of rainfall and did not show signs of water stress until after July 2015.

Differences in amount of herbivory (greater on *T. amazonia* than *O. pyramidale*), arthropod biomass (higher on *T. amazonia*) and trophic cascade strength (cascade only evident on 2016 wet season *O. pyramidale*) are likely driven by species-specific traits. Leaves of *O. pyramidale* are widely spaced and rarely touch each other, which reduces shelter for herbivorous insects from temperature fluctuations and drying winds. Such “open” branch architecture may also leave herbivores insects more exposed to foliage-gleaning predators. In contrast, foliage on *T. amazonia* branches is frequently dense with many overlapping leaves that may create more favorable microclimates for arthropods. The dense foliage may also make it more difficult for vertebrate predators to glean arthropods from *T. amazonia* leaves. In addition, the life history strategies of our two species are different. *Ochroma pyramidale* may be more vulnerable to generalist herbivores which, in turn, may be more vulnerable to vertebrate predators (Singer et al. 2014; Bosc et al. 2018), because it is a short-lived pioneer that may not invest heavily in mechanical or chemical leaf defenses (but see Coley 1983). Although *T. amazonia* had higher herbivory rates than *O. pyramidale*, it may be less palatable to generalist herbivores because it is a longer-lived species common in well-developed secondary forests and has relatively tough leaves (Paul et al. 2011).

We found a demonstrable trophic cascade in one context, despite low predator abundance in the ASP native tree plantation. Insect-eating bird abundance was considerably less than in other land cover types in central Panama, including residential areas, gallery forest, and old-growth forest (Petit et al. 1999; Roels et al. 2018) and a less heavily managed forest restoration of comparable age (see Chapter 1 of this dissertation). A separate study of bird predation pressure in the broader ASP landscape found that bird predation activity in the native tree plantation was second-lowest of any land cover type surveyed, including non-native teak plantation (the lowest), unmanaged secondary growth, gallery forest, old-growth forest, and countryside hedgerows (Roels et al. 2018). Although we did not collect data on bat abundance, other researchers have documented low bat densities in the ASP native tree plantation relative to nearby forests (S. Brändel, personal communication).

Since exclosures on *O. pyramidale* were in place for 24 hours a day, we cannot quantify the proportional contributions of birds and bats to the trophic cascade we observed in the 2016 wet season. We suspect birds were the primary drivers of the trophic cascade because bat species that consume folivorous insects are unlikely to be present in the ASP native tree plantation in substantial numbers. Phyllostomid bats, a major component of Neotropical bat communities, generally avoid areas where understory vegetation has been removed (García-Morales et al. 2013). Furthermore, within the Phyllostomidae, species that are specifically described as foliage-gleaning insectivores (subfamily Phyllostominae) are especially sensitive to forest disturbance (Medellín et al. 2000). However, another phyllostomid subfamily, the Carolliinae, is positively associated with forest disturbance (Medellín et al. 2000) and some species in this generally frugivorous group may consume more insects than has traditionally been assumed (York and Billings 2009). Additional study of bat ecology in tropical forest restorations is clearly needed.

Our results only represent 4–5 weeks of herbivory on newly flushed leaves; measures of standing crop herbivory are likely to be higher. Leaf life span is approximately 100 days for *O. pyramidale* (Selaya et al. 2008) and 200 days or more for *T. amazonia* (Kitajima et al. 2013; K. Sinacore, personal communication). If damage continues to accumulate over leaf life spans, longer experiments may have found greater differences in herbivory between more of the season-treatment comparisons. The difference in magnitude of the exclosure effect on still-expanding and fully flushed *O. pyramidale* leaves in the 2016 wet season also supports the idea that longer experiments may have found more evidence for trophic cascades. The proportional increase in herbivory caused by exclosures was greater for still-expanding leaves than for fully flushed leaves (58.2% vs. 38.0%), despite less herbivory overall on the younger leaves. If the increase in folivorous arthropod biomass on exclosure branches developed over time (i.e. not instantaneously), leaves began flushing near the end of the experiment would have experienced the greatest divergence in folivorous insect biomass between treatment groups, leading to the greater exclosure effect we observed on still-expanding leaves. Given these observations, we recommend that exclosure experiments be run as long as logistically feasible.

Native species timber plantations are becoming increasingly common in tropical regions as human societies seek to restore ecosystem services and reduce logging pressure on dwindling tracts of primary forest. Low abundances of birds and bats at our site, and lack of trophic cascade effects on the tree/season combination with the highest level of herbivory (2016 wet season *T. amazonia*) suggest a missed opportunity to take advantage of a potentially beneficial trophic cascade. Bird- and bat-friendly management of these new forests, such as less aggressive management of understory vegetation and placement of artificial nesting or roosting structures (Lindell et al. 2018), may increase benefits provided by insectivorous wildlife to plantation trees. However, we still have much to learn about multi-trophic level interactions with global-scale environmental patterns like the ENSO cycle before we can manage or manipulate them with confidence. Shifting global climate may change seasonal patterns in rainfall, primary productivity, and wildlife communities, altering trophic cascades in ways that will be difficult to predict with our currently limited understanding of their operation.

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APPENDIX

APPENDIX

Taxon	Authority	Location	a	b	Habitat
Aranae	Johnson & Strong 2000	Jamaica	0.1253	2.039	Various
Blattodea	Wardhaugh 2013	Australia	0.0187	2.760	Rainforest
Coleoptera*	Schoener 1980	Costa Rica	0.1170	2.110	Dry forest
	Schoener 1980	Costa Rica	0.1260	1.910	Wet forest
Diptera*	Schoener 1980	Costa Rica	0.0740	1.640	Dry forest
	Schoener 1980	Costa Rica	0.0680	1.590	Wet forest
Hemiptera*	Schoener 1980	Costa Rica	0.0350	2.480	Dry forest
	Schoener 1980	Costa Rica	0.0270	2.280	Wet forest
Homoptera*	Schoener 1980	Costa Rica	0.0230	2.650	Dry forest
	Schoener 1980	Costa Rica	0.0300	2.230	Wet forest
Hymenoptera (Formicidae)*	Schoener 1980	Costa Rica	0.0120	2.720	Dry forest
	Schoener 1980	Costa Rica	0.0210	2.310	Wet forest
Hymenoptera (non-Formicidae)*	Schoener 1980	Costa Rica	0.0430	2.070	Dry forest
	Schoener 1980	Costa Rica	0.0220	2.290	Wet forest
Lepidoptera (Larval)*	Sample et al. 1993	West Virginia	0.0027	2.959	Forest
	Wardhaugh 2013	Australia	0.0043	2.550	Rainforest
Mantodea	Wardhaugh 2013	Australia	0.0018	3.010	Rainforest
Neuroptera	Sample et al. 1993	West Virginia	0.0113	2.570	Forest
Orthoptera*	Schoener 1980	Costa Rica	0.2220	1.810	Dry forest
	Schoener 1980	Costa Rica	0.0660	2.100	Wet forest
Phasmatodea	Wardhaugh 2013	Australia	0.0027	2.310	Rainforest

Table 2.3. Biometric equations for arthropod length and dry biomass. Arthropod length:mass equations take the form: mass (mg) = a*L^b where a and b are empirically derived constants and L is length in mm. Modern taxonomy regards Homoptera as a clade within Hemiptera. Asterisks denote where the average of two equations was used. Approximate annual rainfall at Schoener's (1980) dry and wet forest sites are 1800 mm and 5500 mm, respectively. Approximate annual rainfall at the Agua Salud Project is 2700 mm.

	Estimate	Std. Error	z value	p
Intercept	-3.684	0.114	-32.21	<0.001*
Season(2016 Dry)	-0.430	0.183	-2.35	0.019*
Season(2015 Drought)	-0.302	0.154	-1.96	0.050*
Treatment(24-hr Exclosure)	0.322	0.152	2.12	0.034*
Treatment(24-hr Exclosure)* Season(2016 Dry)	-0.325	0.249	-1.31	0.192
Treatment(24-hr Exclosure)* Season(2015 Drought)	-0.535	0.216	-2.48	0.013*

Table 2.4. Effects of predator exclosures and seasonality on herbivory for fully flushed *O. pyramidale* leaves. Leaves in the control group during the 2016 wet season are the reference group (intercept). Statistically significance differences (p<0.05) denoted by *.

	Estimate	Std. Error	z value	p
Intercept	-4.167	0.145	-28.756	<0.001*
Season(Dry 2016)	-0.188	0.187	-1.008	0.313
Treatment(24-hr Exclosure)	0.459	0.180	2.546	0.011*
Treatment(24-hr Exclosure)* Season(Dry 2016)	-0.248	0.266	-0.934	0.351

Table 2.5. Effects of predator exclosures and seasonality on herbivory for still-expanding *O. pyramidale* leaves. Leaves in the control group during the 2016 wet season are the reference group (intercept). Statistically significance differences (p<0.05) denoted by *.

	Estimate	Std. Error	z value	p
Intercept	-3.713	0.046	-81.45	<0.001*
Treatment(Daytime Exclosure)	0.037	0.049	0.77	0.440
Treatment(24-hr Exclosure)	-0.026	0.054	-0.49	0.624

Table 2.6. Effects of predator exclosures on herbivory for *T. amazonia* leaves in the 2015 drought. Leaves in the control group are the reference group (intercept). Statistically significance differences (p<0.05) denoted by *.

	Estimate	Std. Error	z value	p
Intercept	-2.800	0.062	-45.44	<0.001*
Treatment(24-hr Exclosure)	-0.124	0.077	-1.61	0.108

Table 2.7. Effects of predator exclosures on herbivory for *T. amazonia* leaves in the 2016 wet season. Leaves in the control group are the reference group (intercept). Statistically significance differences (p<0.05) denoted by *.

Folivorous Insect Biomass	Estimate	Std. Error	z value	p
Intercept	1.499	0.636	2.356	0.019*
Season(2015 Drought)	0.257	0.765	0.336	0.737
Season(2016 Wet)	0.860	0.783	1.098	0.272

Table 2.8. Seasonal differences in folivorous insect biomass on *O. pyramidale*. Branches during the 2016 dry season are the reference group (intercept). Statistically significance differences (p<0.05) denoted by *.

Folivorous Insect Biomass	Estimate	Std. Error	z value	p
Intercept	2.282	0.402	5.672	<0.001*
Season(2015 Drought)	0.194	0.511	0.379	0.705
Season(2016 Wet)	1.510	0.507	2.977	0.003*

Table 2.9. Seasonal differences in folivorous insect biomass on *T. amazonia*. Branches during the 2016 dry season are the reference group (intercept). Statistically significance differences (p<0.05) denoted by *.

Folivorous Insect Biomass	Estimate	Std. Error	z value	p
Intercept	1.807	1.185	1.525	0.127
Period(Post-experiment)	0.361	1.459	0.248	0.804
Treatment(24-hr Exclosure)	-1.782	1.534	-1.161	0.245
Period(Post-experiment) *Treatment(24-hr Exclosure)	1.131	2.051	0.552	0.581

Table 2.10. Predator exclosure effects on folivorous insect biomass on *O. pyramidale* in the 2015 drought. Branches in the control group during the pre-experiment survey period are the reference group (intercept). Statistically significance differences (p<0.05) denoted by *.

Folivorous Insect Biomass	Estimate	Std. Error	z value	p
Intercept	-0.182	0.879	-0.208	0.836
Period(Post-experiment)	2.022	1.248	1.620	0.105
Treatment(24-hr Exclosure)	2.373	1.230	1.929	0.054
Period(Post-experiment) *Treatment(24-hr Exclosure)	-0.991	1.750	-0.566	0.571

Table 2.11. Predator exclosure effects on folivorous insect biomass on *O. pyramidale* in the 2016 dry season. Branches in the control group during the pre-experiment survey period are the reference group (intercept). Statistically significance differences (p<0.05) denoted by *.

Folivorous Insect Biomass	Estimate	Std. Error	z value	p
Intercept	0.649	0.582	1.115	0.265
Period(Post-experiment)	0.687	0.813	0.845	0.398
Treatment(24-hr Exclosure)	-0.226	0.820	-0.275	0.783
Period(Post-experiment) *Treatment(24-hr Exclosure)	3.025	1.144	2.643	0.008*

Table 2.12. Predator exclosure effects on folivorous insect biomass on *O. pyramidale* in the 2016 wet season. Branches in the control group during the pre-experiment survey period are the reference group (intercept). Statistically significance differences (p<0.05) denoted by *.

Folivorous Insect Biomass	Estimate	Std. Error	z value	p
Intercept	2.483	0.699	3.553	<0.001*
Period(Post-experiment)	-0.103	0.988	-0.105	0.917
Treatment(24-hr Exclosure)	0.624	0.988	0.632	0.528
Treatment(Daytime Exclosure)	-0.272	0.988	-0.275	0.783
Period(Post-experiment) *Treatment(24-hr Exclosure)	-0.433	1.397	-0.310	0.757
Period(Post-experiment) *Treatment(Daytime Exclosure)	-0.304	1.399	-0.217	0.828

Table 2.13. Predator exclosure effects on folivorous insect biomass on *T. amazonia* in the 2015 drought. Branches in the control group during the pre-experiment survey period are the reference group (intercept). Statistically significance differences (p<0.05) denoted by *.

Folivorous Insect Biomass	Estimate	Std. Error	z value	p
Intercept	2.209	0.731	3.022	0.003*
Period(Post-experiment)	0.102	1.034	0.098	0.922
Treatment(24-hr Exclosure)	0.800	1.033	0.774	0.439
Treatment(Daytime Exclosure)	0.436	1.055	0.414	0.679
Period(Post-experiment) *Treatment(24-hr Exclosure)	-0.659	1.461	-0.451	0.652
Period(Post-experiment) *Treatment(Daytime Exclosure)	-1.738	1.495	-1.163	0.245

Table 2.14. Predator exclosure effects on folivorous insect biomass on *T. amazonia* in the 2016 dry season. Branches in the control group during the pre-experiment survey period are the reference group (intercept). Statistically significance differences (p<0.05) denoted by *.

Folivorous Insect Biomass	**Estimate**	**Std. Error**	**z value**	**p**
Intercept	3.824	0.539	7.099	<0.001*
Period(Post-experiment)	0.058	0.762	0.077	0.939
Treatment(24-hr Exclosure)	-0.952	0.762	-1.248	0.212
Period(Post-experiment) *Treatment(24-hr Exclosure)	1.645	1.078	1.526	0.127

Table 2.15. Predator exclosure effects on folivorous insect biomass on *T. amazonia* in the 2016 wet season. Branches in the control group during the pre-experiment survey period are the reference group (intercept). Statistically significance differences ($p<0.05$) denoted by *.

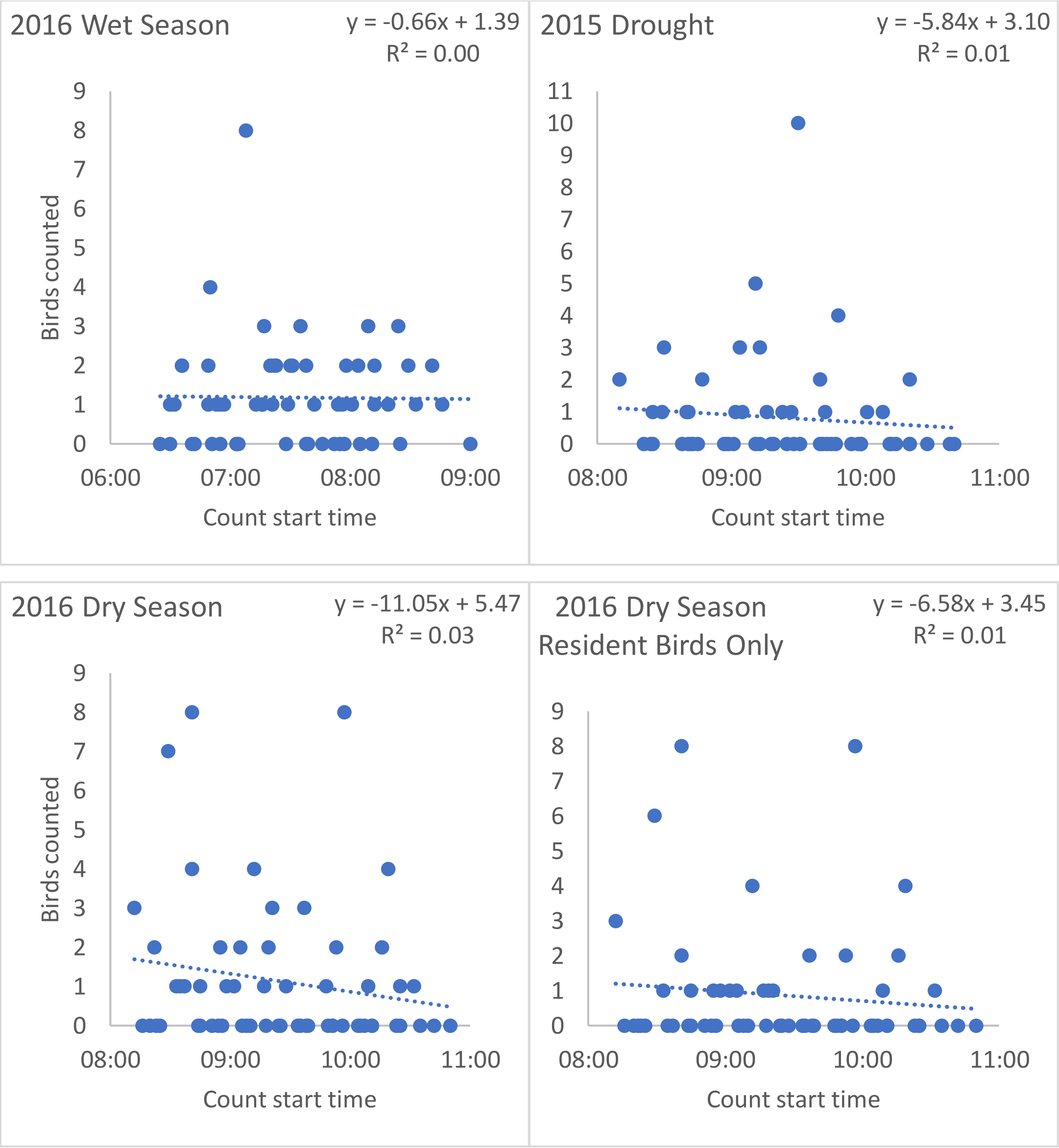

Figure 2.11. Linear regression models for the effect of start time on number of birds counted.

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CHAPTER 3:

Tropical Trophic Cascade Linked to Reduction in Large-bodied Insects by Birds and Bats

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ABSTRACT

In many tropical ecosystems, predation pressure from birds and bats regulates populations of folivorous insects and decreases leaf damage in a trophic cascade that benefits trees. Detailed information regarding bird and bat predation pressure on individual arthropod taxa is necessary for understanding mechanisms underlying these trophic cascades. We conducted a bird and bat exclosure experiment on two tree species, *Ochroma pyramidale* and *Terminalia amazonia*, in a tropical forest restoration. There was a significant trophic cascade on *O. pyramidale*, but not *T. amazonia*. We report the effects of bird and bat exclosures on taxonomic composition and distribution of biomass within arthropod communities on both tree species. On *O. pyramidale*, predation by birds and bats reduced biomass for five folivorous insect orders (Coleoptera, Lepidoptera, Phasmida, Blattodea, and Orthoptera) and numbers of individuals for four of the five orders. Spider (Araneae) biomass and numbers on *O. pyramidale* were also reduced by bird and bat predation. These patterns were noticeably weaker or absent on *T. amazonia*, where a trophic cascade was not observed. We did not find evidence that intraguild predation by birds and bats on spiders dampened trophic cascade effects. Bird- and bat-driven trophic cascades have been found in natural, agricultural, and restoration ecosystems, demonstrating that conservation of bird and bat populations is a critical component of maintaining trophic relationships and ecological function.

INTRODUCTION

Ecological effects of herbivorous insects in the tropics are pervasive. Insects are regarded as drivers of tree community structure and diversity (Janzen 1970; Connell 1971), plant speciation rates (Coley and Kursar 2014), and evolution of plant defenses (Coley and Barone 1996).

Arboreal insects are the primary herbivores of tropical foliage (Coley and Barone 1996), and serve as prey for hundreds of species in two of the most speciose groups of tropical vertebrates; birds and bats. In many tropical ecosystems, predation pressure from birds and bats regulates populations of folivorous (i.e., chewing) insects and decreases leaf damage in a trophic cascade that benefits trees (Van Bael et al. 2008; Mäntylä et al. 2011; Maas et al. 2016).

Detailed information regarding bird/bat predation pressure on individual arthropod taxa is necessary for understanding mechanisms underlying bird/bat-insect-plant trophic cascades. On trees in temperate regions, indirect reductions in plant damage by birds are often attributed to high rates of caterpillar consumption (Atlegrim 1989; Marquis and Whelan 1994; Strong et al. 2000; Mols and Visser 2002; Singer et al. 2014). In tropical forests, Lepidoptera are also important herbivores (Van Bael et al. 2004; Dyer et al. 2007) but studies of arthropod community structure suggest the relative importance of other insect taxa with herbivorous species, such as Coleoptera, Blattodea, Phasmida, and Orthoptera, may be greater than in temperate regions (tropical studies: Stork 1988; Basset 2001; Kitching et al. 2001; Ellwood and Foster 2004, temperate studies: Trieff 2002; Southwood et al. 2004). Predatory arthropods, especially spiders, are also common in tropical arthropod communities and may consume folivorous insects. High intraguild predation by vertebrates on arthropod predators is counterintuitively associated with strong trophic cascades because of positive correlations between vertebrate predation on arthropod predators and herbivores (Mooney et al. 2010). However, there are circumstances where intraguild predation dampens cascade effects (Karp and Daily 2014; Bosc et al. 2018).

Studies on tropical trophic cascades with bird/bat exclosures have typically reported exclosure effects on arthropod density (individuals/unit area; Van Bael et al. 2003; Van Bael and Brawn 2005; Kalka et al. 2008; Williams-Guillén et al. 2008; Maas et al. 2013). Some studies reporting densities have taken an additional step of examining two size classes, “small” and “large” arthropods (large variably defined as body lengths >3 or >5 mm), based on the presumption that larger arthropods are preferred prey items and would, therefore, be more likely to show effects of bird/bat predation (Philpott et al. 2004; Jedlicka et al. 2006; Van Bael et al. 2007; Karp and Daily 2014). While census-based approaches to characterizing arthropods in trophic cascade studies are straightforward, they rely on the assumption that herbivory is proportional to number of individual arthropods, despite the wide range of arthropod body sizes. Correlations between aggregate biomass and census counts vary widely among arthropod communities and metrics of biomass have been recommended over census counts when ecological functions and trophic interactions are of interest (Saint-Germain et al. 2007). Allometric scaling of arthropod body length to body mass causes a two-fold increase in body length to result in a four-fold or greater increase in body mass (Schoener 1980; Sample et al. 1993), with concomitant increases in metabolic demands (Brown et al. 2004). The amount of herbivory caused by 50 mm caterpillar, for example, likely dwarfs that caused by a 10 mm caterpillar because the longer caterpillar may have a mass 60 or even 120 times greater (Sample et al. 1993; Wardhaugh 2013).

Exclosure studies that have accounted for differences in arthropod size by converting census data into total arthropod or folivorous insect biomass are uncommon (Bridgeland et al. 2010; Morrison and Lindell 2012). Bridgeland et al. (2010) reported both counts of individuals and biomass per unit area; one of their research sites showed stronger evidence for exclosure effects on biomass than counts and the other site showed the reverse (Bridgeland et al. 2010: Fig. 4). Effects of predator exclosures will be more evident for biomass instead of count data in cases where predators disproportionately consume large arthropods. Accounting for arthropod size is especially important in tropical studies, where the range of arthropod body size is greater than temperate regions due to the presence of extremely large taxa (Makarieva et al. 2005).

There is some evidence that tropical birds preferentially forage on arthropods larger than 5 mm (Philpott et al. 2004; Jedlicka et al. 2006; Van Bael et al. 2007) and may especially target large prey items during the breeding season for efficient food delivery to nestlings (Greenberg 1995). Preference for large arthropods as prey items is likely also true for tropical foliage-gleaning bats. Kalka and Kalko (2006) studied the diet of the smallest of nine foliage-gleaning bat species occurring on Barro Colorado Island, Panama and found it primarily consumed arthropods larger than 10 mm. This bat species has a body mass (5–7 g, Kalka and Kalko 2006) similar to that of a small insectivorous bird, such as a gnatcatcher (Polioptilidae; Dunning 2008). Gnatcatchers do not usually consume arthropods greater than 10 mm (Burger et al. 1999), suggesting that foliage-gleaning bats in general may be even more focused on large arthropod prey than birds.

We conducted a multi-season bird/bat exclosure experiment on two tree species in a tropical forest restoration to measure trophic cascade strength and evaluate the effects of bird/bat predation on tropical arthropod communities. A measurable trophic cascade was only detectable during the 2016 wet season, which had typical rainfall (see Chapter 2 of this dissertation). One tree species showed greater leaf herbivory in the exclosure treatment (i.e., birds/bats absent) while the other species showed no difference between exclosure and control treatments. Here, we report the effects of bird/bat exclosures on the taxonomic composition and distribution of biomass within the arthropod communities on both tree species during the 2016 wet season.

METHODS

Study site and species

We conducted our study in a plantation-style native species forest restoration at the Agua Salud Project (ASP), Colón Province, Panamá (9°12’52’’ N, 79°43’25’’ W, elevation: 200–300 m a.s.l.). The plantation was established in 2008 with plots containing native species monocultures or polycultures (see Mayoral et al. 2017 for details). We selected two tree species for our study, *Terminalia amazonia* (J.F.Gmel.) Exell (Family: Combretaceae) and *Ochroma pyramidale* (Cav. ex Lam.) Urb. (Family: Malvaceae). Our study occurred in the middle portion of the 2016 wet season (June 11–July 27). Rainfall during June and July was 502 mm, similar to the average of 549 mm (2009–2017, STRI 2018).

Experimental protocol

Exclosure material and design

We constructed predator exclosures out of light-weight plastic netting (Standard BirdNet; Bird-X, Chicago, IL, USA), with mesh large enough (2 x 2 cm) to permit passage of large arthropods but not foraging birds or bats. For each tree species, we paired neighboring trees and randomly assigned trees within pairs to control and exclosure treatments. There were 36 pairs of *O. pyramidale* and 41 pairs of *T. amazonia*. On each tree, we selected a single branch (~50 cm length) that showed evidence of active growth so we could measure herbivory on leaves flushed during the experiment. Exclosures remained in place for 30–31 days on *O. pyramidale* and 34–

35 days on *T. amazonia*. Additional details of exclosure construction are provided in Chapter 2 of this dissertation.

Arthropod surveys

A single observer, S. Roels, censused arthropods just prior to placement of exclosures and again at the end of the experiment. During each survey, S. Roels visually searched for arthropods on all leaves of focal branches, inspecting both upper and lower leaf surfaces. Arthropods were identified to order and categorized into the following body length classes: ≤2 mm, >2–4 mm, >4–6 mm, >6 mm. Arthropods greater than 6 mm were measured with a hand ruler. We did not attempt to count ants (Hymenoptera: Formicidae) due to difficulty of censusing individuals on trees with colonies. We report arthropod counts and biomass per m^2 of leaf area (see Chapter 2 of this dissertation for leaf area calculation methods).

Arthropod biomass estimates

We converted arthropod lengths into dry arthropod biomass using published length:mass regression relationships specific to taxonomic order (Schoener 1980; Sample et al. 1993; Johnson and Strong 2000; Wardhaugh 2013). The biomass of arthropods placed into body length classes was calculated using the midpoint of the range (e.g., 2–4 mm was treated as 3 mm for biomass calculations). Arthropods in the < 2 mm class were treated as having a body length of 1.5 mm because arthropods smaller than 1 mm were unlikely to be counted on visual surveys. Additional details of biomass calculations are provided in Chapter 2 of this dissertation (Methods and Table 2.1).

Preliminary review of the distributions of individual arthropod biomass values on each tree species revealed clear discontinuities at the high end of the distributions. A few extremely large arthropods (>90 mg) on each tree species were over twice as massive, or more, as the next largest individual. We regarded these arthropods as outliers and removed two individuals from the *O. pyramidale* and four from the *T. amazonia* biomass data sets. Biomass estimates with these 'giants' retained are included in the appendix. Sample sizes for individual arthropod orders were too small for statistical analysis and, even with 'giants' removed, individual arthropods sometimes represented large portions of total biomass for their taxa within a survey period. For these reasons, we qualitatively describe the effects of exclosures on the biomass of individual taxa.

RESULTS

We counted 357 arthropods on *O. pyramidale* and 558 on *T. amazonia*. We recorded arthropods in three non-insect orders (spiders: Araneae, scorpions: Scorpiones, pillbugs: Isopoda) and ten insect orders (roaches: Blattodea, beetles: Coleoptera, flies: Diptera, true bugs: Hemiptera, bees and wasps: Hymenoptera, butterflies and moths: Lepidoptera, mantises: Mantodea, lacewings: Neuroptera, grasshoppers and allies: Orthoptera, and stick insects: Phasmida). Diversity within these taxa appeared to be high; although we only identified arthropods to the order level, we did not notice any particular morpho-species that were dominant within their order. The biomass and census count of many orders increased from our pre- to post-experiment surveys on both control and exclosure branches, suggesting a trend driven by environmental conditions unrelated to treatment group (Tables 3.1–3.4).

On *O. pyramidale*, our previous study found a significant increase in folivorous insect biomass on exclosure, but not control, branches (see Chapter 2 of this dissertation: Fig. 2.1). On exclosure branches, biomass increased for each of the five primary folivorous orders (Table 3.1; Fig. 3.1).

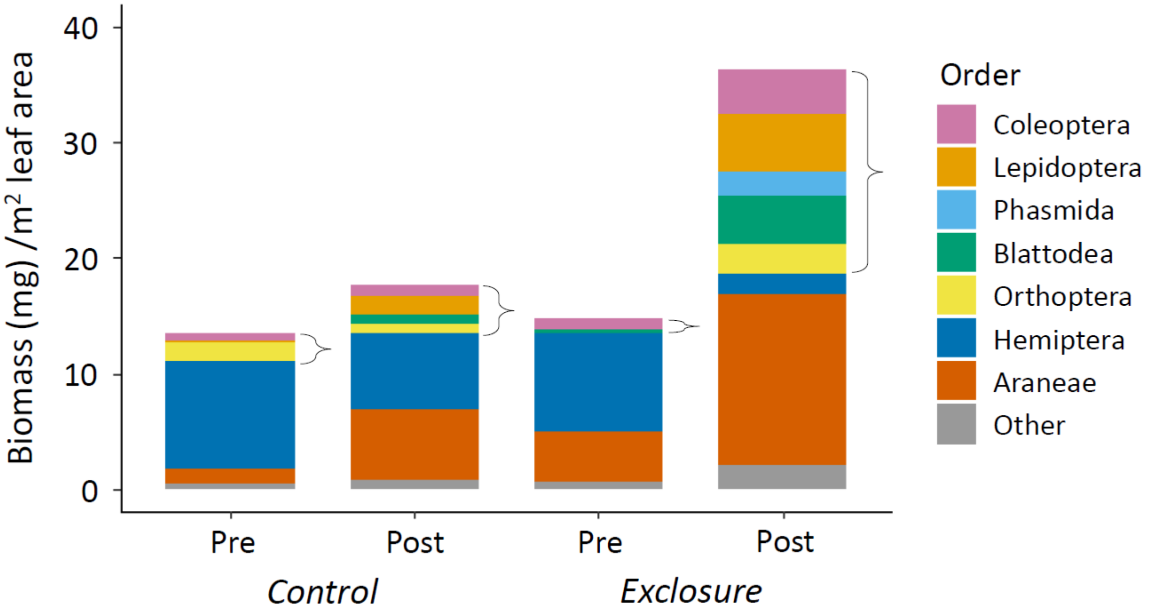

Figure 3.1. Arthropod biomass by order on *O. pyramidale* before (Pre) and after (Post) the exclosure experiment. Two individual arthropods with mass greater than 90 mg were regarded as outliers and removed from the data set. Brackets denote folivorous orders.

On control branches, the direction of change for folivorous orders was not consistent (three increases, one without change, one decrease) and the magnitudes of any positive changes were smaller than for exclosure branches (Table 3.1). Spider biomass increased in both treatment groups but the increase on control branches was less than half that observed on exclosure branches (4.80 mg/m^2 leaf area vs. 10.47 mg/m^2 leaf area) (Table 3.1). The effect of exclosures on biomass may actually be underestimated in Fig. 3.1 because both ‘giants’ removed from the data set were found on exclosure branches in the post-experiment survey (Table 3.1; Appendix, Fig. 3.7).

Taxon	Ctr-Pre	Ctr-Post	Δ Ctr	Exc-Pre	Exc-Post	Δ Exc
Coleoptera	0.62	1.10	0.48	0.96	3.88	2.92
Lepidoptera	0.25	1.47	1.22	0.00	5.02 (18.14)	5.02 (18.14)
Phasmida	0.00	0.00	0.00	0.00	2.08	2.08
Blattodea	0.04	0.84	0.80	0.38	4.14	3.76
Orthoptera	1.62	0.89	-0.73	0.00	2.64 (40.43)	2.64 (40.43)
Hemiptera	9.20	6.52	-2.68	8.55	1.79	-6.76
Araneae	1.36	6.16	4.80	4.28	14.75	10.47
Other	0.43	0.75	0.32	0.66	2.03	1.37
Folivorous	2.53	4.30	1.77	1.34	17.76 (68.67)	16.42 (67.33)
All Arthropods	13.53	17.73	4.20	14.83	36.33 (87.24)	21.50 (72.41)

Table 3.1. Biomass (mg) of arthropod orders per m^2 leaf area during pre- and post-experiment surveys on control (Ctr) and exclosure (Exc) branches of *O. pyramidale*. Numbers in parentheses include the 'giant' arthropods regarded as outliers. "Folivorous" is the total of Coleoptera, Lepidoptera, Phasmida, Blattodea, and Orthoptera. Δ Ctr and Δ Exc are the differences between pre- and post-experiment surveys within treatment group.

Exclosure effects were less obvious using count data because the total number of arthropods increased by over double in both treatment groups between pre- and post-experiment surveys (Table 3.2; Fig. 3.2). However, 93.1% of the increase in arthropod numbers on exclosure branches was due to folivorous insects and spiders while 61% of the increase on control branches was due to Hemipterans (especially small Auchenorrhynchine "hoppers") (Table 3.2).

Taxon	Ctr-Pre	Ctr-Post	Δ Ctr	Exc-Pre	Exc-Post	Δ Exc
Coleoptera	0.19	0.86	0.67	0.28	0.77	0.49
Lepidoptera	0.10	0.31	0.22	0.00	1.08	1.08
Phasmida	0.00	0.00	0.00	0.00	0.23	0.23
Blattodea	0.10	0.08	-0.02	0.09	0.85	0.75
Orthoptera	0.19	0.08	-0.12	0.00	0.31	0.31
Hemiptera	1.07	3.76	2.69	1.50	2.01	0.51
Araneae	0.68	1.80	1.12	1.12	4.01	2.89
Other	0.39	0.23	-0.15	0.47	0.39	-0.08
Folivorous	0.58	1.33	0.75	0.37	3.24	2.87
All Arthropods	2.72	7.12	4.40	3.46	9.64	6.18

Table 3.2. Census counts of arthropod orders (individuals per m^2 leaf area) during pre- and post-experiment surveys on control (Ctr) and exclosure (Exc) branches of *O. pyramidale*. "Folivorous" is the total of Coleoptera, Lepidoptera, Phasmida, Blattodea, and Orthoptera. Δ Ctr and Δ Exc are the differences between pre- and post-experiment surveys within treatment group.

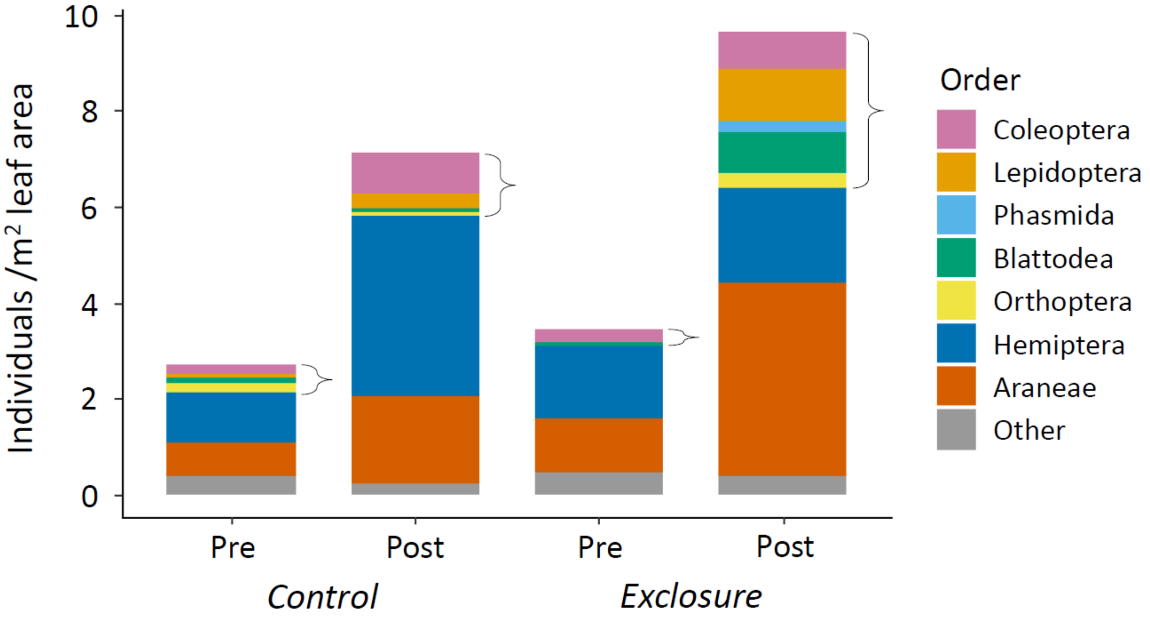

Figure 3.2. Census counts of arthropod orders on *O. pyramidale* before (Pre) and after (Post) the exclosure experiment. Brackets denote folivorous orders.

On *T. amazonia*, our previous study did not find significant exclosure effects on folivorous insect biomass. There were no consistent patterns in the direction of change for individual order biomass in either treatment group (Table 3.3; Fig. 3.3). Considering biomass totals with ‘giants’ included suggests a greater increase in folivore biomass on exclosure than control branches (exclosure: 79.89 mg/m^2 leaf area vs. control: 14.73 mg/m^2 leaf area) but the large change on exclosure branches was due to a single roach and single caterpillar (Table 3.3; Appendix, Fig. 3.8). Without those two individuals, the change in folivore biomass is lower on exclosure than control branches (exclosure: 6.12 mg/m^2 leaf area vs. control: 14.73 mg/m^2 leaf area) (Table 3.3).

Taxon	Ctr-Pre	Ctr-Post	Δ Ctr	Exc-Pre	Exc-Post	Δ Exc
Coleoptera	7.99	5.59	-2.40	4.09	2.54	-1.55
Lepidoptera	1.05 (32.40)	9.65	8.60 (-22.75)	4.12	4.33 (26.91)	0.21 (22.79)
Phasmida	0.00	0.00	0.00	0.00	8.20	8.20
Blattodea	0.06	16.20 (36.56)	16.20 (36.56)	6.83	9.28 (60.46)	2.44 (53.62)
Orthoptera	8.47	0.86	-7.60	3.35	0.17	-3.17
Hemiptera	9.83	1.38	-8.45	1.48	5.78	4.30
Araneae	4.20	11.28	7.08	10.63	21.59	10.96
Other	0.97	0.14	-0.83	0.36	0.06	-0.30
Folivorous	17.57 (48.91)	32.30 (52.66)	14.73 (3.75)	18.39	24.51 (98.28)	6.12 (79.89)
All Arthropods	32.57 (63.91)	45.10 (65.46)	12.53 (1.55)	30.85	51.94 (125.71)	21.09 (94.85)

Table 3.3. Biomass (mg) of arthropod orders per m^2 leaf area during pre- and post-experiment surveys on control (Ctr) and exclosure (Exc) branches of *T. amazonia*. Numbers in parentheses include the 'giant' arthropods regarded as outliers. "Folivorous" is the total of Coleoptera, Lepidoptera, Phasmida, Blattodea, and Orthoptera. Δ Ctr and Δ Exc are the differences between pre- and post-experiment surveys within treatment group.

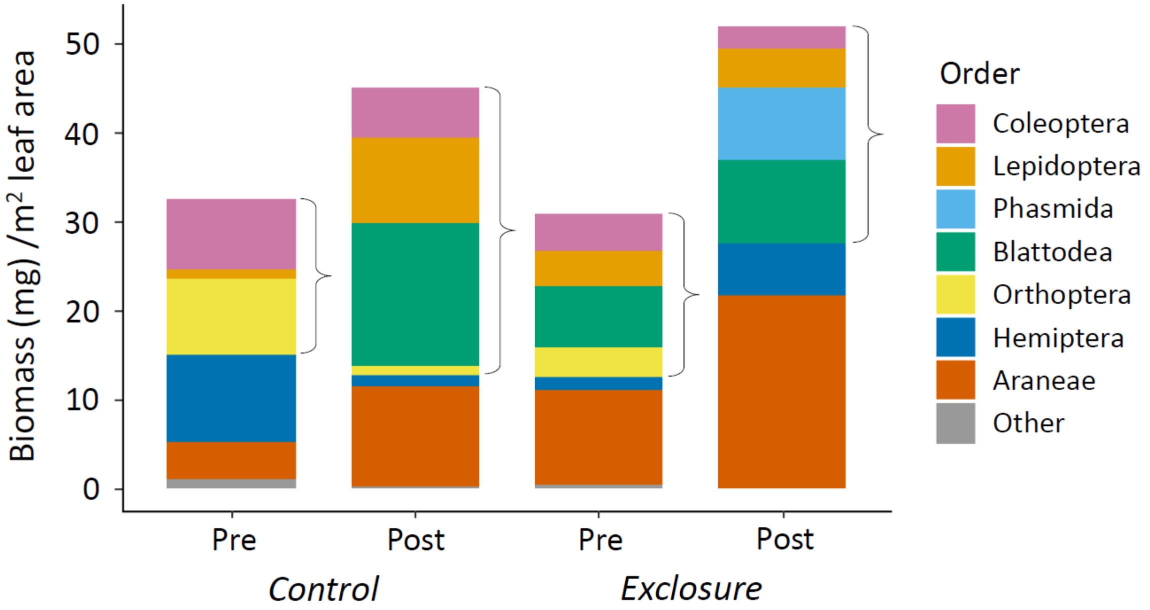

Figure 3.3. Arthropod biomass by order on *T. amazonia* before (Pre) and after (Post) the exclosure experiment. Four individual arthropods with mass greater than 90 mg were regarded as outliers and removed from the data set. Brackets denote folivorous orders.

Examining count data, there is also a lack of evidence that exclosures affected the arthropod community (Table 3.4; Fig. 3.4). Changes in census counts for individual orders were largely parallel between control and exclosure branches. For example, the increases in Blattodea and spiders on exclosure branches were similar to increases observed on control branches, suggesting dynamic populations of these taxa but not exclosure effects (Table 3.4; Fig. 3.4).

Taxon	Ctr-Pre	Ctr-Post	Δ Ctr	Exc-Pre	Exc-Post	Δ Exc
Coleoptera	1.97	1.51	-0.46	1.70	1.05	-0.65
Lepidoptera	0.66	0.60	-0.05	0.46	0.60	0.14
Phasmida	0.00	0.00	0.00	0.00	0.30	0.30
Blattodea	0.16	1.96	1.80	0.62	2.25	1.63
Orthoptera	0.49	0.15	-0.34	0.15	0.15	0.00
Hemiptera	2.46	0.76	-1.70	1.08	2.40	1.31
Araneae	2.46	6.34	3.88	4.80	8.10	3.30
Other	2.30	0.76	-1.54	1.55	0.60	-0.95
Folivorous	3.28	4.23	0.95	2.94	4.35	1.41
All Arthropods	10.49	12.08	1.59	10.38	15.44	5.07

Table 3.4. Census counts of arthropod orders (individuals per m^2 leaf area) during pre- and post-experiment surveys on control (Ctr) and exclosure (Exc) branches of *T. amazonia*. "Folivorous" is the total of Coleoptera, Lepidoptera, Phasmida, Blattodea, and Orthoptera. Δ Ctr and Δ Exc are the differences between pre- and post-experiment surveys within treatment group.

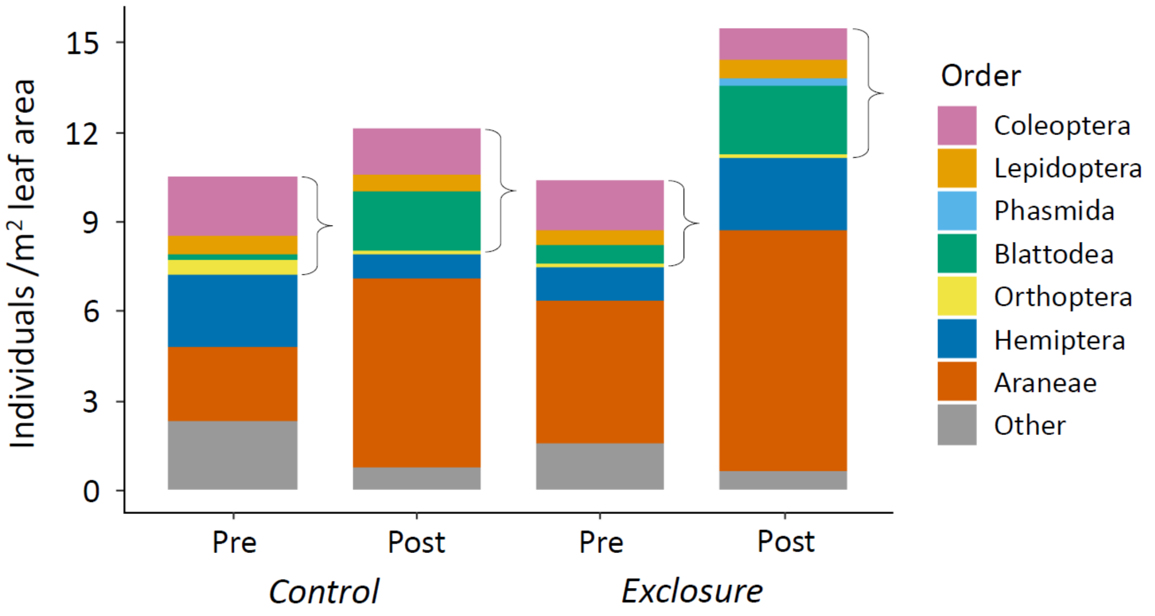

Figure 3.4. Census counts of arthropod orders on *T. amazonia* before (Pre) and after (Post) the exclosure experiment. Brackets denote folivorous orders.

Examining the distribution of body sizes for *O. pyramidale*, we found that individuals with small body size (square root of biomass (mg) < 2) increased for both control and exclosure groups between survey periods, indicating a temporal effect unrelated to our experimental treatments (Fig. 3.5). For arthropods with larger body sizes (square root of biomass (mg) > 1.5), exclosure branches showed clearly increased numbers in the post-experiment period while control branches demonstrated only a weak positive trend (Fig. 3.5).

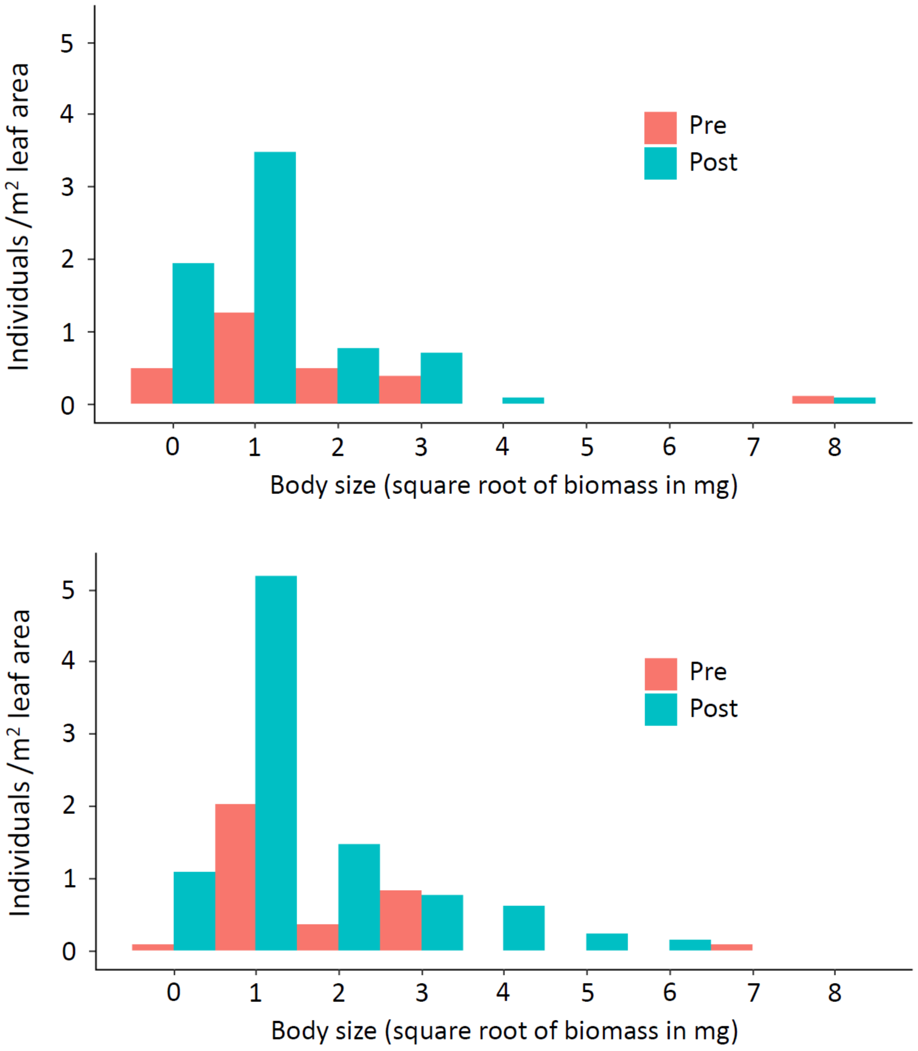

Figure 3.5. Distribution of arthropod sizes on *O. pyramidale* for control branches (top panel) and exclosure branches (bottom panel) before (Pre) and after (Post) the exclosure experiment. Two individual arthropods with mass greater than 90 mg were regarded as outliers and removed from the data set. Bins are centered on whole numbers (e.g. bin 2 includes values from 1.5 to < 2.5). The x-axis is on the square root scale.

Like *O. pyramidale*, distributions of body sizes on *T. amazonia* (Fig. 3.6) also showed slight increases in the number of small-bodied individuals in post-experiment surveys for both treatment groups. Unlike *O. pyramidale*, there was not a clear signal of exclosure effects on the number of larger-bodied individuals as neither treatment group demonstrated substantial changes in numbers between survey periods (Fig. 3.6).

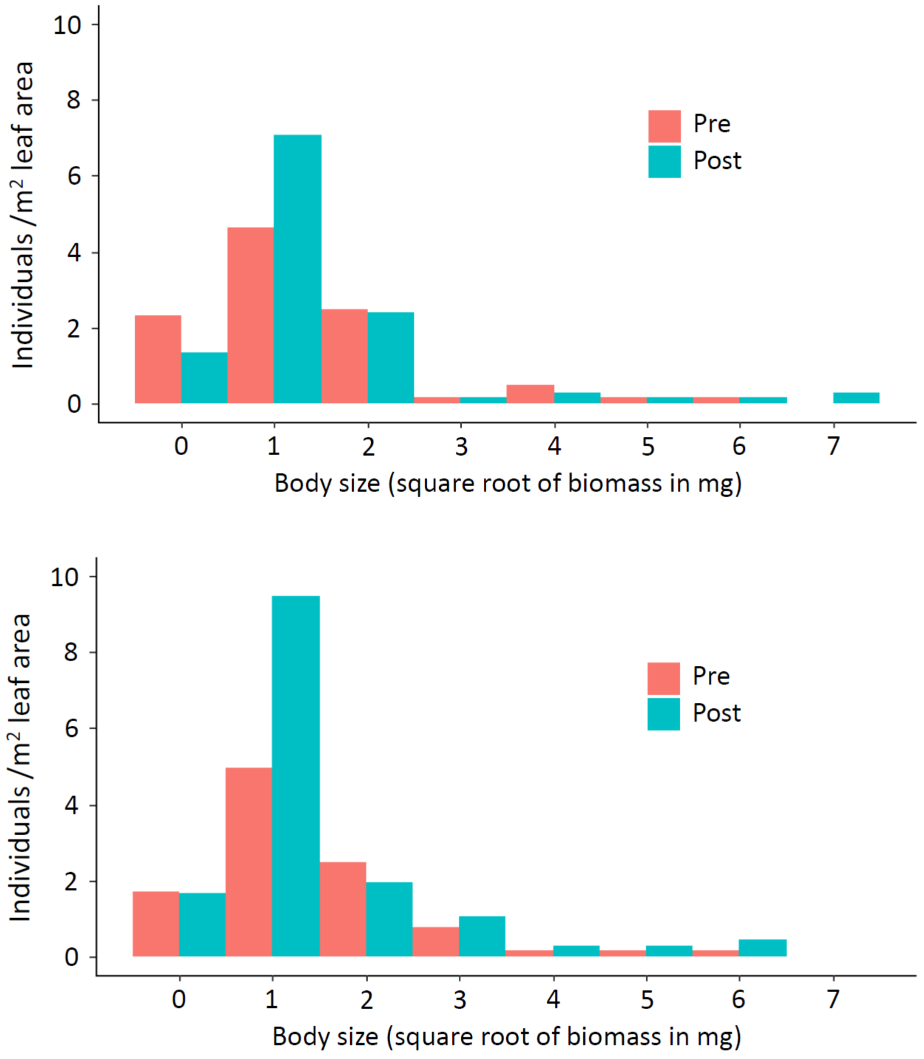

Figure 3.6. Distribution of arthropod sizes on *T. amazonia* for control branches (top panel) and exclosure branches (bottom panel) before (Pre) and after (Post) the exclosure experiment. Four individual arthropods with mass greater than 90 mg were regarded as outliers and removed from the data set. Bins are centered on whole numbers (e.g. bin 2 includes values from 1.5 to < 2.5). The x-axis is on the square root scale.

DISCUSSION

Predation by birds/bats appeared to reduce biomass for each of five folivorous insect orders (Blattodea, Coleoptera, Lepidoptera, Phasmida, Orthoptera) on *O. pyramidale*, the tree species where we detected a trophic cascade. Birds and bats also reduced number of individuals for four of the five orders (the positive change in Coleoptera on exclosure branches was not more than observed on control branches). Others have also suggested these taxa are regular prey items of tropical birds and bats (Greenberg 1995; Kalka and Kalko 2006) and exclosure studies have found these taxa are likely to be affected by bird/bat predation (Van Bael et al. 2003; Morrison and Lindell 2012; Maas et al. 2013). These patterns were noticeably weaker or absent on *T. amazonia*, where no trophic cascade was present. Possible reasons for differences in bird/bat effects between tree species are discussed in Chapter 2 of this dissertation. A study in the broader ASP landscape found a positive correlation between insectivorous bird abundance and attack rates by birds on artificial caterpillars (Roels et al. 2018). Out of six land cover types studied, attack rates in the native species plantation were second-lowest (Roels et al. 2018). This suggests the magnitude and pervasiveness of vertebrate predator effects on arboreal folivorous insects in central Panama may generally be higher than what we observed in this study, in a context with low bird abundance.

Phloem-feeding (also called sap-sucking) herbivores (Hemiptera) were one of the more common herbivorous taxa on both tree species but assessing their effect on plants is difficult since they do not leave obvious damage. Leigh (1999) speculated that, given their abundance and metabolisms, phloem-feeders in tropical forests may actually remove more plant biomass than chewing insects. Other authors agree that the functional significance of phloem-feeders has been overlooked (Coley and Barone 1996). In a temperate forest, presence of birds had a significant, but weaker, negative effect on phloem-feeders than on folivorous insects (Bridgeland et al. 2010). In our study, phloem-feeders did not appear to increase in bird/bat absence, matching prior results from central Panama (Van Bael et al. 2003). High biomass and counts of Hemiptera on *O. pyramidale* relative to folivorous orders may be related to the life history strategy of the tree. Schowalter (1994) proposed that higher abundances of phloem-feeders and lower abundances of chewing insects may be a characteristic of disturbed areas in tropical forests. *Ochroma pyramidale* is regarded as a short-lived pioneer species that specializes on disturbed areas. However, it is unclear if the association between phloem-feeders and disturbance is a function of abiotic conditions in disturbed areas or characteristics of host plants that colonize such areas (Schowalter 1994).

Like folivorous insect orders, spiders demonstrated positive exclosure effects on *O. pyramidale* (increased biomass and numbers relative to changes on control) while exclosure effects on *T. amazonia* were equivocal (slightly greater change in biomass but smaller change in numbers than control). Intraguild predation of intermediate predators, especially spiders, by birds/bats has been cited as a mechanism that potentially negates top-down trophic cascades on herbivorous insects (Mooney et al. 2010; Karp and Daily 2014; Bosc et al. 2018). Our finding that bird/bat predation on spiders was associated with reductions in both folivorous insects and herbivory aligns with the general conclusions of Mooney et al. (2010), who found that high rates of vertebrate insectivore predation on predatory arthropods were positively correlated with vertebrate insectivore predation on herbivorous arthropods. Thus, intraguild predation did not dampen trophic cascade strength (Mooney et al. 2010). Unlike Bosc et al. (2018), we did not notice a decline in numbers of phloem-feeders on exclosure branches in response to an increase in intermediate predator numbers.

We did not census ants during our surveys but multiple species were regularly observed. A small portion of our selected trees, mostly *T. amazonia*, were colonized by a tree-nesting species (*Azteca* sp.) and dozens of individual ants could sometimes be observed on study branches. We are uncertain regarding the ecology of those ants, but ants in general are strong interactors in tropical food webs that can act as predators or tenders of herbivorous insects (Floren et al. 2002; Davidson et al. 2003; Philpott et al. 2004; Gras et al. 2016). Intermediate predators other than ants and spiders on our trees were uncommon, including Hymenoptera (Vespidae), Hemiptera (Reduviidae) and possibly a few Coleoptera (e.g., Lampyridae) and Neuroptera (Chrysopidae).

Authors that have suggested meaningful distinctions between ‘small’ and ‘large’ arthropods as prey items for birds have delineated body length categories at either 3 or 5 mm (Philpott et al. 2004; Jedlicka et al. 2006; Van Bael et al. 2007; Karp and Daily 2014). Dry biomass of 1–3 mg is approximately equivalent to a 5 mm body length, although there is wide variation by taxon due to differences in stereotypical body shape (e.g., long and thin for Phasmida) and water content (e.g., high in Lepidopteran larvae). In our study, exclosure effects on *O. pyramidale* were most evident on arthropods larger than 2.25 mg (square root > 1.5 on Fig. 3.5, lower panel), equivalent to individuals with body lengths longer than 5–11 mm, depending on order. Birds and bats likely select prey based on a number of characteristics, including body size, conspicuousness, nutritional content, and palatability, so it is unclear whether distinctions made using body length or biomass would be more relevant when seeking to characterize availability of preferred prey items. However, we find that using biomass > 2.25 mg as the mark of preferred insectivorous bird prey is functionally similar to using > 5 mm.

We concur with Saint-Germain et al. (2007) that studies focused on ecological function of arthropod feeding guilds or higher-level taxa like orders should consider using biomass values in addition to census counts. This approach is commonly taken by studies investigating general arthropod community structure in tropical forests (Basset 2001; Ellwood and Foster 2004; Dial et al. 2006). Presenting biomass per unit of leaf area accounts for arthropod size and would allow for more direct comparisons between trophic cascade studies occurring in locations with different mean arthropod sizes (e.g., temperate vs. tropical regions, dry vs. wet forests). Published allometric equations are available for spiders and most insect taxa but researchers should take care to use equations from latitudes and climates similar to their field site due to variation in coefficient values between ecosystems (Schoener 1980).

The extremely large (> 90 mg) arthropods we treated as biomass outliers were rare but may be functionally significant components of folivorous insect communities on the tree species studied. The ‘giants’ found during our surveys were in the orders Lepidoptera, Blattodea, and Orthoptera. One exceptional insect (Orthoptera: Proscopiidae) found on *O. pyramidale* had a body length of 70 mm. Its estimated mass was nearly equivalent to the combined mass of all other folivorous insects found on *O. pyramidale* exclosure branches during the post-experiment survey period. Two other individuals of this species were encountered on *O. pyramidale* during related field work, including one measuring 130 mm; it is possible this species is an important herbivore of *O. pyramidale*, despite low population density. Whether such ‘giants’ have reached a size sufficiently large to reduce predation likelihood is uncertain. Consumption by smaller species of insectivorous bird seems improbable but foliage-gleaning bats demonstrate a remarkable ability to consume very large prey items relative to their own body size (Kalka and Kalko 2006). Studies seeking to accurately quantify effects of ecological experiments on arthropod biomass in tropical regions should expect to be challenged by the presence of extremely large, but rare, individuals.

Bird and bat effects are confounded in our study because we did not use diurnal and nocturnal exclosures, but kept exclosures in place continuously. Thus, patterns we report characterize the net effects of both predator groups. Prior studies have found mixed results regarding whether bird/bat effects on arthropod communities are additive or functionally distinct (Williams-Guillén et al. 2008; Morrison and Lindell 2012; Maas et al. 2013; Karp and Daily 2014). Our arthropod surveys occurred during the daytime hours, when temperatures are higher and humidity is lower. It is possible that some arthropod species present on our study trees take refuge from abiotic conditions and risk of bird predation during the day and are more active at night. Nocturnal sampling may have provided a different perspective on relative abundance of each arthropod order or on their contributions to overall arthropod biomass, especially for Blattodea and Orthoptera, which are often nocturnal (Novotny et al. 1999; Mass et al. 2013).

Precise mechanisms of bird/bat-driven trophic cascades are variable between ecosystems yet the beneficial relationship between vertebrate predators and trees has been revealed at a variety of latitudes on at least five continents. These cascades have been found in natural (Marquis and Whelan 1994; Van Bael et al. 2003; Bridgeland et al. 2010), agricultural (Van Bael et al. 2007;

Williams-Guillén et al. 2008; Maas et al. 2013) and restoration (Morrison and Lindell 2012, this study) ecosystems, demonstrating that conservation of bird and bat populations is a critical component of maintaining trophic relationships and ecological function.

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APPENDIX

APPENDIX

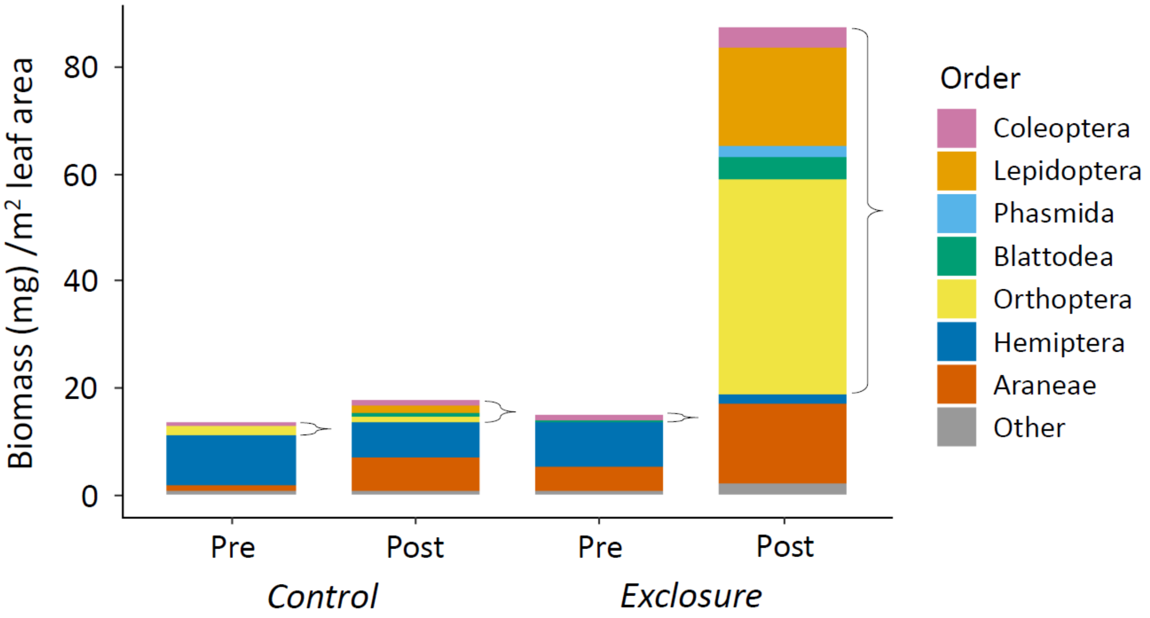

Figure 3.7. Arthropod biomass on *O. pyramidale* by order before (Pre) and after (Post) the exclosure experiment without arthropods >90 mg removed. Brackets denote folivorous orders.

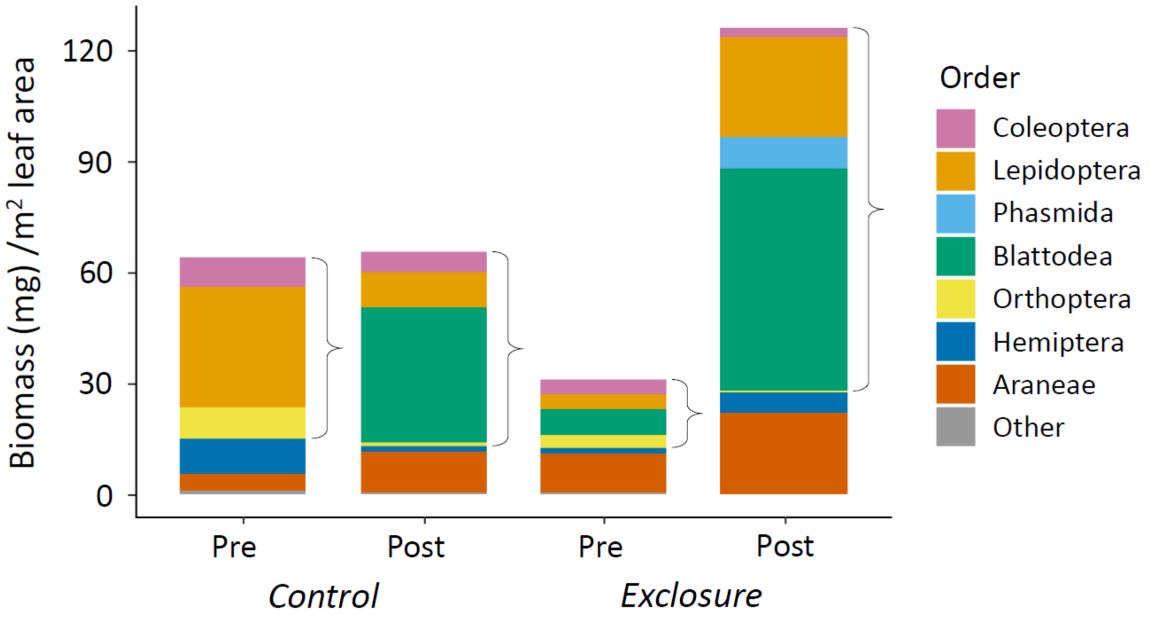

Figure 3.8. Arthropod biomass on *T. amazonia* by order before (Pre) and after (Post) the exclosure experiment without arthropods >90 mg removed. Brackets denote folivorous orders.

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CHAPTER 4:

Predation Pressure by Birds and Arthropods on Herbivorous Insects Affected by Tropical Forest Restoration Strategy

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ABSTRACT

Recovery of animal-dependent ecosystem functions is a key component of ecological restoration on degraded tropical forest lands. One of these functions, regulation of herbivorous insects by predators, shapes tropical communities through cascading trophic effects. An improved understanding of how predation pressure on herbivorous insects varies with reforestation strategy, management decisions, and landscape context would guide restoration practice. We measured predation pressure by birds and arthropods on dummy caterpillars in five forest types in Panama. These land covers represent natural and managed forest conditions: non-native monoculture plantation, native multi-species plantation, young natural forest succession, secondary gallery forest, and old-growth forest. We also placed dummy caterpillars in residential countryside, a heavily disturbed non-forest land cover. In three land covers, we surveyed bird communities to examine the relationship between predator abundance and predation pressure. Predation pressure from birds was lowest in the intensively managed plantations and highest in land covers with structurally complex vegetation: successional forest, gallery forest, and residential countryside. In the non-native plantation, bird predation increased with proximity to gallery forest. We found strong correspondence between bird abundance and bird attacks on dummy caterpillars. Arthropod predation pressure was highest in the native plantation but, unlike bird predation pressure, did not vary strongly by land cover. Our results suggest that ecosystem functions by insectivorous birds can be enhanced on reforestation lands by incorporating unmanaged areas and tolerating non-planted understory vegetation. We recommend that, regardless of management objectives, forest managers adopt a holistic approach to reforestation to facilitate recovery of animal-dependent ecosystem functions.

INTRODUCTION

The restoration of degraded tropical forest lands is essential to long-term maintenance of global biodiversity and potentially a significant contributor to global climate stabilization via carbon sequestration (Lamb et al. 2005; Chazdon 2008). Attempts at ecological restoration exist along a spectrum of escalating strategies from basic soil rehabilitation to re-creation of reference site species compositions (Ciccarese et al. 2012). In hyper-diverse tropical forest regions, full restoration of species composition is, at best, a long-term goal. Furthermore, the vast amount of land needing restoration requires scalable and cost-effective strategies. Several authors argue that plantations of one or a few tree species can initiate rapid restoration of key ecological functions, such as erosion control, nutrient retention, and carbon sequestration, while reducing forest resource extraction pressure on remaining native forests (Parrotta et al. 1997; Redondo-Brenes 2007; Paquette & Messier 2010). Multi-species native tree plantations are an intermediate step on the “forest restoration staircase” (Chazdon 2008: Fig. 1), with expected total ecological function greater than monoculture plantations of non-native trees, but lower than naturally regenerated secondary forests. Some empirical studies support this notion, demonstrating more animal biodiversity in native versus non-native plantations (Volpato et al. 2010) and greater plant biomass accumulation in plantation polycultures versus monocultures (Erskine et al. 2006; Kelty 2006; Potvin & Dutilleul 2009; Mayoral et al. 2017).

How tropical forest restoration strategy affects development of animal-dependent ecosystem functions is not well-studied. Animals drive important ecological functions in restorations like pollination, seed dispersal, and regulation of herbivorous insects (Lindell 2008). Herbivores and their predators shape tropical communities (Floren et al. 2002; Coley & Kursar 2014); herbivory can affect survival and growth of young tropical trees (Clark & Clark 1985; Plath et al. 2011; Riedel et al. 2013) and predators of herbivores can create top-down trophic cascades that benefit plants in tropical ecosystems (reviewed in Pace et al. 1999; Van Bael et al. 2008). While a number of studies have demonstrated the important ecological functions of insect-eating birds and bats in tropical agroforest ecosystems (reviewed by Maas et al. 2016), there has been little evaluation of predation pressure on herbivores in communities along the restoration staircase (Morrison & Lindell 2012). Plantation-style forest restorations are in many ways analogous to agroforest ecosystems like shade coffee and cacao; both feature reduced ecological complexity relative to natural forest and have specific management goals (e.g. crop or timber production).

For insectivorous birds and other ecologically important predator groups, such as bats and predatory arthropods, the degree of herbivorous insect regulation they provide depends on landscape context (Tscharntke et al. 2008; Maas et al. 2016). The simplified communities in tree plantations and other young restoration areas often provide insufficient habitat resources to independently support many forest wildlife species (Dunn 2004; Lindenmayer & Hobbs 2004). However, native forest patches and riparian corridors could act as sources of predation pressure to forest restoration areas via spillover of foraging activity by mobile predators. Previous studies in tropical agroforest ecosystems found predation by insectivorous birds increased with native forest proximity (Karp et al. 2013; Maas et al. 2015; Milligan et al. 2016).

We used model (dummy) caterpillars to compare predation pressure on herbivorous insects in a mosaic tropical landscape comprising non-native monoculture plantations, native multi-species plantations, young natural forest succession, secondary gallery forest, old-growth forest, and residential countryside. The first three land covers represent possible entry points on the restoration staircase, the next two represent potential longer-term restoration targets, and the last is of interest due to the persistence of high bird diversity in neotropical countryside habitats (Hughes et al. 2002). In the non-native and native plantations, we examined the effect of distance to natural forest on predation pressure.

Model caterpillars can record attacks by virtually any predator taxa, but are particularly effective at signaling predation pressure by birds and arthropods (Howe et al. 2009; Low et al. 2014). This method has been used to study latitudinal and elevational gradients in predation pressure (Sam et al. 2015a; Roslin et al. 2017), effects of forest age and fragmentation on predation pressure (Tvardikova & Novotny 2012), seasonal variation in predation pressure (Molleman et al. 2016), and predation pressure in tropical agroforest ecosystems (Howe et al. 2015; Maas et al. 2015; Milligan et al. 2016). Few studies to date have used model caterpillars to compare predation pressure across many tropical land cover types (Posa et al. 2007; Tvardikova & Novotny 2012) or between different forest restoration strategies (Solis-Gabriel et al. 2017).

We anticipated the rank order of caterpillar attack frequency for four of our land covers would correspond to that land cover's position on the restoration staircase. Specifically, we expected attack rates to increase in the following order: non-native monoculture plantation < native multi-species plantation < young natural forest succession < secondary gallery forest. This expectation was based on our observations of plant diversity and structure. Prior studies of predation pressure on insect herbivores found that higher plant diversity and structural heterogeneity are correlated with increased attacks on real and artificial sentinel caterpillars (Perfecto et al. 2004; Poch &

Simonetti 2013; Bereczki et al. 2014). In both plantation types, we expected attack frequency would increase with proximity to forest due to a predator spillover effect.

We left out two land covers, old-growth forest and residential countryside, from our prediction. How old-growth forest would rank relative to plantations and less mature forests was difficult to predict; diversity and heterogeneity in this land cover are high but trophic activity (by both herbivores and predators) is concentrated in the canopy. We only measured predation pressure in the understory, where predation pressure may be lower than in the canopy (Loiselle & Farji-Brener 2002; Van Bael & Brawn 2005). Studies in tropical forest understory have produced a wide range of predation pressure estimates (Loiselle & Farji-Brener 2002; Koh & Menge 2006; Richards & Coley 2007; Posa et al. 2007; Tvardikova & Novotny 2012). Whether this variability is due to methodological differences or real variation in ecosystem function is unclear.

The countryside in our study is not, even in the broadest sense, a “forest” and cannot be placed on the forest restoration staircase. We included it as an example of a heavily modified land cover that nonetheless features high plant diversity and structural heterogeneity. Posa et al. (2007) found a trend of increasing attacks on model caterpillars along a disturbance gradient from tropical forest to countryside and attributed this trend to increased bird abundance. Similarly, we anticipated a relatively high attack frequency in countryside because we previously observed a conspicuous abundance of birds in countryside, in contrast to a paucity of birds in plantations.

To investigate this potential mechanism underlying variation in caterpillar attack rates we conducted bird surveys in non-native plantation, native plantation, and residential countryside.

We hypothesized caterpillar attacks by birds would be positively related to local abundance of insect-eating birds. Positive relationships between insectivorous bird abundance and predation pressure on herbivorous insects have been documented in tropical agroforest and managed temperate forest (Perfecto et al. 2004; Bereczki et al. 2014; Maas et al. 2015).

Finally, we tested the effect of model posture on attack rate. While not explicitly stated in many published model caterpillar studies, some researchers deployed models that are straight-bodied (e.g. Howe et al. 2009; Tvardikova & Novotny 2012), while others deployed models with a humped posture (e.g. Bereczki et al. 2014; Low et al. 2016; Roslin et al. 2017). The latter posture mimics Lepidopteran larvae commonly called “inchworms” or “loopers” (Families: Geometridae and Noctuidae). Whether this methodological difference is significant has not been explored. We predicted models with a humped posture would be attacked more than straight-bodied models as they may be more conspicuous to birds and other visually-oriented predators.

METHODS

Study site

We conducted our study in and near the Agua Salud Project (ASP), Colón Province, Panamá (9°12’52” N, 79°43’25” W, elevation: 200–300 m a.s.l., Appendix, Fig. 4.5). The ASP contains many land covers including plantations, secondary forests at various ages, and old-growth forest fragments. The plantations and youngest secondary forest (successional) areas represent active and passive experimental approaches to restoring ecological function and ecosystem services on degraded land (STRI, 2017). Plantation areas are former pasture cleared of woody vegetation prior to tree planting in 2008. Non-planted understory growth is cleared approximately quarterly.

Successional forest areas are also former pasture but have been unmanaged since initial clearing in 2008. The ASP is embedded in a countryside landscape matrix containing the aforementioned land covers as well as active pasture, recently abandoned agricultural land, and the heavily forested Soberanía National Park (Figs. 4.2 and 4.3).

Experimental land covers

We placed caterpillars in six land covers: non-native monoculture plantation, native multi-species plantation, successional forest, secondary gallery forest (width ranging 20–120 m), old-growth forest, and residential countryside (Appendix, Figs. 4.6 and 4.7). The first five land covers were present within the ASP. The non-native plantation was teak (*Tectona grandis*: Lamiaceae). Native plantation areas were patchworks of experimental plots (45 x 39 m) with planting treatments ranging from 1 to 6 tree species (full description in Mayoral et al. 2017). The countryside was a typical rural neighborhood in the town of Giral, approximately 6 km from the ASP, and featured a mix of lawns, gardens, hedgerows, pastures, and small secondary forest fragments. The non-native plantation included two distance-to-forest treatments: near gallery forest and far from gallery forest. The native plantation included three distance-to-forest treatments: near gallery forest, far from gallery forest, and at the boundary of Soberanía National Park. Caterpillars placed near forest edges (either gallery or park) were 0–10 m from the plantation–forest interface while caterpillars placed far from forest were 60–105 m away from the interface. In each plantation type, the far-from-forest treatment reflected the maximum distance from forest that could be achieved within the ASP. This range of distance from forest was previously found to be meaningful for variation in predator pressure in coffee (Milligan et al. 2016). Our prior observations of birds at the ASP suggested bird activity decreased rapidly over this distance.

Caterpillar construction

We constructed dummy caterpillars from non-toxic, oven-bake modeling clay, which does not melt or dry out at ambient temperatures (Sculpey III, Polyform Products Company, Elk Grove Village, IL, USA). We chose a medium green color ("String Bean") to simulate a generalist species lacking significant anti-predator defenses, a common modeling strategy (Low et al. 2014; Roslin et al. 2017). We manufactured uniform caterpillar models (hereafter "caterpillars") with consistent diameter and smooth surface by extruding clay through a modified potato ricer (Metaltex SA; Genestrerio, Switzerland). Strands of extruded clay were cut into sections and the ends were rounded by hand. The resultant caterpillars were 4 x 25 mm. We hand-shaped clay balls of equivalent volume (diameter = 8.43 mm) for use as experimental controls to test the possibility that some property of the clay itself (rather than the caterpillar-like shape) attracted predators (Tvardikova & Novotny 2012). We wore surgical gloves during caterpillar construction and placement to limit imparting human scents to the clay which might influence predators driven by chemical cues (recommended by Sam et al. 2015b).

Following Low et al. (2014), we threaded thin wire (26 Ga brown floral wire) length-wise through the caterpillars to facilitate attachment, wrapping the wire ends around vegetation to secure the caterpillar. To make the inchworm posture, we bent the clay and interior wire, creating a hump in the center of the caterpillar (Fig. 4.1).

Figure 4.1. Caterpillar models wired onto branch tips. Left: A model in the standard posture. Note the real caterpillar to the left of the model. Center: A control clay ball. Right: A model in the inchworm posture.

Concurrent observations of the real caterpillar community at the ASP revealed a diverse assemblage of species, including many Geometrids. Although we did not design our caterpillars to mimic a particular species, we did encounter real Lepidopteran larvae that closely matched the size and color of our caterpillars.

Caterpillar placement criteria

In each land cover, caterpillars were placed on trees at least 3 m apart with a single caterpillar or a control clay ball per tree. In multi-species native plantation areas, we placed caterpillars on a single species, *Terminalia amazonia*, which was the fastest growing of the principle native species planted (Mayoral et al. 2017). The non-native plantation was a monoculture, so caterpillars were only placed in teak. In other land covers, plant diversity was much higher and there were no focal tree species for caterpillar placement. In the residential countryside, we placed caterpillars in roadside hedgerows and live fences. We placed each caterpillar at a height of 1.5–3.0 m, generally on a twig near the branch tip. In teak however, branch architecture made twig placement impractical so we placed caterpillars on the central vein of a terminal leaf, with the wire threaded through the leaf and secured on the underside. All branches were chosen so that caterpillars were not obscured by overhanging vegetation and had at least 1 m of open space above the placement location. We alternated straight-bodied and inchworm postures and placed clay ball controls every tenth location. We marked caterpillar locations with flagging tape tied to ground stakes or near-ground vegetation directly below the branch. This approach facilitated recovery while limiting the risk that flagging would obstruct or influence predator behavior.

Exposure season, exposure duration, and model recovery

We conducted our study during July 2016, mid-wet season in central Panama. Data from an earlier pilot study in the native species plantation was used to determine an appropriate exposure duration. We used an exponential decay function assuming a constant daily predation rate to calculate an expected caterpillar half-life of approximately 10 days. Planning for half of the caterpillar population to be attacked balances study efficiency (length) with power to distinguish between attack probabilities of different treatment groups; studies with exposure periods that are too long lose power as treatment groups asymptotically converge toward 100% of caterpillars attacked. Caterpillars in most land covers remained in place for 10 days before recovery and damage assessment. Due to unanticipated logistical challenges and wet weather, exposure duration for caterpillars in the residential countryside was shorter than planned; countryside caterpillars were exposed for either 5 or 8 days. Two observers (S. Roels and J. Porter) worked together to recover caterpillars. Each observer independently assessed whether the caterpillar was attacked and used damage patterns to assign attacks to predator class. Observers prepared by reviewing predator attack reference photos in Low et al. (2014) and followed their recommendation that predator classes be taxonomically broad. Based on prior clay caterpillar studies in the tropics, we anticipated predator classes would include birds, mammals, lizards, and arthropods, but did not a priori limit interpretation of damage to those categories. Assignment of damage to multiple predator classes on the same caterpillar was allowed. Photographs were taken to serve as a permanent record of any caterpillar regarded as attacked by either observer.

Bird surveys

In June–July 2016, S. Roels conducted 10-minute point counts of birds in the non-native plantation, native plantation, and residential countryside. In each land cover, survey points were located a minimum of 85 m apart (mean distance to nearest neighboring point = 113 m, max = 177 m) and spatially overlapped with caterpillar placement areas. During each survey, all birds detected by sight or sound within a 25 m radius were recorded. Birds flying through or over the count circle were not counted. In the native plantation, 15 points were surveyed four times each between 0630–0900 hrs. In the non-native plantation, 9 points were surveyed two times each between 0700–1100 hrs. In countryside, 12 points were surveyed two times each between 1600–1720 hrs. The number of sampling points in each land cover was the most points feasible given the total area of each cover type, land cover configuration, and minimum inter-point distance. Doves (Family: Columbidae) and hummingbirds (Family: Trochilidae) were removed from the data set as they are highly unlikely to attack a caterpillar. All other species we detected are capable of eating caterpillar-sized insects, although insects may not be a primary component of their diet (Stiles & Skutch 1989). Birds not identified to species were left in the data set as they were unlikely to be doves or hummingbirds.

Statistical analyses

All statistical tests were performed in R v3.3.3 (R Core Team, 2017). We assessed our ability to consistently assign attacks to predator class with a metric of the interrater reliability, Krippendorff's alpha (function "kripp.alpha" in package "irr", Gamer et al. 2012). This metric, ranging from 0 to 1, evaluates the ability of independent observers of subjective phenomena to consistently code observations and accounts for observer agreement simply due to chance (Krippendorff 2004).

We examined the effects of model shape, posture, land cover, proximity to forest, and on caterpillar attacks using generalized linear models with a binomial distribution and Tukey a posteriori tests for pairwise contrasts between land covers (function "glht" in package "multcomp", Hothorn et al. 2008). An exception to this method was made for tests of bird attacks involving the non-native plantation far-from-forest treatment. No bird ever attacked a caterpillar in this treatment and having a zero count in binomial logistic regression models inflates standard error estimates. As an alternative, we used Barnard's Unconditional Test, which can accommodate zero counts and has more statistical power than the traditional Fisher's exact test (Barnard 1945; function "barnard.test" in package "Barnard", Erguler 2016).

Although caterpillars in residential countryside had shorter exposure periods, we used unadjusted countryside attack data in our statistical model as a conservative approach to examining differences between land covers. However, for visualization of the data, we present daily attack rates, calculated with an exponential decay function ($N(t) = N_0 * e^{-\lambda t}$, where N = caterpillars placed, t = number of days exposed, and λ = daily attack rate); this approach accounts for differences in exposure time. In some land covers, but not others, there were multiple caterpillar placement areas because suitable patches of vegetation varied in size; caterpillars within each land cover are pooled for analysis (see Table 4.1 for sample sizes by land cover and Figs. 4.2 and 4.3 for a map of caterpillar placement areas).

Model	Caterpillars	Control
Non-native Plantation		
- Near gallery forest	55	7
- Far from gallery forest	53	6
Native Plantation		
- Near gallery forest	88	10
- Far from gallery forest	88	9
- Near national park	91	9
Successional Forest	108	11
Gallery Forest	106	12
Old-growth Forest	108	12
Residential Countryside (8 days)	34	3
Residential Countryside (5 days)	35	3

Table 4.1. Caterpillars and controls recovered by land cover and distance-to-forest treatment.

To compare insect-eating bird abundance in the two plantations and countryside we calculated mean birds counted for each point and used a Kruskal-Wallis test with Tukey a posteriori tests for pairwise contrasts (function “posthoc.kruskal.nemenyi.test” in package “PMCMR”, Pohlert 2014). We believe detectability of birds was high and similar in each land cover surveyed, all are fairly open habitats with good sightlines and our survey radius was short, so we used raw count data in statistical analyses of bird abundance. We used $\alpha = 0.05$ for all hypothesis testing.

RESULTS

Caterpillars exposed, recovered, and attacked

We exposed a total of 863 caterpillars and spherical controls and recovered 98.3% (n=848; caterpillar n=766; control ball n=82). Of those unrecovered, four were cases where the clay had been stripped from the wire, indicating a likely attack, and two were crushed by a falling tree. Other unrecovered caterpillars may have been due to lost flagging or, in residential countryside, human tampering. Unrecovered caterpillars were not included in analyses. Overall attacks on caterpillars and controls were 43.6% (334/766) and 43.9% (36/82), respectively (Fig. 4.2). We categorized attacks into four classes: arthropods, birds, mammals, and lizards. Attacks by the latter two groups were rare (7/766 caterpillars, 0/82 controls) so we did not analyze those data in depth.

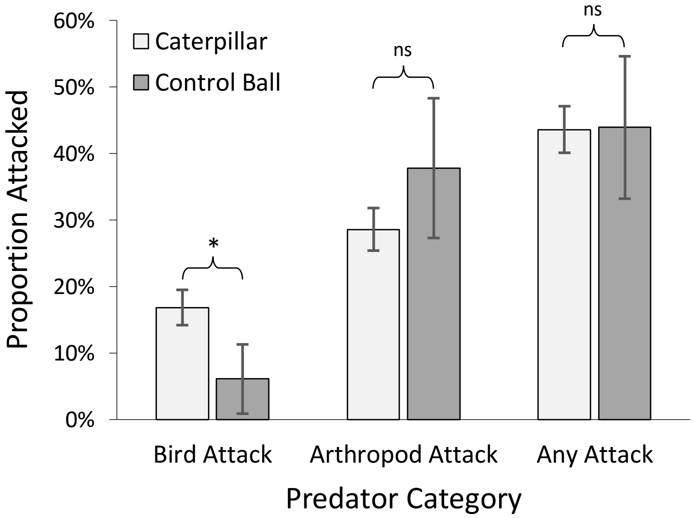

Figure 4.2. Attacks on models by shape (caterpillar vs. control ball) and predator class. Attacks by predators other than birds and arthropods were rare and are not depicted separately. Error bars depict ± 95% CI. Statistically significance differences (p<0.05) denoted by *.

Reliability of observers

The two independent observers agreed on caterpillar and control status (attacked or not) 94.5% (801/848) of the time. When both observers agreed that a caterpillar or control was attacked, they also agreed on attacker identity 92.1% (314/341) of the time. In 44.4% (12/27) of disagreements regarding attacker identity, the disagreement was only partial in that both observers agreed on one predator class but one observer believed an additional predator class attacked the caterpillar. Interrater reliability was high (Krippendorff's alpha = 0.887, 0.830, and 0.890 for observer concordance of attack status, arthropod assignment, and bird assignment, respectively); values of alpha above 0.80 are regarded as indicative of reliable scoring systems (Krippendorff 2004). For simplicity, subsequent results presented are based on attack data from S. Roels only.

Effect of shape and posture on attack probability

Birds were significantly more likely to attack caterpillars than controls (change in log odds = 1.14 ± 0.472 SE, $z = 2.41$, $p = 0.0158$) while arthropods showed a non-significant tendency to attack controls more often (Fig. 4.2; Appendix, Table 4.2). There was no significant difference in attack probability by posture for either arthropods or birds (Appendix, Table 4.2) so we lumped postures together in subsequent analyses.

Land cover and attack probability

We detected differences in bird and arthropod attack rates by land cover type (Fig. 4.3). Daily attack rates for birds were more variable by land cover (range: 0% to 5.90%) than for arthropods (range: 2.07% to 4.94%). There was little correspondence between bird and arthropod attack rates; the highest bird rate was in residential countryside, which had a moderate arthropod rate, and the highest arthropod rates were in native plantation treatments, which had low bird rates.

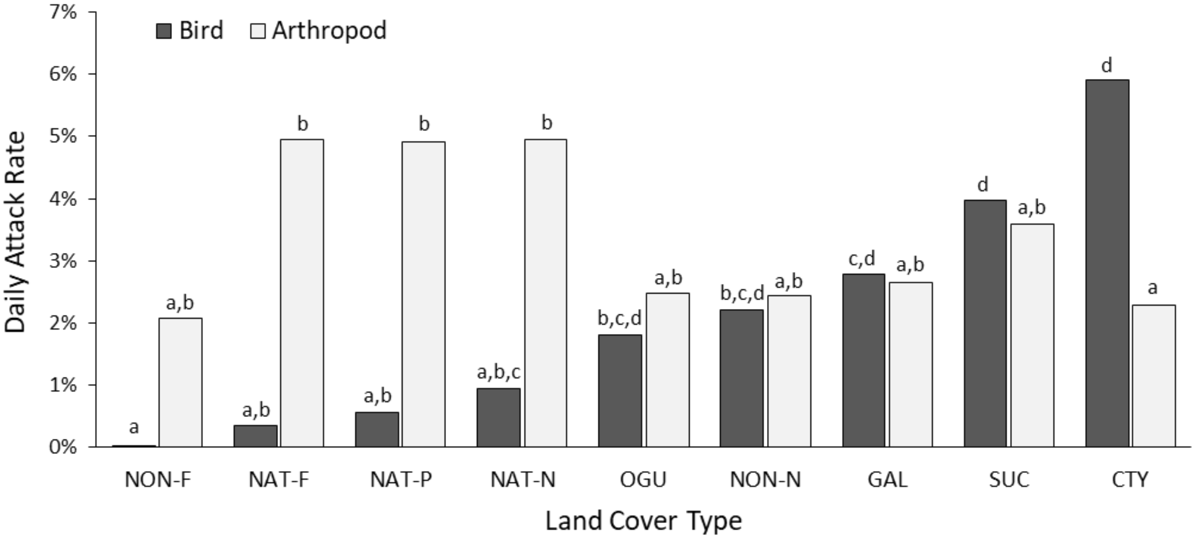

Figure 4.3. Daily attack rates by bird and arthropods on model caterpillars vary by land cover. Attack rates were calculated from multi-day exposure periods of model caterpillars using an exponential decay formula. All exposure periods were 10 days except for residential countryside where exposure was 8 or 5 days. For countryside, we present the mean of attack rates calculated independently for the two exposure lengths. Land covers are ordered from lowest to highest daily bird attack rate. Statistically significant differences by land cover within predator group are denoted by shared letters. Land covers are non-native plantation (NON), native plantation (NAT), old-growth understory (OGU), secondary gallery forest (GAL), successional forest (SUC), and residential countryside (CTY). Caterpillars in plantations were placed far from gallery forest (-F), near gallery forest (-N), or near national park forest (-P).

Evidence for spillover predation

Attacks by birds in non-native plantation near gallery forest were significantly more common than far from forest (Barnard’s Unconditional Test, Score = -3.435, two-sided nuisance parameter = 0.5, $p < 0.001$). In native plantation there were no significant differences in bird attacks between distance-to-forest treatments (Appendix, Table 4.3). Arthropod attacks did not differ by distance-to-forest treatment in either plantation type (Appendix, Table 4.3).

Bird surveys

In 101 avian point counts of non-native plantation, native plantation, and residential countryside, we detected 283 insect-eating birds of 48 species. The abundance of insect-eating birds was significantly different between land covers (mean birds/point ± 1 SE; non-native plantation = 0.722 ± 0.426, native plantation = 1.18 ± 0.141, countryside = 8.46 ± 0.811; Kruskal-Wallis test: $\chi^2 = 26.13$, df = 2, $p < 0.001$; Fig. 4.4).

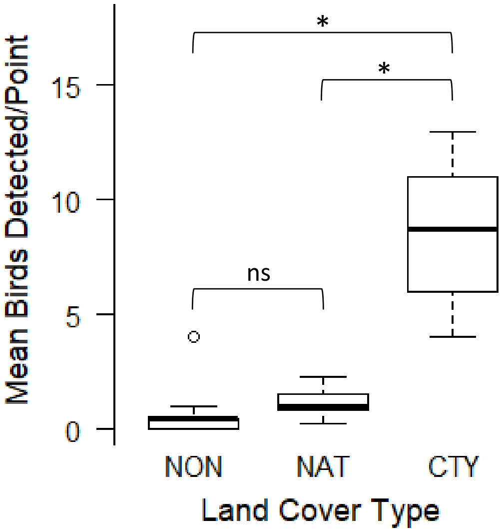

Figure 4.4. Insect-eating bird abundance in three land covers. Plots depict minimum, first quartile, median, third quartile, and maximum values. Outliers determined with 1.5 x interquartile range. Statistically significance differences ($p<0.05$) denoted by *. Land covers are non-native plantation (NON), native plantation (NAT), and residential countryside (CTY).

Countryside had more birds than either plantation type while the plantations did not significantly differ from each other (Tukey comparisons: non-native–native, p = 0.22; non-native–countryside, $p<0.001$; native–countryside, $p<0.001$). Although survey effort was unequal between land covers, we have strong evidence that species richness was greatest in countryside (41 species recorded in 24 point counts), intermediate in native plantation (21 species in 60 counts), and lowest in non-native plantation (4 species in 17 counts).

DISCUSSION

We predicted predation pressure in the restoration land covers would follow the restoration staircase conceptual model (non-native monoculture plantation < native multi-species plantation < young natural forest succession < secondary gallery forest). For birds, we found more predation pressure in the successional and gallery forest than in either plantation, but did not find an increase in predation pressure moving from non-native to native plantations. For arthropods, a "step up" in ecological function did occur between non-native and native plantations, but predation pressure in successional and gallery forest was intermediate to the two plantation types.

Although another dummy caterpillar study concluded that arthropods are the primary driver of predation pressure in the tropics (Roslin et al. 2017), we found caterpillars had higher rates of attacks by birds than arthropods in successional forest, gallery forest, and residential countryside. Predation pressure from birds was highest and reached its largest share of total attacks in countryside, similar to the findings of Posa et al. (2007). Two other dummy caterpillar studies in forest regions found greater attacks from birds associated with disturbance in the form of fragmentation (temperate forest, González-Gómez et al. 2006; tropical forest, Tvardikova & Novotny 2012). Like our study, González-Gómez et al. (2006) associated increased bird attacks in fragments with increased birds present. However, unlike our study, those authors found more birds and attacks by birds in plantations than in native forest. The manner in which birds and bird-associated ecological functions respond to disturbance in forested landscapes warrants further investigation.

Predation pressure from arthropods was highest and reached its largest share of total attacks in native plantation. We noticed a particularly high density of ants on *Terminalia amazonia* in native plantation which may have contributed to this finding. Whether intraguild predation (birds eating predatory arthropods) is responsible for any part of the somewhat inverse relationships between bird and arthropod attack rates is beyond the scope of our study. However, we note that both bird and arthropod attack rates were high in successional forest, suggesting that birds and arthropods can simultaneously make strong contributions to ecological function.

Daily attack rates by birds strongly corresponded to insect-eating bird abundance in non-native and native plantations and residential countryside. In countryside, where bird attack rates were highest, bird detections were approximately twelve times greater than in non-native plantation and seven times greater than in native plantation. On a daily basis, caterpillars were over five times more likely to be attacked by birds in countryside than in either plantation type. The relative abundance estimates we obtained in residential countryside (8.46 birds/point) and non-native plantation (0.72 birds/point) are comparable to those obtained in a previous study in central Panama using a similar point count methodology (Petit et al. 1999; residential areas, ~6.7 non-migratory birds/point; non-native plantation, ~0.3 non-migratory birds/point). Although we did not conduct bird surveys in gallery forest or old-growth forest, the abundance estimates for those habitats given by Petit et al. (1999) align with the intermediate predation pressure from birds we observed in those habitats (gallery forest, ~3.1 non-migratory birds/point; old-growth forest, ~2.8 non-migratory birds/point). Like studies in tropical agroforest ecosystems, we found evidence that proximity to natural habitat can increase predation by birds (Karp et al. 2013; Maas et al. 2015; Milligan et al. 2016); bird attack rates in plantations were low, but higher nearby natural forest.

Implications for ecosystem management and restoration

Some restoration ecologists have criticized tree plantations as “green deserts” that provide few resources for native wildlife (Janzen 1986; see discussion in Bremer & Farley 2010). Indeed, we found very low bird abundances in ASP plantations and bird ecological function, as measured by caterpillar attacks, was correspondingly low. We posit the paucity of birds in the plantations was due to the management regime of quarterly clearing, which suppressed understory vegetation. Prior studies recording high bird species richness or abundance in tree plantations documented structurally complex understory vegetation (e.g. Diaz et al. 1998; Poch & Simonetti 2013). Our experience has been similar; in another native species plantation in central Panama (Mamoní Valley, Panamá Province) we detected nearly three times more birds per survey point as in the ASP native plantation (Roels & Lindell unpublished data). The Mamoní Valley site was of similar age and tree species richness to the ASP native plantation but management of non-planted vegetation was much less aggressive and the site featured unmanaged buffer strips between plantation blocks. Tolerance of non-planted vegetation and buffer strips are recommendations made by Lamb (1998) and Hartley (2002) as ways to enhance plantation biodiversity.

Our results suggest that plantations interspersed with bird-friendly features such as unmanaged successional areas or dense hedgerows could facilitate plantation use by birds and enhance the ecological function of herbivorous insect consumption. Other authors have previously noted the significance of hedgerows to ecological functioning in fragmented tropical landscapes (Harvey et al. 2005; Zahawi 2005; Pulido-Santacruz & Renjifo 2011). Given that predation pressure by birds declined noticeably in tree plantations over a distance of 60–105 m from gallery forest, such habitat features should be spaced at relatively small intervals. One promising observation is that the total land area that would need to be dedicated to such features may be small; the riparian corridors in our study that enhanced predation pressure in adjacent plantation trees were as narrow as 20 m and the countryside hedgerows that demonstrated the highest bird attack rates were as narrow as a single row of trees. High predation pressure in countryside suggests that bird-driven ecological functions can be compatible with high levels of human activity. Other authors have commented upon the high abundance and species richness of birds in the neotropical countryside, likely due to high land cover heterogeneity favorable to habitat generalists (Harvey et al. 2005; Pulido-Santacruz & Renjifo 2011).

Methodological considerations

Our interrater reliability results provide a high level of confidence that we consistently assessed attack status and assigned damage patterns to predator classes. This suggests trained observers can operate independently, allowing for increased study sample sizes or efficiency. Birds, a group of visually-oriented predators, responded as predicted to variations in shape and posture. We were initially surprised that any birds attacked clay balls; however, we found shrubs in the field with berries of similar size and some birds may have perceived our clay balls as fruit. In contrast, the lack of difference in arthropod attacks between caterpillars and controls suggests the arthropod community as a whole did not respond to model mimicry of real prey items and that arthropods may simply sample many potential diet items. We concur with others who recommend interpreting attacks by arthropods as a relative measure of arthropod foraging activity rather than a reliable measure of predation pressure *per se* (Howe et al. 2009; Sam et al. 2015a). We assumed daily attack rate to be constant; one recent study with a four-day exposure period suggests that attacks on model caterpillars do occur with a constant daily rate, at least over the span of a short study (Roslin et al. 2017, supplemental material).

Conclusion

Tropical reforestation includes a number of initiation and management alternatives and a range of potential outcomes. While ambitious forest restoration initiatives like the Bonn Challenge on Forest Landscape Restoration and REDD+ encourage biodiverse restored forests, other carbon forestry schemes and rising global demand for forest products may push for more biologically simplified reforestation. What is certain is that the area of managed forest in the tropics will continue to increase. High levels of ecosystem functioning in these new forests cannot be assumed; our work indicates that simply planting native species and planting multiple species are insufficient tactics to fully restore ecosystem function of predators of herbivorous insects if these approaches are not coupled with more holistic management. However, management strategies such as reduced understory clearing could lead to substantial gains in bird activity and ecosystem function even in large-scale plantations.

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APPENDIX

APPENDIX

Factor	Estimate	SE	z	*p*
Shape				
Bird	1.137	0.472	2.412	0.0158*
Arthropod	-0.418	0.241	-1.730	0.0837
Posture				
Bird	0.319	0.195	1.635	0.102
Arthropod	0.020	0.160	0.125	0.900

Table 4.2. Generalized linear model for effects of shape (caterpillar vs. control) and posture (straight-bodied vs. inchworm) on attack probability. For tests of shape, the reference group was control. For tests of posture, the reference group was straight-bodied. The estimate is the change in log odds of attack by changing from the reference group. Statistically significant differences (p<0.05) denoted by *.

Model		Estimate	SE	z	*p*
Non-native Plantation					
Bird		alternative test used, see text			<0.001*
Arthropod		0.182	0.479	0.380	0.704
Native Plantation					
Bird:	Near Gallery	1.042	0.695	1.499	0.134
	Near Park	0.499	0.746	0.669	0.504
Arthropod:	Near Gallery	<0.001	0.308	0.000	1.000
	Near Park	-0.008	0.306	-0.029	0.977

Table 4.3. Generalized linear model for effects of proximity to natural forest (gallery or national park) on attack probability. For tests in both non-native and native plantation, the reference group was Far-from-forest. The estimate is the change in log odds of attack by changing from the reference group. Statistically significant differences (p<0.05) denoted by *.

Figure 4.5. Agua Salud Project location. The Agua Salud Project (red star) is located within the Panama Canal watershed approximately 35 km northwest of Panama City.

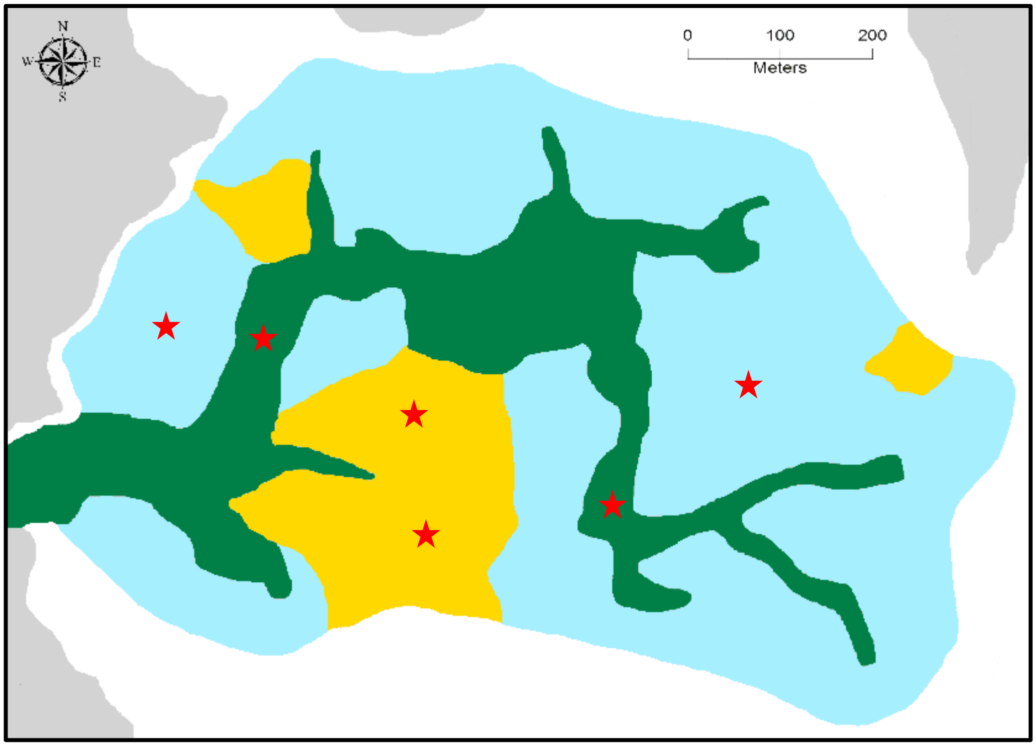

Figure 4.6. Agua Salud Project map of land cover types, Area A (9°12’52” N, 79°43’25” W). Area A is approximately 3 km northeast of Area B (Figure 4.3). Land cover types in and near Area A were native plantation (NAT, blue), old-growth (OGU) mixed with other secondary forest (both are gray), secondary gallery forest (GAL, green), successional forest (SUC, yellow), cleared areas and pasture (white). The residential countryside location (CTY, not depicted) was approximately 6 km northeast of Area A (9°15’05” N, 79°41’40” W). Red stars denote general areas where caterpillars were placed.

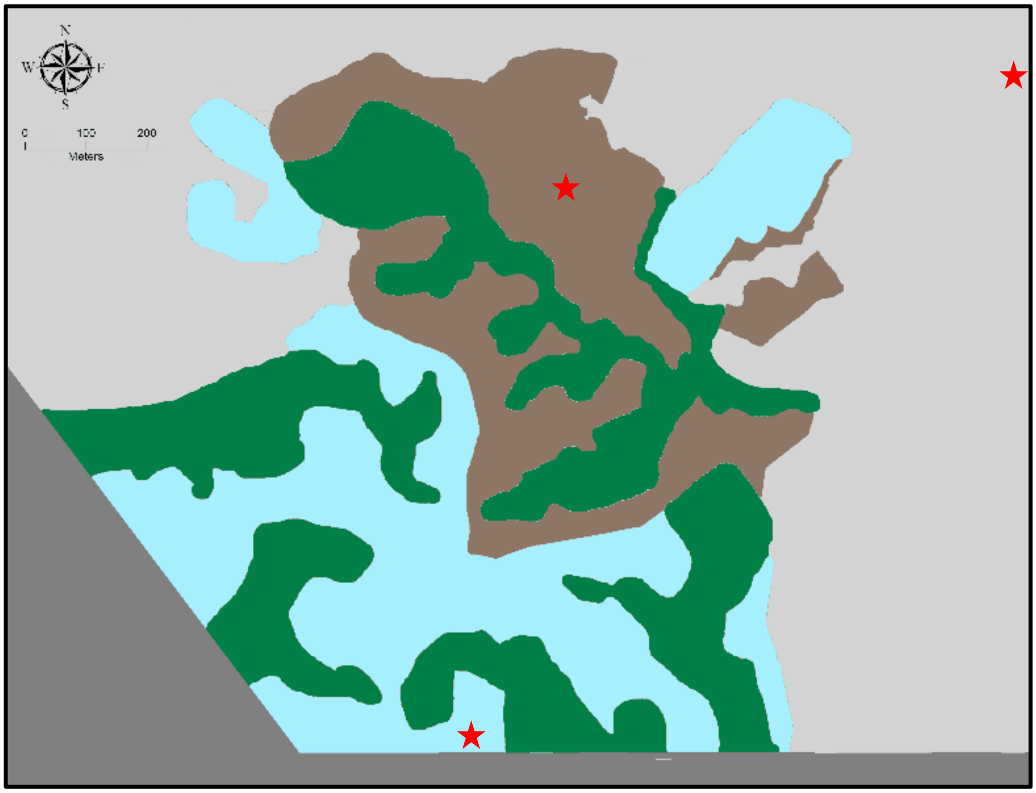

Figure 4.7. Agua Salud Project map of land cover types, Area B (9°11’49’’ N, 79°44’55’’ W). Land cover types in and near Area B are non-native plantation (NON, brown), native plantation (NAT, blue), old-growth (OGU) mixed with other secondary forest (both are gray), secondary gallery forest (GAL, green), and Soberanía National Park (forest, dark gray). Red stars denote general areas where caterpillars were placed.

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