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EFFECT OF ANTS ON ELEVATIONAL DIVERSITY PATTERN OF BIRDS IN THE EASTERN HIMALAYA

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Dedicated to the legendary Indian botanist Dr. Janaki Ammal

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Acknowledgments

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I dedicate this child, oops, I mean this dissertation to all the people that make up this village.

Introduction

The latitudinal species diversity gradient, i.e. an increase in species diversity towards the equator is one of the oldest known diversity patterns. Because changes in climate observed while moving away from equator are similar to those observed while moving up a mountain, the elevational pattern of species diversity was thought to mirror the latitudinal pattern of species diversity (MacArthur, 1972; Stevens, 1992; Zhang, 2013b). Indeed, many elevational species diversity gradients follow this expectation and show a decline in diversity with increase in elevation. However, several other studies report a hump-shaped pattern of species diversity along elevational gradients with a peak in diversity at mid-elevations (Rahbek, 1995; Lomolino, 2001; McCain and Grytnes, 2010; Guo et al., 2013). In this dissertation, I examine how these patterns of species diversity along elevational gradients may be shaped by the distribution of resources and competitors.

Insects and other arthropods are a major food resource for many other groups, such as insectivorous birds. Therefore, examining patterns of arthropod abundance can give valuable insights into diversity patterns of taxa that depend on them. For example, bird diversity peaks at mid-elevations in the eastern Himalaya and this peak coincides with a mid-elevational peak in overall arthropod abundance (Ghosh-Harihar, 2013; Price et al., 2014). However, the pattern of arthropod abundance along elevational gradients varies globally with some studies reporting maximum arthropod abundance at low elevations (e.g. Collins, 1980; Wolda, 1987), and others show a mid-elevational peak (e.g. Janzen, 1973a; Ghosh-Harihar, 2013). In order to understand this variation and assess if it is shaped by seasonality or productivity, I conducted a formal meta-analysis on the global patterns of summer arthropod abundance along elevational gradients for the first chapter

of this dissertation. I found that arthropod abundance tends to peak at higher elevations at mid-latitudes. Shorter growing seasons at these sites leading to synchronous emergence and reproduction of arthropods might be responsible for this observed pattern.

In addition to environmental factors, presence of competitors can play a major role in shaping resource abundance patterns. Studies of resource competition often focus on closely related taxa (Terborgh and Weske, 1975; Jankowski et al., 2010; Pasch et al., 2013), but distantly related taxa also compete for resources, and such interactions can have large impacts on diversity patterns (e.g. Brown and Davidson, 1977). One such case might be ants and birds in the eastern Himalaya. In stark contrast to the mid-elevational peak in bird species diversity in the eastern Himalaya, ants are extremely abundant at the moist tropical low elevations, but they are essentially absent at mid-elevations. This is consistent with their near-absence in cool moist tropical montane habitats all across the world (Janzen, 1973b; Samson et al., 1997; Bruhl et al., 1999), where songbirds and small mammals tend to be very abundant and diverse (Heaney, 2001; Price et al., 2014). Could competition from ants for food and nesting space contribute to the observed lower diversity of birds at low elevations? I examined this question in chapters 2 and 3 of my dissertation.

Low elevations in the eastern Himalaya are home to a highly aggressive insectivorous arboreal ant species, the Asian weaver ant (*Oecophylla smaragdina*). These ants are even used to control pest populations in orchards (Way and Khoo, 1992; Peng and Christian, 2005; Van Mele, 2008). Therefore, in chapter 2, I examined competition between Asian weaver ants and birds for insect prey by conducting weaver ant removal and exclusion experiments and examining diet overlap between these ants and birds at low and mid-elevations. I found that removal of these ants from a tree increases the abundance of large arthropods (>4mm) and their diet overlaps significantly with diets of birds from low and mid-elevations. Thus, competition for arthropod prey from these ants could be a factor causing the lower diversity of birds at low elevations.

While food is an important resource for breeding birds, nesting space could also be a limiting factor, especially for secondary cavity nesting species i.e. species that use pre-

existing cavities. Thus, in chapter 3, I assessed whether availability of nesting cavities contributes to the mid-elevational peak of bird species richness in the eastern Himalaya and if ants play a role in reducing the availability of cavities at low elevations. I found no evidence for lower cavity production at low elevations. However, I recorded extensive use of nest boxes by birds at 200m elevation and none at 1200m, suggesting nest-site limitation at low elevations. Moreover, ants occupied about 70% of the nest boxes at 200m elevation compared to only 13% at 1200m. Thus, I found some preliminary evidence that competition between ants and birds for nesting cavities contributes towards the mid-elevational peak in bird species richness.

Overall, these results suggest that resource abundance patterns play an important role in shaping the diversity and distribution of species. Moreover, patterns of resource abundance are influenced both by abiotic factors such as seasonality and biotic factors such as presence of competitors. These competitors need not be closely related species, as exemplified by ants and birds in the eastern Himalaya. Competitive interactions between distantly related groups are often understudied in terrestrial ecosystems and might be key to understanding large-scale diversity patterns.

1. Global analysis of elevational gradients in arthropod abundance

1.1. Abstract

Arthropods are a major component of ecosystems, in terms of both their biomass and the variety of functional roles they play. Yet we lack a clear understanding of how arthropod abundance changes along environmental gradients. We compiled published literature on overall arthropod abundances along elevational gradients and performed a formal meta-analysis on the role of latitude, climatic variables and interactions with ants, in shaping the pattern of arthropod abundance. Specifically, we asked if patterns of arthropod abundance along different elevational gradients are associated with gradients of seasonality and productivity, and whether ant abundance affects other arthropods. Arthropod abundance peaks at higher elevations at mid-latitudes than low latitudes, and the correlation between arthropod abundance and elevation shifts from negative to positive with an increase in latitude. We suggest these patterns reflect a steep elevational gradient in the length of growing season at mid-latitudes, with the short growing season at high elevations in mid-latitudes generating a large arthropod flush. Precipitation has no consistent effect on arthropod abundance along most elevational gradients. However, on gradients with a very dry base and sharp increase in precipitation with elevation, arthropod abundance peaks at higher elevations. Both gradients in seasonality and productivity drive arthropod abundance along elevational gradients.

1.2. Introduction

Arthropods are the most diverse phylum of animals, not just in terms of the number of species, but also in their form and function, containing groups as different as butterflies, ants, spiders, springtails, millipedes, crabs and scorpions (Zhang, 2013a). Despite their small size relative to vertebrates, arthropods constitute a much larger proportion of animal biomass in many ecosystems (Fittkau and Klinge, 1973; Brockie and Moeed, 1986). Still, we do not have a clear understanding of how arthropods are distributed across environmental gradients. Because of their enormous diversity, it is difficult to examine patterns of species richness across all arthropods and most studies focus on one (Niemalä et al., 1992; Brehm et al., 2003; Sanders et al., 2007) or a few taxonomic groups (e.g. Peters et al., 2016a). Here we address a different question, that of patterns in the total number of arthropod individuals instead of patterns in the number of arthropod species. The processes that shape arthropod abundance patterns have important ramifications for understanding ecological communities as well as predicting future change. First, arthropods play myriad roles in ecosystems: as prey (Poulin and Lefebvre, 1997), predators (Sabelis, 1992), competitors (Kaplan and Denno, 2007), pollinators (Kevan and Baker, 1983), parasites (Hoogstraal, 1985) and disease vectors (Kalluri et al., 2007). Therefore, their numbers should have major effects on the diversity and distribution of the taxa they interact with (Terborgh, 1977; Morton and James, 1988; Heaney, 2001; Bagchi et al., 2014). Second, several studies have reported sharp recent declines in arthropod abundance, up to 75% over the course of 27 years (Conrad et al., 2006; Shortall et al., 2009a; Dirzo et al., 2014a; Hallmann et al., 2017; Sánchez-Bayo and Wyckhuys, 2019). This is a major conservation concern, because such declines can have a large effect on ecosystem function, even in the absence of species extinction (Ceballos et al., 2017). Indeed, reduction in arthropod abundance has been linked to declines in vertebrate populations that depend on arthropods for food (Benton et al., 2002; Wickramasinghe et al., 2004; Gibbons et al., 2015; Lister and Garcia, 2018) and to lower, less stable crop yields for plants pollinated by insects (Allen-Wardell et al., 1998; Aizen et al., 2009; Garibaldi

et al., 2011a). Given rapid ongoing environmental changes, understanding the effect of environmental gradients on arthropod abundance becomes crucial in effective conservation planning.

Here, we address patterns of arthropod abundance during the growing season, i.e. temperate summer or tropical wet season, which roughly corresponds to the breeding season of most terrestrial vertebrate and invertebrate species Wolda (1988). We focus on elevational gradients because they encompass rapid changes in several climatic variables, notably temperature but often also precipitation, over a short distance (McCain and Grytnes, 2010; Graham et al., 2014). Moreover, elevational gradients allow us to decouple effects of temperature from seasonality, because tropical gradients are less seasonal, at least with respect to temperature (Janzen, 1967; Körner, 2007a). Typically, seasonality increases and minimum temperatures decrease away from the equator, making it difficult to tease apart the role of seasonality and temperature (Körner, 2000). However, along tropical mountains, mean temperature drops with elevation without a corresponding decline in seasonality and hence the length of the growing season (Körner, 2007b).

Some previous studies have reported highest arthropod abundance at low elevations (e.g. Collins, 1980; Wolda, 1987), while others show highest summer arthropod abundance at mid-elevations (e.g. Ghosh-Harihar, 2013; Janzen, 1973b). We examine three hypotheses to explain the variation in arthropod abundance along elevational gradients:

1. Seasonality: We derive this hypothesis from patterns along latitudinal gradients. In places that experience winter frost, many arthropods spend the winter in a state of diapause (Schaefer, 1977; Denlinger, 1991; Bale and Hayward, 2010). Roughly synchronous emergence and reproductive activity of such arthropods in the spring or summer creates a sharp peak in abundance in temperate areas that can surpass tropical maxima (Janzen and Pond, 1975; Hails, 1982; Thiollay, 1988). For example, peak arthropod abundance as assessed using suction traps was 16x higher in Scotland (56°N) than peak arthropod abundance in Malaysia (3°N), but winter arthropod abundance in Malaysia was 22x that in Scotland (Hails, 1982). Thus,

greater seasonality in temperate sites can cause sharper peaks in summer arthropod abundance because of the constraints imposed by a short growing season (Rabenold, 1978; Lowman, 1982). Elevational gradients in the temperate and sub-tropical zone might reflect this latitudinal pattern and show summer abundance maxima at higher elevations. In other words, higher elevations in seasonal (i.e. temperate) environments are expected to show a relatively short growing season, which is expected to be accompanied by a large arthropod flush. Hence, our first hypothesis is that the peak in arthropod abundance should be at higher elevations at higher latitudes. This is expected to apply most strongly on gradients that include sites that frost in the winter

2. Productivity: More arthropods are found in warm, wet, highly productive regions than cold, dry, low productivity regions (Rypstra, 1986; Kaspari et al., 2000; Gibb et al., 2015). Because temperature declines monotonically with elevation, deviations from a monotonic decline in productivity with elevation must be largely set by precipitation. Such deviations are likely to be observed for mountains with dry bases but wetter mid-elevations (McCain, 2007, 2009), leading to the prediction that arthropod abundance will peak at higher elevations on mountains with dry bases than on ones with wet bases.

3. Biotic interactions: Apart from abiotic environmental variables, population sizes are influenced by biotic interactions. Several studies have pointed to ants as important predators on other arthropods, especially in tropical lowlands (Floren et al., 2002; Mooney, 2007; Tvardikova and Novotny, 2012; Sam et al., 2015; Rodríguez-Castañeda et al., 2016). Experimental exclusion of ants from selected trees or plots has been shown to result in increased abundance of other arthropods (Schmitz et al., 2000; Mooney, 2007; Piñol et al., 2012; Singer et al., 2017). Patterns of ant abundance might be an important factor shaping non-ant arthropod abundance patterns at a larger spatial scale as well (Olson, 1994; Heaney, 2001; Kumar et al., 2009; Yu et al., 2013), leading to the prediction that ant abundance across elevations should correlate negatively with abundance in other groups.

In this paper, we first describe arthropod abundance patterns along elevational gradients and then evaluate these three hypotheses.

1.3. Materials and methods

1.3.1. Data collection

We searched for papers on arthropod abundance along elevational gradients using the Google Scholar search engine with "arthropod abundance elevation", "arthropod abundance altitude", "insect abundance elevation" and "insect abundance altitude" as keywords. We then searched bibliographies of those papers for additional relevant studies, as well as ecological databases including Dryad, knb, GBIF, DataOne, ecological data wiki and re3data. Finally, we consulted researchers that have worked on arthropods in mountains regarding unpublished datasets or studies we may have missed. Our compilation was last updated in November 2018.

We only included studies that reported abundance (i.e. number of individuals) for all arthropods collected, sampled at a minimum of four elevations and that had equal sampling effort with identical sampling methods at each elevation. We excluded studies limited to specific taxa or specific microhabitats but included studies that only used one particular method (e.g. pitfall traps). For example, we excluded data from Garibaldi et al. (2011b) because they only sampled arthropods from a single tree species over a restricted elevational range at three elevations. Similarly, we excluded all studies that only provide information on species richness but do not report abundance (e.g. Peters et al., 2016b).

Because this search yielded a small number of studies (n = 21), we did not filter them based on other potentially relevant criteria such as the proportion of gradient sampled and lowest elevation covered. However, all but two of the studies included in our analyses sampled at least one site within the lowest 400m of the elevational gradient for that

region. The only exceptions were the elevational gradients in western Himalayas sampled by Ghosh-Harihar (2013) and northwestern Argentina sampled by González-Reyes et al. (2017), where the lowest elevations sampled were 1350m and 1586m respectively; in both regions the elevational gradient extends to below 400m. Across four North American gradients, the lowest elevation sampled is over 1400m, but the lowest elevation in the region is at about 1000m. Seventeen out of the 21 studies we included in our analysis were conducted during the temperate summer or the wet season in the tropics, which corresponds with the growing season (Table S1.1). The other two studies were conducted during the dry season in the tropics, but the dry season is generally mild at these sites. One study did not specify the month of sampling and the final study sampled in all seasons but did not present the data for each season separately (Table S1.1).

The studies we found did not use the same methods to estimate arthropod abundance and did not sample the same substrates (Table S1.1), but we assume that the overall pattern of abundance along elevational gradients is similar across substrates (see discussion). We evaluate patterns within each study, then compare these patterns (notably where the maximum abundance is reached on the gradient). Therefore, we standardized measurements of arthropod abundance across each gradient to a mean of 0 and standard deviation of 1 before analysis. Hence differences in absolute abundances due to different methods and intensities of sampling are not an issue. Complete data used for the analyses are given in Table S1.2.

We extracted data on five climatic variables (mean annual temperature, annual precipitation, minimum temperature, temperature seasonality and precipitation seasonality) from the worldclim2 database (Fick and Hijmans, 2017) using spatial coordinates for sampled sites based on the original papers. Seven of the papers did not include latitude and longitude information for every site, and in such cases we either contacted the authors or inferred co-ordinates from other sources. For example, Collins (1980) sampled along a regular hiking route to the summit of Gunung Mulu, so we obtained GPS co-ordinates from a hiking website and corroborated some of the points from a study of birds along the same elevational gradient (Burner et al., 2016). For three studies, we estimated the

latitude and longitude of the sampling sites using Google Earth based on the study site description provided in the paper. For Janzen (1976), we could not estimate the location co-ordinates and used the precipitation and minimum temperature data as provided in the paper .Hence we could not use this data set for all the analyses. We also could not estimate locations for Leakey and Proctor (1987) and so had to exclude this study from several analyses.

We used annual temperature and precipitation data extracted from worldclim to calculate Actual Evapotranspiration using Turc's formula: $AET = P/[0.9 + (P/L)^2]^{1/2}$ where $L = 300 + 25T + 0.05T^3$ and Tstands for mean annual temperature and P is annual precipitation (Turc, 1954; Yu et al., 2013). We used AET instead of measures such as NDVI, EVI or NPP from the MODIS data, because the sampling sites within elevational gradients are not far enough apart to fall into different grids in the MODIS data. Finally, we gathered data on ant abundance from the same studies where available. All compiled data are available on Dryad and as a supplement to this paper.

1.3.2. Data analysis

Our dataset included one study in Sweden at 67°N (Franzén and Dieker, 2014), while all the other studies fell between 0-40°. We excluded the Sweden outlier from all analyses. To visualize patterns, we first fit a loess smoother to each gradient using the R package ggplot2 (Wickham, 2011). Next, following Werenkraut & Ruggiero (2014), we evaluated the pattern of abundance along individual elevational gradients by comparing the regression coefficients and P-values for (1) a null model ($y = a$), (2) a linear model of declining abundance with elevation ($y = a - bx$), (3) a quadratic model with high arthropod abundance from low to mid-elevations followed by a gradual decline i.e. low plateau ($y = a - cx^2$) and (4) a full quadratic model with mid-elevational peak in abundance ($y = a \pm bx - cx^2$) (note that $y = a + bx$ would indicate an increase in abundance with elevation and $y = a \pm bx + cx^2$would indicate a U-shaped pattern). Note that one study could potentially fit all three models (i.e. models 2, 3 and 4). We estimated spatial autocorrelation for each of the gradients as Moran's I, using the R package Ape

(Paradis et al., 2004; R Core Team, 2014). For gradients with statistically significant spatial autocorrelation, we assessed the fit of models 1, 2, 3 and 4 accounting for spatial autocorrelation by incorporating spatial correlation structures using corSpher, corExp and corGaus in linear mixed effects models using the R package nlme (Pinheiro et al., 2014). If incorporating spatial correlation structures led to a better-fit model assessed conservatively using AICc values, we used the spatial models to identify the pattern of arthropod abundance with elevation.

Next, we conducted a formal meta-analysis (Cooper et al., 2009; Harrison Freya, 2010; Koricheva et al., 2013) to examine the effect of latitude, climatic variables related to temperature and precipitation on arthropod abundance along elevational gradients. We also analyzed the effect of ant abundance on abundance of other arthropods, after standardizing non-ant arthropod abundance data. We calculated linear correlations between arthropod abundance, all six climatic variables, and ant abundance for all the gradients for which we had these data. We converted these correlations to effect sizes using Fisher's z transformation with the function escalc in the R package metafor Viechtbauer (2010). Effect sizes are correlations between variables normalized and corrected for sample size to enable comparisons across studies Harrison Freya (2010). Because spatial autocorrelation was low for most of the studies included in our analyses, we did not account for it in calculations of the effect sizes.

We asked if the effect size of any of these variables on arthropod abundance differed significantly from zero using a meta-analytic random-effects model. Next, we used these effect sizes and conducted a meta-regression with latitude as a modifier to ask if the relationship between arthropod abundance and climatic variables is associated with latitude. For all of these analyses, we had to exclude three studies that sampled only 4 locations (the variance of the effect size for these studies is $1/(n - 3) = 1$ which prevents the estimation of sampling variance across studies (Field, 2005)). In our analyses of climatic variables and ant abundance, we were unable to include one and 10 studies respectively because the relevant data were lacking.

Finally, to ask if seasonality or productivity best predicts the elevation of maximum

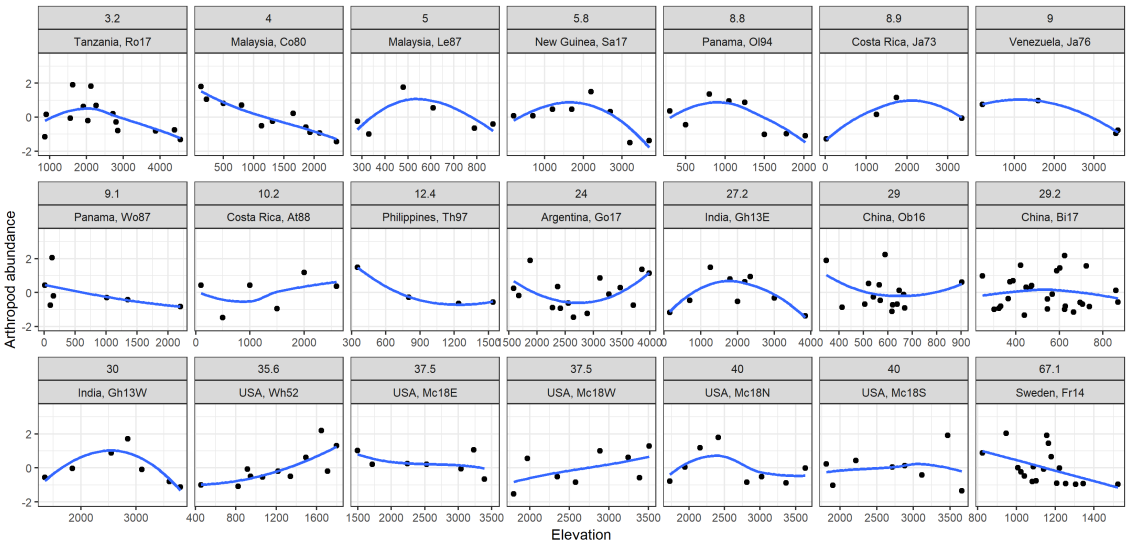
non-ant arthropod abundance in the datasets, we used a general linear model (GLM) approach. Specifically, we used the following independent variables in our full models: (1) precipitation at lowest elevation. We chose precipitation at the lowest elevation as a measure of productivity instead of annual evapotranspiration (AET), because we had precipitation data for more studies and the two variables were highly correlated in those studies where both measures are available (r= 0.97, P $<$ 0.0001, N= 19), (2) "freezing fraction" i.e. fraction of sampled gradient that freezes over, calculated as (maximum elevation sampled – lowest freezing elevation)/elevational range sampled. We used a step-wise model reduction approach and dropped variables one by one from the full model until the dropping of a variable increased AIC values (Burnham and Anderson, 2002). We used AICc values to compare the best model to an intercept-only null model to assess the explanatory power of the model. All analyses were done in the R programming environment (R Core Team, 2014) using the packages raster (Hijmans et al., 2017), rgdal (Bivand et al., 2015), plyr (Wickham, 2016), Rmisc (Hope, 2013), metafor (Viechtbauer, 2010), nlme (Pinheiro et al., 2014), ape (Paradis et al., 2004), MuMIn (Bartoń, 2016) and ggplot2 (Wickham, 2011).

1.4. Results

1.4.1. Patterns of abundance

We found 21 studies that reported data on overall arthropod abundance along elevational gradients at a total of 206 sites (Table S1.1). The lowest elevation sampled by these studies ranged from 20m to 1811m and the highest elevation sampled ranged from 869m to 4550m (Fig. A.1). The elevational range covered by the studies varied from 590m to 3690m. All but two of these studies focused on only one substrate for arthropod collection, i.e. ground, air, or leaves. Patterns of arthropod abundance varied greatly. They included a monotonic decline in abundance with elevation (Collins, 1980; Wolda, 1987; Franzén and Dieker, 2014), a mid-elevation peak (Janzen et al., 1976; Olson, 1994;

Figure 1.1.: Pattern of arthropod abundance along elevational gradients. Latitude, location and Study ID (see Table S1) are indicated on top of each panel arranged from lowest to highest latitude. Elevation in meters is indicated on the bottom of each panel. The curves show loess smooth fits to the data. Abundance data were standardized to have a mean of zero and standard deviation of one before plotting. See Figure S1 for a version of this figure where all plots cover the same elevational range on the x-axis.

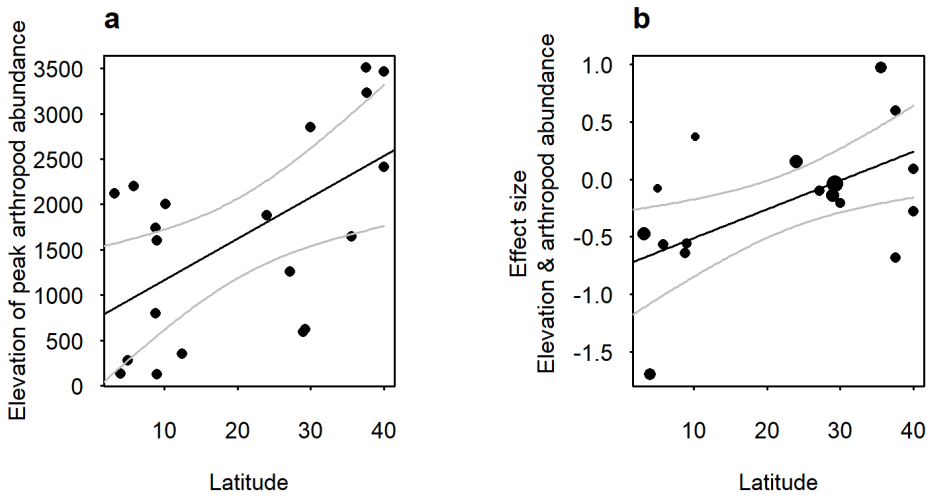


Ghosh-Harihar, 2013; Röder et al., 2017; Sam et al., 2017; Janzen, 1973b), a monotonic increase in abundance (Whittaker, 1952; Atkin and Proctor, 1988), a U-shaped pattern with greater abundance at low and high elevations (Leakey and Proctor, 1987; Thomas and Proctor, 1997; González-Reyes et al., 2017) and no obvious pattern (O'Brien et al., 2017; Binkenstein et al., 2017; McCain et al., 2018)(Fig. 1.1 & Figs. S1.1 & S1.2). We found significant support for a linear model of declining abundance in only two studies (Table S1.1). Four studies showed significant support for mid-elevational peak and low-plateau models for arthropod abundance, one of which showed significant support for both (Table S1.1). Moran's I was positive and significant for 6 of the 19 gradients. However, the values were low (Table S1.1) and a model with spatial correlation structure performed better than a non-spatial model for only one study (Binkenstein et al., 2017).

1.4.2. Predictors of abundance

Consistent with the expectations from our seasonality hypothesis, the correlation between elevation and arthropod abundance shows a linear increase with latitude i.e. abundance

Figure 1.2.: a. Relationship between elevation of maximum arthropod abundance and latitude **b.** Relationship between effect size of the correlation between arthropod abundance and elevation and latitude. Size of each point in b indicates sample size of the gradient. Grey lines in both plots indicate 95% confidence interval.



decreases with elevation in the tropics but increases with elevation at mid-latitudes (Fig. 1.2, meta-regression, correlation of elevation and arthropod abundance, N= 17, R2 = 53%, slope (latitude) = 0.025 ± 0.009 SE, z = 2.69, P = 0.007). Correspondingly, mean annual temperature, minimum temperature and actual evapotranspiration are positively correlated with arthropod abundance along gradients in the tropics, decreasing to a weak or negative correlation at higher latitudes (Fig. 1.3, all $P < 0.01$). Correlations between arthropod abundance and annual precipitation, precipitation seasonality and temperature seasonality are not related to latitude (Fig. 1.3, all $P > 0.7$). Finally, the correlation between ant abundance and non-ant arthropod abundance was not significantly different from zero across all studies (Fig. A.2, average ES = -0.018 ± 0.11, P = 0.87) and was also not significantly affected by latitude (meta-regression, ant abundance x arthropod abundance: slope = -0.014 ± 0.009 SE, N= 10, P = 0.15).

The finding that temperature correlates of abundance vary with latitude, but precipitation correlates do not, suggest that some feature of absolute temperature is affecting the position of peak abundance. Indeed, the best model for position of peak abundance supports a positive relationship between arthropod abundance and the fraction of the gradient that freezes over (Table 1.1, Fig 1.4). However, the model with precipitation

Table 1.1.: General linear models for elevation of peak arthropod abundance (meters above sea level). Model 1 is the best model based on AICc values.

Model ID	Independent variables	Slope ±S.E.	P	AICc
Model 1	Freezing fraction	1728.8 ± 457.6	0.002	314.58
Model 2	Precipitation at lowest elevation	-0.59 ± 0.18	0.004	316.73
Model 3	Latitude	42.45 ± 16.34	0.019	319.8
Full model 1	Precipitation at lowest elevation	-0.17 ± 0.32	0.6	317.49
	Freezing fraction	1326 ± 886.2	0.15	
Full model 2	Precipitation at lowest elevation	-0.48 ± 0.27	0.09	319.62
	Latitude	12.64 ± 22.74	0.59	
Null model	Intercept-only			323.31

at the lowest elevation as a predictor was a close second (ΔAICc = 2.15), lending some support to the idea that dry mountain bases do tend to have peak abundances at higher elevations than those with wetter bases.

1.5. Discussion

In the introduction, we considered three possible explanations for why arthropod abundance along elevational gradients should vary geographically: seasonality, productivity and interactions with ants. Across 20 studies of arthropod abundance along elevational gradients spanning 0-40° latitude, we found that correlation of elevation and arthropod abundance increases with latitude (Fig. 1.2). Moreover, we found that arthropod abundance peaks at higher elevations on gradients where freezing temperatures are recorded over a greater fraction of the gradient (Table 1.1, Fig. 1.4). We suggest that this elevational shift is driven by variation in seasonality along elevational gradients, with high variation in the length of growing season along gradients at mid-latitudes, but little variation along gradients in the tropics. A relatively short growing season at high elevations and latitudes leads to a large arthropod flush. We also found some support for the productivity hypothesis as peak arthropod abundance is higher on gradients with an arid base (Table 1.1, Fig. A.3). However, precipitation did not emerge as an important factor

across all gradients, which might be explained by low variation in precipitation most individual gradients (Table S1.2). Lastly, we found no evidence that ants influence abundance of other arthropods. However, ant abundance data was not available for seven of the 20 gradients, reducing our ability to evaluate this hypothesis.

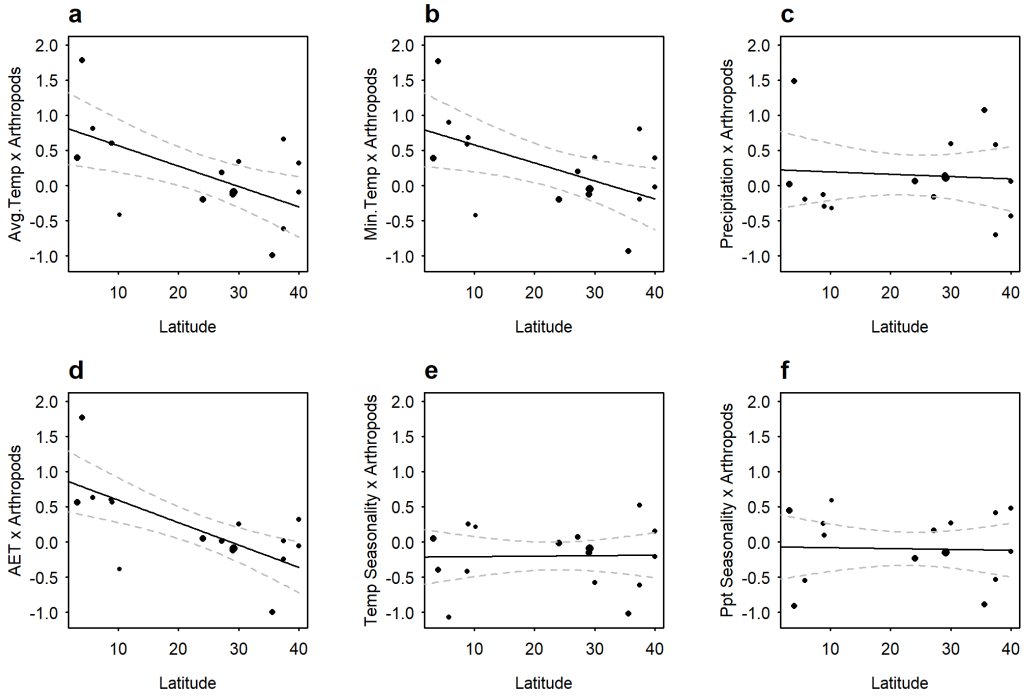


Figure 1.3.: Relationship between effect size of the correlation between arthropod abundance and various climatic variables and latitude. Size of each point indicates number of sampling stations along the gradient. Meta-regression results: mean temperature x arthropod abundance: slope ± SE = -0.029 ± 0.01, P = 0.005; minimum temperature x arthropod abundance: slope ± SE = -0.026 ± 0.011, P = 0.014; annual precipitation x arthropod abundance: slope ± SE = -0.003 ± 0.011, P = 0.76; actual evapotranspiration x arthropod abundance: slope ± SE = -0.032 ± 0.009, P = 0.0002; temperature seasonality x arthropod abundance: slope ± SE = -0.007 ± 0.008, P = 0.93; precipitation seasonality x arthropod abundance: slope ± SE = -0.0012 ± 0.009, P = 0.89. Dashed grey lines indicate 95% confidence interval.

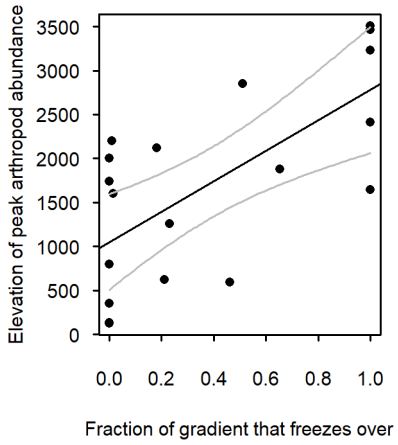
We suggest that the abundance peaks at higher elevations at higher latitudes are caused largely by synchronous emergence and reproduction due to the constraints on the growing season. These abundance peaks may be underlain by large numbers of individuals belonging to a few species and may not necessarily correlate with species richness peaks. Discordant patterns of abundance and species richness along elevational gradients have been widely reported. At temperate latitudes, maximum insect species richness often

occurs at low elevations (McCoy, 1990), whereas abundance peaks at intermediate elevations (Figs. 1.1 & 1.2). For example, in the Smoky mountains, Whittaker (1952) found that insect species diversity is highest at about 945m elevation while total abundance peaks at about 1645m. Similarly in New South Wales, Australia (≈30°S), Lowman (1982) sampled three sites at 760, 900 and 1200m elevation and found a sharp spring arthropod abundance peak at 1200m elevation which was seemingly constituted of fewer species. Similar findings have been reported for specific arthropod groups. Brehm et al. (2007) found a near monotonic increase in moth abundance along an elevational gradient from 40m to 2730m in Costa Rica, but recorded highest species richness at mid-elevations. Kumar et al. (2009) found almost twice as many paper wasp species at 500m compared to 1100m elevation in Costa Rica, despite finding more than 5x as many individuals at 1100m elevation compared to 500m elevation in their malaise and flight-intercept traps.

Together, these findings suggest that the abundance peak at higher elevations in mid-latitudes is constituted of larger populations of relatively few species, akin to the latitudinal pattern of more arthropod individuals but fewer species in the temperate versus the tropics (Janzen and Pond, 1975). This is consistent with expectations that seasonality, i.e. a short growing season and synchronous emergence are responsible for greater arthropod abundance at mid- or high elevations at mid-latitudes. This effect may diminish towards polar latitudes where growing seasons at different elevations might not vary much. Indeed, the only study in our dataset in the frigid zone (Franzén and Dieker, 2014), which we omitted from all analyses, showed a strong negative correlation between elevation and arthropod abundance (r = -0.49).

Our findings come with caveats. First, the studies included in our analyses sampled different substrates and used different methods. Thus, the component of arthropod fauna measured could be quite different from each other, and we have assumed that the estimates obtained correlate generally with arthropod abundance. However, previously published work in the Andes (Guevara and Avilés, 2007) and our own unpublished studies from the eastern Himalayas show that arthropod abundances do vary similarly across methods (Schumm et al., MS in review). The second caveat is that we did not account

Figure 1.4.: Correlation between elevation of peak arthropod abundance and fraction of the sampled gradient that experiences freezing temperatures. Grey lines indicate 95% confidence interval.



for the effect of human disturbance on arthropod abundance in our analyses. This could have a particularly large impact at low elevations, which tend to have larger human settlements (Lee et al., 2004; McCain, 2009). Because the studies included in our analyses spanned a long timescale (1952 - 2017), it was difficult to include a meaningful measure of human disturbance for all the gradients at the time that they were sampled. However, the correlates we uncovered with latitude seem most likely to be driven by climatic factors.

Our study also demonstrates the limited number of published datasets on arthropod abundance patterns. Given the importance of arthropods and the reported declines in arthropod population in some places (Conrad et al., 2006; Shortall et al., 2009b; Dirzo et al., 2014b; Hallmann et al., 2017), more studies of arthropod abundance along environmental gradients would be valuable, using similar sampling methods across different gradients. Data on arthropod abundance across all seasons at different sites are also needed. Some studies show sharper peaks of arthropod abundance in temperate regions compared to the tropics (Janzen and Pond, 1975; Hails, 1982). However, Lowman (1982) is the only study we could find that compares seasonal patterns of arthropod abundance across different substrates at different elevations.

In conclusion, we find that arthropod abundance peaks at higher elevations on elevational gradients at higher latitudes, and attribute this pattern to a negative relationship

between the length of growing season and arthropod abundance maxima (Table 1.1, Fig. 1.4). Length of growing season has been increasing in many places over the past few years (Walther et al., 2002; Ims et al., 2008; Cooper, 2014). Our interpretation suggests that this ongoing change will reduce maxima in arthropod abundance with potentially cascading effects, including effects on the populations of insectivorous vertebrate species and transmission of diseases with insect vectors. Hodkinson (2005) came to a similar conclusion in his review of single-species abundance patterns along elevational gradients. Global changes in precipitation patterns might also affect the shape of elevational patterns of arthropod abundance, with hump-shaped patterns becoming more common in regions where the low elevations become drier over time.

Global climate change is likely to have an enormous impact on species distributions, abundances and interactions in mountains (Pounds et al., 1999; Konvicka et al., 2003; Gottfried et al., 2012; Radenković et al., 2017). Moreover, stable or positive abundance trends of species over time appear to be necessary to allow species range expansion in response to climate change (Mair et al., 2014). Only with increased documentation of arthropod abundance patterns along elevational gradients and across different seasons will we be able to predict the changes in arthropod abundance patterns and their consequences.

2. Competition with insectivorous ants as a cause of low songbird diversity at low elevations in eastern Himalaya

2.1. Abstract

If competitive interactions exist between distantly related clades, it may result in complementary diversity patterns of these clades over large spatial scales. One such example might be ants and birds in the eastern Himalaya, where ants are very common at low elevations but almost absent at mid-elevations, whereas bird diversity peaks between about 1200m and 2000m. Here, we test if the presence of ants at low elevations contributes to the lower diversity of birds through competition for arthropod prey. First, we compared arthropod abundance on trees and leaf damage due to herbivory on 17 pairs of trees with or without Asian weaver ants (*Oecophylla smaragdina*), the most common and aggressive ant in the eastern Himalaya. We found greater arthropod abundance and greater leaf damage on trees without weaver ants. Next, we conducted a weaver ant removal and exclusion experiment at a low- elevation site replicated across 15 pairs of trees and found that removal of weaver ants from a tree increases non-ant arthropod abundance significantly. Finally, we examined the diets of weaver ants and songbirds at the low elevation

using 16S rDNA amplicon sequencing and found significant diet overlap. Increase in arthropod abundance after removal of weaver ants and diet overlap between weaver ants and birds suggests that competition from weaver ants is an important factor lowering insectivorous bird diversity at low elevations in eastern Himalaya. Competition with ants may shape vertebrate diversity patterns in other tropical and sub-tropical regions as well.

2.2. Introduction

Biotic interactions such as mutualism, commensalism, competition and predation, affect diversity and distribution of species at different scales in different ways (Schemske et al., 2009; Wisz et al., 2013; Araújo and Rozenfeld, 2014; Lany et al., 2018; Nelsen et al., 2018). While the role of these interactions in shaping large-scale biodiversity patterns is often acknowledged, it is rarely examined along environmental gradients (Schemske et al., 2009; McCain and Grytnes, 2010; Wisz et al., 2013). This paucity of studies may be attributed to the fact that biotic interactions are often difficult to quantify (McCain and Grytnes, 2010) and that cause and effect can be difficult to distinguish in the relationship between biotic interactions and species diversity (Fischer, 1960; Schemske et al., 2009). However, there is a growing realization of the need to study the role of these interactions in shaping diversity patterns in the light of predicted shifts in species ranges due to climate change (Blois et al., 2013; Wisz et al., 2013; Valiente-Banuet et al., 2015; Anderson, 2017; Gavish et al., 2017), especially as the strength and effects of these interactions are themselves susceptible to climate change (Tylianakis et al., 2008; Faldyn et al., 2018).

One of the key biotic interactions that can influence diversity patterns in various ways is competition. Competition may reduce diversity by competitive exclusion (Goldberg and Barton, 1992; Valone and Brown, 1995)or enhance diversity through increasing specialization of species (Abbott et al., 1977; Futuyma and Moreno, 1988; Emerson and Kolm, 2005). Closely related taxa often compete for similar resources and these competitive interactions can influence range limits of these taxa (Terborgh and Weske, 1975; Jankowski

et al., 2010; Pasch et al., 2013). However, interactions between distantly related taxa can have even greater impacts on diversity patterns because these taxa may interact with each other in multiple ways simultaneously including predation, competition and even mutualism (Polis et al., 1989; Ingram et al., 2012).

Although a few studies have demonstrated competition between distantly related taxa such as ants and rodents (Brown and Davidson, 1977), frog tadpoles and mosquito larvae (Mokany and Shine, 2003), waterfowl and fishes (Eriksson, 1979; Eadie and Keast, 1982), birds and lizards (Wright, 1981), birds and bats (Palmeirim et al., 1989), squirrels and grasshoppers (Hansen and Ueckert, 1970), plants and spiders (Jennings et al., 2010) and large animals and microbes (Janzen, 1977; Hochberg and Lawton, 1990), moths and hummingbirds Carpenter (1979), this subject has not received much attention in macroecology. In fact, the presence of closely related species in a place has been used as evidence against the role of competition in structuring the community (Webb et al., 2002; Gómez et al., 2010; Tucker et al., 2017). However, recent advances in ecological coexistence theory suggests that a weak difference in competitive ability between closely related species could allow for coexistence, despite little niche differentiation Chesson (2000). On the other hand, strong differences in competitive ability between distantly related competitors could cause competitive exclusion despite substantial niche differentiation (Chesson, 2000; Mayfield and Levine, 2010; Gerhold Pille et al., 2015).

Several studies have found no support for a correlation between strength of competition and phylogenetic relatedness (Cahill Jr. et al., 2008; Fritschie et al., 2013; Godoy et al., 2014; Venail et al., 2014). Moreover, the effect of competition between distantly related taxa on diversity patterns has also been observed in the fossil record Jablonski (2008). For example, existing data suggest that rodents competitively replaced multituberculate mammals over a period of about 20 million years in the early Cenozoic (van Valen and Sloan, 1966; Krause, 1986). Thus, distantly related taxa may strongly compete and influence each other's diversity and abundance over a long timescale (Wilcox et al., 2018). Here, we present evidence for the ecological role of competition between two distantly related clades in shaping their complimentary diversity patterns: songbirds (Phylum

Chordata, Class Aves, Subfamily Oscines) and ants (Phylum Arthropoda, Class Insecta, Family Formicidae). While several studies have presented evidence for competition or amensalism between ants and birds (Supplementary table S2.1), they have not assessed the effect of these interactions on patterns of diversity. Ants are important predators, especially in tropical and sub-tropical lowland forests (Floren et al., 2002; Sam et al., 2014) and have been shown to limit populations of other arthropod taxa (Piñol et al., 2010; Karban et al., 2017). However, ants are often absent or very low in abundance in tropical and sub-tropical montane cloud forests across the world (Janzen, 1973b; Samson et al., 1997; Longino et al., 2014), for reasons that remain unclear. One proposed explanation is that ground-nesting ants cannot survive in places that are wet throughout the year whereas arboreal nesting ants cannot survive freezing winters (Wheeler, 1917; Janzen, 1973b; Samson et al., 1997). On the other hand, songbirds and small mammals are often very diverse and abundant in these cloud forests (Heaney, 2001; Price et al., 2014). One mechanism for this mid-elevation diversity and abundance maximum could be the lack of competition with ants for arthropod prey in the cloud forests (Heaney, 2001; Price et al., 2014). We investigated this hypothesis in the eastern Himalaya.

In the eastern Himalaya, songbird diversity peaks at the mid-elevations between about 1200m and 2000m; by contrast, ants are highly abundant and diverse at the low elevations but almost absent at mid-elevations. The mid-elevation peak of songbirds in the eastern Himalaya consists largely of insectivores. Among ants, the low elevations are dominated by an aggressive arboreal insectivorous species, the Asian weaver ant *Oecophylla smaragdina*. The dominance of weaver ants at the warm low-elevations could lead to lower diversity of birds at these elevations due to competition for food resources. To test this idea, we compared arthropod abundance and leaf damage due to insect herbivory on trees with and without weaver ants, conducted weaver ant removal and exclusion experiment using a paired design and compared the diet of weaver ants and birds at low and mid elevations.

2.3. Methods

2.3.1. Study sites

We carried out the comparison of trees with and without weaver ants in June 2014 and May 2015. We followed it up with the weaver ant removal and exclusion experiment from April-June 2015 and 2016 at a low elevation site in Chapramari Wildlife Sanctuary (26.8858°N, 88.8341°E, ~ 200m) in West Bengal, India. For diet analyses, we conducted fieldwork at additional sites at mid-elevations in Neora Valley National Park (27.0611°N, 88.7707°E, ~ 2000m) in West Bengal.

2.3.2. Effect of weaver ants on arthropod abundance

Field Methods To assess the effect of weaver ants on arthropod abundance, we used a paired design. We measured arthropod abundance at trees with weaver ants and trees without weaver ants, where the trees were paired by species, height and girth. In Chapramari (200m elevation), we sampled 10 pairs of trees in June 2014 and 7 other pairs of trees in May 2015. We collected arthropods by beating the foliage of a tree with a stick, and collecting all the insects that fell on an upturned umbrella, which is similar to the method used by Piñol et al. (2012) in assessing ant impacts in a citrus orchard in Spain. We used the same umbrella at all trees and beat the foliage three times before collecting insects and repeated the process at another part of the tree. We collected the arthropods in vials containing 95% ethanol. Later in the field camp, we counted all the collected arthropods, measured body length to the nearest mm, and classified them to taxonomic order. To control for observer bias, the person counting the arthropods was unaware of the identity of the source tree and the presence or absence of weaver ants on the tree.
We also estimated leaf damage on the pairs of trees as a longer-term proxy of insect herbivore abundance, with greater arthropod abundance implied by higher leaf damage. Leaf damage may not accurately represent herbivory when leaf lifespans are different

among tree species and habitats (Moles et al., 2011) and may not reflect arthropod abundance if the arthropod communities on the trees are very different and have different herbivory rates. However, using similar-sized trees belonging to the same species in similar habitats for comparison should control for these confounding factors. We used two methods to assess leaf damage: (1) visual estimation of leaf damage (% removed) on 10 leaves from different parts of each tree, and (2) visual estimation of leaf damage on each leaf on a short (~0.5m) clipped branch of the tree.

Data analysis We used paired t-tests to compare arthropod abundance and leaf damage between trees with or without weaver ants. Arthropod abundance data were log-transformed before analysis with one added to all values to avoid zeroes in the data. All analyses were done in the RStudio programming environment (R Core Team, 2014).

2.3.3. Weaver ant removal and exclusion experiment

Field Methods First, we located pairs of trees of the same species with roughly the same height and girth that had weaver ants and were not connected to other trees at the canopy level. In some cases, we had to prune the branches of a tree slightly to isolate it from other trees in the area. Next, we measured arthropod abundance at each of these trees using beating (as described in the previous section) and branch-clipping (Ozanne, 2005). In the branch clipping method, we used a tree pruner to clip a short branch from a tree and let it fall on an upturned umbrella and collected all the arthropods from the surface of the umbrella and from the clipped leaves. We also recorded leaf damage as an index of insect herbivory on the clipped branch and on 16 random leaves at each tree. Then, we randomly assigned trees in each pair to experimental or control treatment using coin tosses. On trees in the experimental treatment group, we removed all weaver ant nests using our tree pruner and then applied a band of Tanglefoot^{TM} around the trunk of the tree at about 1 m height from the base of the tree. We plugged all the holes in the trunk crevices under the Tanglefoot band with cotton. On trees receiving the control treatment, we stuck a band of brown paper to make them appear similar to trees receiving

the experimental treatment and pruned a few branches to mimic the disturbance caused by the removal of weaver ant nests. We applied treatments to 15 pairs of trees in May 2015 and then measured arthropod abundance and leaf damage at each of the trees in June 2015 using the same methods to assess the effect of weaver ant removal and exclusion one month after the treatment. We checked the trees every week during the field season in April-June 2015 to ensure the treatments were working and re-applied Tanglefoot or added cotton to the crevices as and when necessary. Between July 2015- April 2016, our assistants checked the trees monthly to maintain the treatments. In May 2016, we measured arthropod abundance and leaf damage at each of the trees again to assess the effect of weaver ant removal and exclusion after one year. An elephant destroyed one tree, so we only had 14 pairs of trees for the one-year after dataset. In some cases, we were not able to completely remove or exclude weaver ants, because of the nature of the bark of the tree trunk or the canopy of the tree.

Data analysis We used paired t-tests to compare the change in arthropod abundance and leaf damage over the period of one month and over the period of one year between trees in the weaver ant exclusion and control treatments. All analyses were done in the RStudio programming environment R Core Team (2014).

2.3.4. Molecular diet analysis

Field and lab methods To examine bird diet, we caught 103 birds and collected 41 fecal samples at low and mid elevations in the eastern Himalaya between April- June 2016 (see Supplementary table S2.2 for detailed information on the birds we collected fecal samples from). We used mist nets to catch birds and upon extracting them from the net, we put them in a brown bag for one minute, weighed them, took them out, measured their wing and tarsus length and released them. After the bird was released, we tore up the brown bag, scraped the feces off and put them in a 2 ml plastic tube with 95% ethanol. Average processing time for a bird was about two minutes. All fecal samples were stored in 95% ethanol until DNA extraction. We used Qiagen QIAamp DNA Stool Mini kit

to extract DNA from these fecal samples with some minor modifications in the protocol following Zeale et al. (2011). To examine weaver ant diet, we collected items of food that the weaver ants were carrying to their nest from 25 different colonies between April- June 2016. We collected food from each colony either for an hour or until we had collected 10 items, whichever happened first. We extracted DNA from these samples by taking a small part of each of the prey items, crushing it and then using the Qiagen DNeasy blood and tissue kit and following the manufacturer's protocol for extraction.

We carried out a 25μL PCR (polymerase chain reaction) to amplify a segment of the 16S rDNA using the lns16S-short primer pair (5'-3' TRRGACGAGAAGACCCTATA; ACGCTGTTATCCCTAAGGTA) described by Clarke et al. (2014). We used this primer set because it is invertebrate specific, so successful DNA amplification using this primer set indicated presence of prey DNA in the DNA extract. For the reactions, we used 10μL of the DNA extract from bird feces or 2μL of the DNA extract from weaver ant food samples as the template. We visualized 3μL of the PCR products on a gel to identify successful amplifications. We sent the successful PCR products to the Sequencing core at the University of Illinois at Chicago, Chicago, Illinois, for barcoding, pooling, size selection and sequencing on an Illumina Miniseq platform. All PCR products had strong primer dimer bands that were removed at the sequencing center just before sequencing with a size-selection procedure that selected for fragments longer than 150 bp.

Data analysis We followed the dada2 pipeline (Callahan et al., 2016) to filter and trim our sequences, identify unique sequences, merge paired reads, remove chimeras and construct an amplicon sequence variant (ASV) table. Because our amplicon varies in length, we did not trim sequences based on the quality profiles and instead just trimmed 20 bp from both the forward and reverse sequences to remove the primer sequences. Using the amplicon sequence variant table generated by dada2, we created a FASTA file with all the unique sequences recovered from our samples. We used blastn in blastplus to BLAST this FASTA file against the NCBI nr database with word size (i.e. length of initial region of exact sequence match) set to 9 bp and e-value set to 1-10. Next, we used the NCBI-taxcollector script (Dias et al., 2014) to get detailed taxonomic information for the top

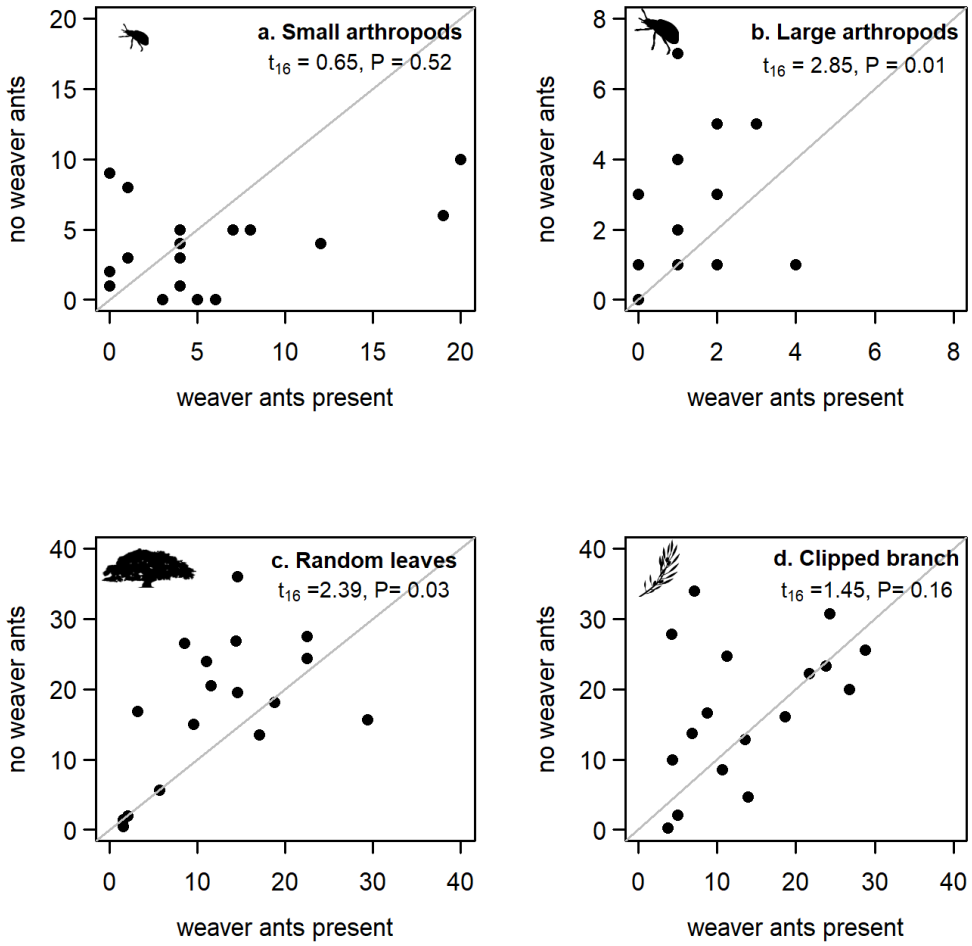
hit of our BLAST results. We filtered out sequences that were identified as bacteria or rotifers and removed potential contaminants such as sequences identified as human. Finally, we estimated overlap between the diets of weaver ants and birds at low and mid-elevations at order and family level using EcoSimR (Gotelli et al., 2015) and visualized the overlap at order, family, genus and species levels using venn diagrams and non-metric multidimensional scaling (NMDS) in R. EcoSimR is used to estimate niche overlap between species and compare it to a null distribution of niche overlap given information on resource utilization (in columns) by each species (rows). The algorithm randomizes resource utilization for each species by reshuffling the row values and generates a null distribution of niche overlap. In our case, we considered birds at low elevations, birds at mid elevations and weaver ants at low elevations as "species" and used the frequency of occurrence of different orders or families in diets as the resources. All the analyses were done in the R programming environment and in the shell using the R packages dada2 (Callahan et al., 2016), DECIPHER (Wright, 2016), VennDiagram (Chen and Boutros, 2011), ggplot2 (Wickham, 2011), vegan (Oksanen et al., 2018) and EcoSimR (Gotelli et al., 2015). All scripts and details of the steps are available as supplements to this paper.

2.4. Results

2.4.1. Effect of weaver ants on arthropod abundance

There was no significant difference in the number of small arthropods on trees with or without weaver ants (Fig. 2.1a). However, we caught almost twice as many large arthropods (>4mm length) on trees without weaver ants than in trees with weaver ants (Fig. 2.1b). Moreover, leaf damage was significantly greater on trees without weaver ants than on trees with weaver ants when leaf damage was estimated on 10 leaves from different parts of the tree (Fig. 2.1c). The difference was not statistically significant when the leaf damage on a clipped branch was compared, but it showed a similar trend (Fig.

Figure 2.1.: Non-ant arthropod abundance and leaf damage data for pairs of trees differing in the presence of Asian weaver ants. The grey line shows a slope of 1.0, i.e. points on this line indicate pairs that do not differ. **a.** Number of small arthropods (< 4mm) **b.** Number of large arthropods (> 4mm) **c.** Leaf damage estimated on 10 leaves distributed around the tree **d.** Leaf damage estimated on a clipped branch



2.1d). Overall, the results indicate that more large arthropods and greater herbivory occurs on trees without weaver ants.

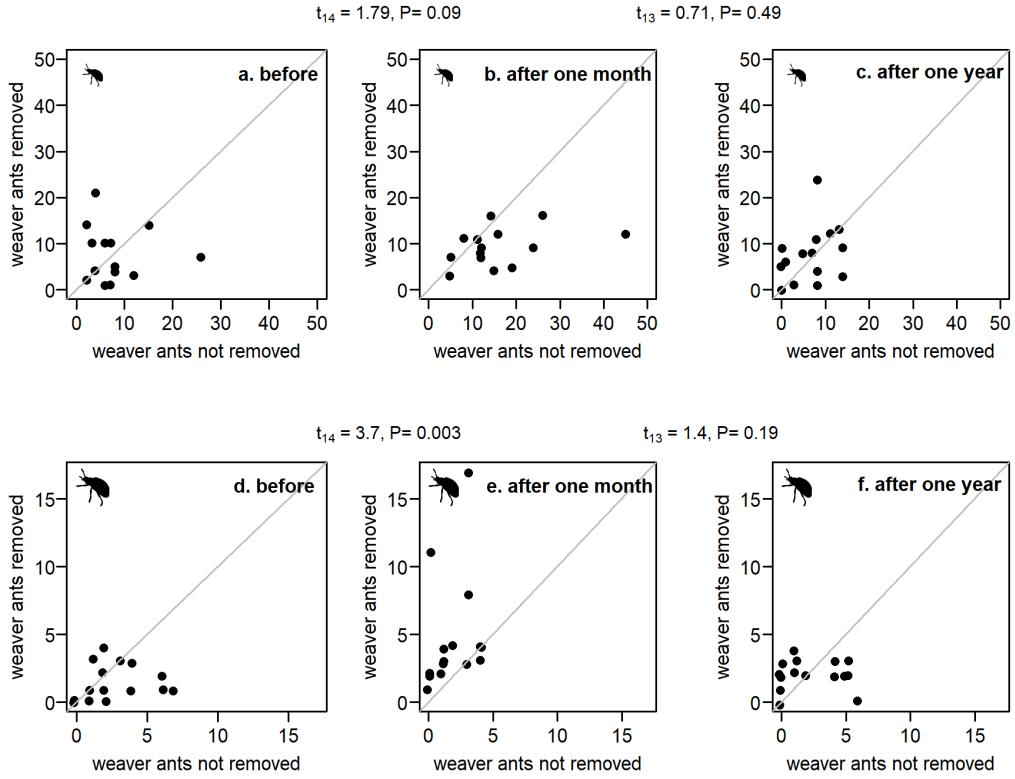
2.4.2. Weaver ant removal and exclusion experiment

Small arthropod abundance did not change significantly due to weaver ant removal and exclusion in either of the timeframes examined, although it was higher on control trees at the end of the one-month period (Fig. 2.2a-c, paired t-test results: number of arthropods one month after - before, n= 15 pairs, mean difference (control) = 11.8 ± 4.6 SE, mean difference (treatment) = -3.4 ± 5.6 SE, t = 1.79, P = 0.09; number of arthropods one year after - before, n= 14 pairs, mean difference (control) = -1.1 ± 1.9 SE, mean difference (treatment) = -5.7 ± 5.9 SE, t = 0.71, P = 0.49). We found significantly greater abundance of large arthropods (>4mm) one month after weaver ant removal and exclusion (Fig. 2.2d-e, paired t-test results: number of arthropods one month after - before, n= 15 pairs, mean difference (control) = -0.93 ± 0.69 SE, mean difference (treatment) = 3.27 ± 1.29 SE, t = 3.7, P = 0.003). However, there was no effect of the treatment on large arthropod abundance after one year of treatment (Fig. 2.2d & 2.2f, paired t-test results: number of arthropods one year after - before, n= 14 pairs, mean difference (control)= -0.5 ± 0.65 SE, mean difference (treatment) = 0.64 ± 0.4 SE, t = 1.4, P = 0.19). There was no effect of weaver ant removal and exclusion on leaf damage estimated using either 16 leaves from different parts of the tree or a clipped branch (Supplementary Fig. B.1).

2.4.3. Molecular diet analysis

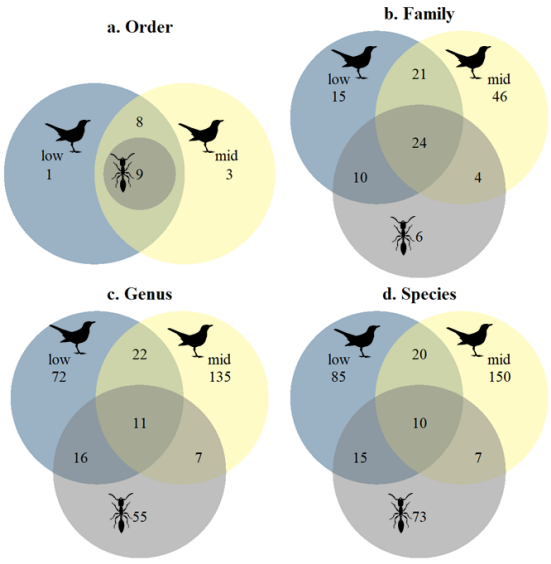
Of the 41 fecal samples collected, we were able to amplify and sequence prey DNA from 33 samples belonging to 5 bird species at low-elevations and 9 bird species at mid-elevations (Supplementary table S2.2). We were also able to amplify and sequence prey DNA from all 25 weaver ant food samples. We recovered 836 amplicon sequence variants (ASVs) from the dada2 pipeline. Of these, 695 sequences yielded BLAST matches and after filtering

Figure 2.2.: Number of small (<4mm, **a-c**) and large (>4mm, **d-f**) non-ant arthropods for each pair of control and treatment trees before (**a,d**), one month after (**b,e**) and one year after (**c,f**) weaver ant removal and exclusion. The grey line shows a slope of 1.0, i.e. points on this line indicate pairs that do not differ in arthropod abundance.



for bacteria and contaminants, we had a total of 665 sequences. Some of these BLAST matches are obviously incorrect, because the taxon identified by BLAST is not known to occur in the region. For example, our results show the order Vetigastropoda in the diet of birds at low elevation, but Vetigastropoda are exclusively marine. Such misclassifications likely arise from the lack of availability of DNA sequences for organisms in our study area. However, we think the taxonomic identifications are still valuable, because all the ASVs that are grouped together likely belong to taxonomic groups closely related to the group they are misclassified into.

Figure 2.3.: Venn diagram showing diet overlap as assessed with molecular metabarcoding between weaver ants, birds at low elevations and birds at mid-elevations at multiple taxonomic levels.



Overall, our results show that birds have an overlapping but wider diet than weaver ants. At the order level, all the orders present in weaver ant diet also occur in bird diets at low elevations (Fig. 2.3, Supplementary tables S2.3-S2.7). All of the nine orders that were found in bird diet at low elevations but absent in weaver ant diet were either relatively larger animals such as centipedes (order Scolopendromorpha), annelids (order Haplotaxida), molluscs (class Gastropoda), lizards (order Squamata) or very small arthropods such as springtails (order Entomobryomorpha), stoneflies (order Plecoptera), booklice (order Psocoptera), thrips (order Thysanoptera) and earwigs (order Dermaptera). Three

orders were detected in bird diet only at mid-elevations: lacewings (order Neuroptera), nemertean worms (order Monostilifera) and mayflies (order Ephemeroptera). The most common orders in the bird diet were the same as the orders that increased in frequency when weaver ants were removed from trees (Fig. 2.4). The one order common in bird diet that decreased dramatically after weaver ant exclusion was Hemiptera, which is expected given that it contains the suborder Homoptera and weaver ants tend Homopterans.

Table 2.1.: EcoSimR results showing observed and simulated values of diet overlap between Asian weaver ants (*Oecophylla smaragdina*) collected from 200m elevation and birds caught at about 200m and 2000m elevations in the eastern Himalaya.

Level	**Diet overlap**	**Birds 200m-Birds 2000m**	**Birds 200m-Ants 200m**	**Birds 2000m-Ants 200m**	**All three**
Order	Observed	0.86	0.87	0.73	0.82
	Simulated	0.47	0.32	0.35	0.38
	SES (P-value)	3.57(**0.001**)	3.96(**0.001**)	2.98(**0.005**)	6.12(**0.001**)
Family	Observed	0.62	0.61	0.40	0.54
	Simulated	0.39	0.24	0.30	0.31
	SES (P-value)	4.17(**0.001**)	5.67(**0.001**)	1.67(0.06)	6.76(**0.001**)
Genus	Observed	0.34	0.38	0.13	0.28
	Simulated	0.28	0.20	0.25	0.24
	SES (P-value)	1.45(0.08)	3.96(**0.003**)	2.99(0.99)	1.56(0.06)
Species	Observed	0.32	0.33	0.11	0.25
	Simulated	0.27	0.21	0.27	0.25
	SES (P-value)	1.49(0.08)	2.38(0.01)	3.9(0.99)	0.23(0.39)
ASV	Observed	0.43	0.23	0.09	0.25
	Simulated	0.17	0.24	0.27	0.23
	SES (P-value)	8.57(**0.001**)	0.20(0.58)	6.89(0.99)	1.46(0.07)

Finally, our EcoSimR results showed that the diets of birds at low elevations and weaver ants overlapped significantly more than expected at all taxonomic levels, albeit not at the ASV level. Diets of birds from low and mid-elevations also overlapped significantly or near significantly at all taxonomic levels, but the diet of birds from mid-elevations

and the diet of weaver ants did not overlap significantly at finer taxonomic scales (Table 2.1). In general, the overlap in diet is lower at finer taxonomic scales (Fig. 2.3), but that could merely be a function of sampling as indicated by the absence of asymptote in accumulation curves at finer taxonomic levels (Supplementary Fig. B.2).

2.5. Discussion

Several lines of evidence suggest that weaver ants compete strongly with birds for arthropod prey. First, we found lower abundance of large arthropods and lower herbivory on trees with Asian weaver ants at the low elevation. Next, we found that weaver ant exclusion and removal from trees results in greater abundance of large arthropods after a month, which is important because insects, particularly larger ones, are an important component of the diet of many birds (Davies, 1977; Moreby, 2004; Shortall et al., 2009b). Finally, we found significant overlap in the diet of ants and birds at low elevations at all taxonomic levels and found that the two most common orders in bird diets at low elevations, increase in abundance after weaver ant removal. Together, these results suggest that weaver ants could significantly reduce food availability for birds at low elevations, resulting in lower bird abundance and species diversity.

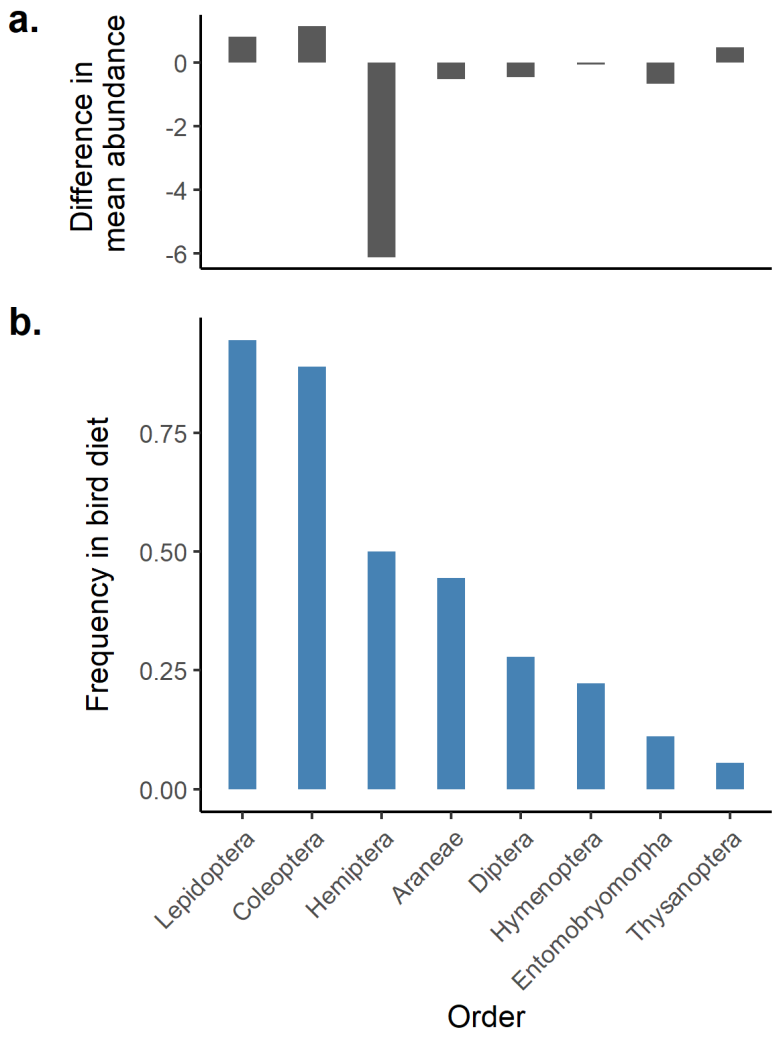
Reduced herbivory and abundance of large arthropods on trees with weaver ants is consistent with other results in the literature. Asian weaver ants are very aggressive and are used to control pest populations in orchards (Way and Khoo, 1992; Peng and Christian, 2005; Van Mele, 2008). Offenberg et al. (2004b) showed that a leaf beetle species avoided eating leaves with weaver ant pheromones on them. As in the eastern Himalaya, the presence of weaver ants is negatively correlated with leaf damage due to herbivores in mangrove forests (Offenberg et al., 2004a). More broadly, many plant species form strong mutualistic associations with ants to reduce the risk of herbivory by offering them rewards such as food bodies, extra-floral nectaries and domatia (i.e. nesting sites) (Janzen, 1966; Fiala et al., 1989; Webber et al., 2007; Chomicki et al., 2016). Even facultative or oppor-

tunistic ant-plant interactions are known to reduce herbivory and deter other arthropods from the plants occupied or visited frequently by ants (Bentley, 1977; Fiala et al., 1994; Chamberlain and Holland, 2009; Rosumek et al., 2009; Trager et al., 2010).

We confirmed the effect of weaver ants on arthropod abundance using a weaver ant removal and exclusion experiment and observed an increase in the abundance of large arthropods one month after weaver ant removal. This is consistent with other ant exclusion studies, some of which have shown that ant exclusion can have a larger impact on arthropod abundance than vertebrate exclusion (Schmitz et al., 2000; Mooney, 2007; Piñol et al., 2010). Surprisingly, we did not record any difference in large arthropod abundance one year after removal. This might be caused by the reappearance of weaver ants on some of the treatment trees and disappearance of weaver ants from many of the control trees over the course of the year. The size of weaver ant colonies changes across the year with larger extent in the wet season when brood production is high and smaller extent in the dry season when the ants evacuate from peripheral trees in their territory (Lokkers, 1990). We did not record any difference in the abundance of small arthropods, because weaver ants are omnivores and tend homopterans, so weaver ant removal often leads to a reduction in abundance of homopterans that almost balances out the increase in abundance of other small arthropods.

Finally, our molecular diet analyses showed significant overlap in the diet of weaver ants and low elevation birds at all taxonomic levels and significant overlap in the diet of weaver ants and mid-elevation birds at higher taxonomic levels. While many previous studies have presented evidence for competition between birds and ants (Supplementary table S2.1), to our knowledge, this is the first study that has directly quantified the overlap in diet between an ant species and insectivorous songbirds. Our work also demonstrates the utility of molecular diet analyses to examine dietary niche overlap between distantly related organisms. Studies of dietary niche partitioning among species are increasingly using molecular tools to get fine-scale taxonomic information on diet composition (Razgour et al., 2011; Brown et al., 2014; Kartzinel and Pringle, 2015; Arrizabalaga-Escudero et al., 2018). Due to PCR and sequencing biases, these methods do not give accurate

Figure 2.4.: a. Difference in mean abundance of major arthropod orders in control and treatment trees one month after ant exclusion and removal (derived from the data in Fig. 2.2a, 2.2b, 2.2d & 2.2e) **b.** Frequency of different arthropod orders in bird diet at low elevations



information on the quantity of dietary items (Pompanon et al., 2012; Shokralla et al., 2012). Still, we think that information on the identity and frequency of dietary items obtained using these methods can be very useful to understand the diversity patterns of dietary guilds along environmental gradients.

Overall, our results lend strong support to the idea put forth by Price et al. (2014) that absence of ants may be responsible for mid-elevational peak in songbird diversity in the eastern Himalaya. Similar competition for food may be responsible for the mid-elevational peak in small- mammal diversity in the Philippines as suggested by Heaney (2001). Other studies have shown patterns of complementary diversity patterns between ants and other arthropod groups, such as staphylinid beetles, carabid beetles and spiders (Hölldobler and Wilson, 1990; Halaj et al., 1997; Noreika and Kotze, 2012). More generally, the near-absence of ants in cloud forests (Longino et al., 2014) could be an important explanatory factor for the high diversity of many other taxa there. This still leaves the question of why ants are so rare in montane cloud forests. Previous studies have suggested that the combination of cool temperatures and humidity make cloud forests unsuitable for ants (Wheeler, 1917; Janzen, 1973b; Samson et al., 1997). However, competition from endotherms such as birds and mammals, better able to cope with cold weather, might also be an important factor. Explicit tests to compare the importance of abiotic versus biotic effects in shaping the pattern of ant abundance along elevational gradient are much needed.

Even when ants are present, they may not be behaviorally dominant in places with extreme temperatures compared to places with moderately high temperatures (Cerdá et al., 1997, 1998; Bestelmeyer, 2000; Stringer et al., 2007; Lessard et al., 2009). Patterns of ant diversity, especially pertaining to the behaviorally dominant species, might therefore be important in shaping arthropod abundance patterns and diversity patterns for competing taxa globally, and not just along tropical and sub-tropical elevational gradients (Rodríguez-Castañeda et al., 2016). A similar link between competition with ants and diversity patterns was recorded by Brown and Davidson (1977) who found complementary diversity patterns in response to annual precipitation in seed-eating ants and rodents

along a north-south gradient in the US.

Competitive interactions with ants could also have influenced the diversification patterns of birds and other taxa. Fossil evidence shows that there were many more tropical ant species in Europe during the Eocene (Wheeler, 1915; Dlussky et al., 2008; LaPolla et al., 2013)before the arrival of passerine birds in the Oligocene (Mayr and Manegold, 2004). Future studies should examine whether ants and birds have correlated diversification patterns in different regions, with care taken to separate differential responses to abiotic factors from direct biotic interactions. More broadly, the role of ecological interactions between distantly related taxa in shaping diversity patterns is especially important because these interactions could damp (Suttle et al., 2007) or enhance the effect of climate change on species abundance and range distributions, depending on the actors involved (Davis et al., 1998). Our work illustrates that competition between distantly related taxa needs to be considered more often in macroecological and macroevolutionary studies.

3. Do birds and ants compete for nesting cavities at low elevations in the eastern Himalaya?

3.1. Abstract

In the previous chapter, we showed that competition between Asian weaver ants and birds for insect prey contributes to an observed mid-elevational peak in bird species richness at about 1200 to 2000m elevation in the eastern Himalaya. In this chapter, we test whether birds and ants also compete for nesting space, a crucial resource for breeding birds, especially secondary cavity-nesters. First, we compared the abundances of primary and secondary cavity nesters at 200m, 1200m and 2000m elevation. We found relatively higher abundance of primary cavity nesters compared to secondary cavity nesters at 200m elevation but not at 1200m and 2000m. This suggests that cavity production should be higher, and cavities should be abundant at 200m elevation. Next, we asked if birds prefer or avoid using nest boxes located on trees with Asian weaver ants and found no evidence for either. We recorded extensive use of nest boxes by birds at 200m elevation and none at 1200m, suggesting nest-site limitation at low elevations for secondary cavity nesters. This nest-site limitation might be caused by the extremely high abundance of arboreal ants at low elevations. Ants occupied many nest boxes at 200m elevation but less so at 1200m. Ants preferentially used nest boxes following bird use due to the presence of

nesting material left in those boxes. Overall, we find some preliminary evidence suggesting that ants reduce availability of nesting spaces for birds at low elevations in the eastern Himalaya.

3.2. Introduction

In the eastern Himalaya, species richness of breeding birds peaks at the cooler mid-elevations around 2000m, instead of the warmer and equally wet low elevations (Price et al., 2014). In the previous chapter, we showed that competition for arthropod prey between birds and Asian weaver ants at low elevations might contribute to this pattern. While food is an important resource for breeding birds, nesting space could also be a crucial limiting factor. Nesting space is especially important for cavity- nesting species that depend on pre-existing cavities, i.e. secondary cavity nesters (Newton, 1994; Cockle et al., 2010; Robles et al., 2012). In this chapter, we assess if availability of nesting cavities contributes to the mid-elevational peak of bird species richness in the eastern Himalaya, and if ants play a role in reducing the availability of cavities at low elevations.

Availability of nesting cavities might be limited by the rate of cavity production and persistence or by factors that reduce desirability or accessibility of the cavities. Cavities are produced either by primary cavity-nesting birds such as woodpeckers or by mechanical or invertebrate damage and fungal decay (Aitken et al., 2002; Gibbons and Lindenmayer, 2002; Wesołowski, 2007; Cooke and Hannon, 2011; Cockle et al., 2012). Therefore, cavity production might be affected by abundance and behavior of cavity excavating birds, amount of fungal activity or traits of trees such as girth (Cockle et al., 2010, 2011). On the other hand, an area might be cavity-rich but many of the cavities may not be desirable due to biotic interactions such as a higher risk of predation (Brightsmith, 2005). Alternatively, many cavities might simply not be accessible because of occupation by other animals (Walker et al., 2005).

Most studies on nest-site limitation have focused on inter-specific competition between

bird species (Merilä and Wiggins, 1995; Edworthy, 2015; Kattan, 2016; Wiebe, 2016), but more distantly related taxa could also compete with birds for cavities. Indeed, cavities are an important resource for many taxa, including small mammals, reptiles, amphibians, social hymenopterans and spiders (Gibbons and Lindenmayer, 2002; Lindenmayer et al., 2009; Warakai et al., 2013; Bonaparte and Cockle, 2017; Manikandan and Balasubramanian, 2018; Veiga et al., 2013a). Despite being distantly related, these cavity users often overlap in their nesting or roosting niche and might compete for high-quality cavities. For example, Bonaparte and Cockle (2017) found high overlap in nesting niche and cavity reuse between birds, opossums, social bees and wasps. In a nest box study, Jablonski et al. (2013) found that bumblebees use warning signals to oust breeding birds from their nests and take over the nest box. However, interactions between these cavity users are not always competitive; mutualistic, facilitative or neutral interactions have also been observed Veiga et al. (2013a). For example, Myczko et al. (2017) reported coexistence between noctule bats and European starlings in natural cavities. Overall, these interactions could play an important role in shaping patterns of cavity availability across environmental gradients.

Specifically, we are interested in the role of interactions between birds and ants on the pattern of cavity availability along an elevational gradient in the eastern Himalaya. Ants are extremely abundant at the low elevations, but almost absent at the mid-elevations, coincident with the peak in bird species richness(Price et al., 2014). Therefore, we ask if ants might play a role in limiting the availability of cavities to birds at low elevations. Ants may reduce the desirability or accessibility of cavities, i.e. birds might avoid nesting near aggressive arboreal ants (Davis et al., 2008) or the presence of ants in a nesting cavity might preclude use of that cavity by birds (Walker et al., 2005; Lambrechts and Schatz, 2014). Alternatively, birds might prefer nesting on trees with colonies of aggressive ants in order to reduce predation risk (Janzen, 1969; Young et al., 1990; Quinn and Ueta, 2008). Preferences may vary with the intensity of that risk. For example, Haemig (1999) showed that birds prefer nesting on trees with ants in forest edges where predation risk is higher but otherwise avoided trees with ants. At low elevations in the eastern Himalaya,

Asian weaver ants *Oecophylla smaragdina* occur in almost 15% of trees (pers. comm. Vinod Shankar) and are known to be very aggressive (Basu, 1997; Peng and Christian, 2004; Van Mele, 2008). In Africa, some bird species preferentially nest near colonies of African weaver ants *Oecophylla longinoda* (Maclaren, 1950; Grimes, 1973), and we hypothesize that similar protective associations might be formed with the Asian weaver ants, to reduce predation risk. Finally, birds might facilitate the use of a nesting cavity by ants (Mitrus et al., 2016).

Here, we ask if cavity availability could contribute to the lower diversity of breeding birds at these elevations in the eastern Himalaya. First, we evaluate the distribution of cavity nesting species across the elevational gradient. Then, to assess if cavity production is lower at low elevations, we compared the abundance of secondary cavity nesting birds (i.e. birds that use pre-existing cavities) to primary cavity nesting birds (i.e. birds that excavate their own cavities). If cavity production is lower at low-elevations compared to mid-elevations, we would expect the ratio of primary cavity nesters to secondary cavity nesters to be lower. Next, we deploy nest boxes to test whether arboreal ants play a role in reducing the desirability or accessibility of cavities at low elevations. We evaluate whether birds prefer or avoid nest boxes on trees with high frequency of the extremely aggressive Asian weaver ants. We compare the use of nest boxes by ants and birds at low and mid-elevations and assess whether use of a nest box by ants at low elevations reduces the likelihood of its use by birds. Finally, we test if birds facilitate the use of nest boxes by ants by examining whether presence of a bird nest increases the likelihood of ants using a nest box.

3.3. Methods

3.3.1. Comparison of primary & secondary cavity-nesters at low and mid-elevations

We collected data on species richness and abundances of birds at about 200m (Chapramari wildlife sanctuary, 26.89°N, 88.83°E), 1200m (Eaglenest wildlife sanctuary, 27.03°N, 92.41°E) and 2000m elevations (Neora Valley national park, 27.06°N, 88.77°E) in eastern Himalaya from the supplement in Price et al. (2014) (see grids B1, B4, B5 and A4 in supplement S11 and S12). From these data, we derived the average abundance of each bird species per 5 Hectare grid at 200m, 1200m and 2000m elevations. We also compiled bird species lists expected at these elevations based on elevational range interpolation data from the supplement in Price et al. (2014) (supplement S10). Next, we compiled information on bird nesting behavior from the Birds of South Asia: the Ripley guide (Rasmussen and Anderton, 2005), Barve and Mason (2015), van der Hoek et al. (2017), Ali and Ripley (1972) and Ali and Ripley (1973). We carried out a chi-square test to assess if the ratio of primary and secondary cavity nesting species is similar at all three elevations using both the grid survey and range interpolation data. Next, we repeated the chi-square test using the data on abundances (i.e. number of individuals) of primary and secondary cavity-nesting birds. Some secondary cavity nesting species are facultative cavity nesters, i.e. they are not entirely dependent on cavities. Therefore, we repeated our chi-square analyses using abundances of primary and obligate secondary cavity nesters.

3.3.2. Evaluating the role of weaver ants on nest box choice

In June 2015 and April 2016, we put up 128 open-fronted nest boxes at a height of about 1.5m in Chapramari wildlife sanctuary (26.89°N, 88.83°E, elevation 200m; see Fig. C.1 for a diagram of the nest box and Fig. C.2 for a map showing location of the nest boxes).

We monitored the next boxes at weekly intervals during the bird breeding season between mid-April and June in 2016 and 2017. At each visit, we recorded the presence or absence of weaver ants on the tree and bird eggs or chicks in the nest boxes. Three nest boxes were damaged by elephants early in the breeding season in 2016 and an additional 36 were destroyed by the beginning of the 2017 breeding season, so we excluded those from analyses. To ask if the frequency of weaver ant presence on trees affects the probability of use of a nest box by birds, we fit generalized linear mixed models using the package lme4 (Bates et al., 2015) in the R programming environment (R Core Team, 2014). We fit three models with weaver ant frequency as the fixed effect and either year or nest box identity or both as crossed random effects. We also fit a random-effects only model with nest box identity as the random effect. We used the package MuMin (Bartoń, 2016) to compare AICc values of the four models.

3.3.3. Evaluating the role of arboreal ants on limiting nesting cavities at low elevation

In addition to open-fronted nest boxes at the low-elevations described in section 3.3.2, in May 2016, we put up 30 open-fronted nest boxes at a 1200m elevation site in Neora Valley National Park (Mouchaki camp: 27.03°N, 88.78°E; see Fig. C.3 for a map showing the location of these nest boxes). Note that this 1200m elevation site is not the same as the 1200m elevation site in section 3.3.1 because it was not sampled by Price et al. (2014). However, we conducted our nest box study here because it is closer to our low-elevation site, and bird composition is similar to the sampled site (Price et al., 2014). Because different bird species prefer different nest box designs, we added additional hole-type nest boxes at both elevations in April 2017. We put up 60 nest boxes each at low and mid-elevations, half of which had a hole diameter of 25mm and the rest had a hole diameter of 30mm.

In 2016, when we only had open-fronted nest boxes, we recorded the identity of the

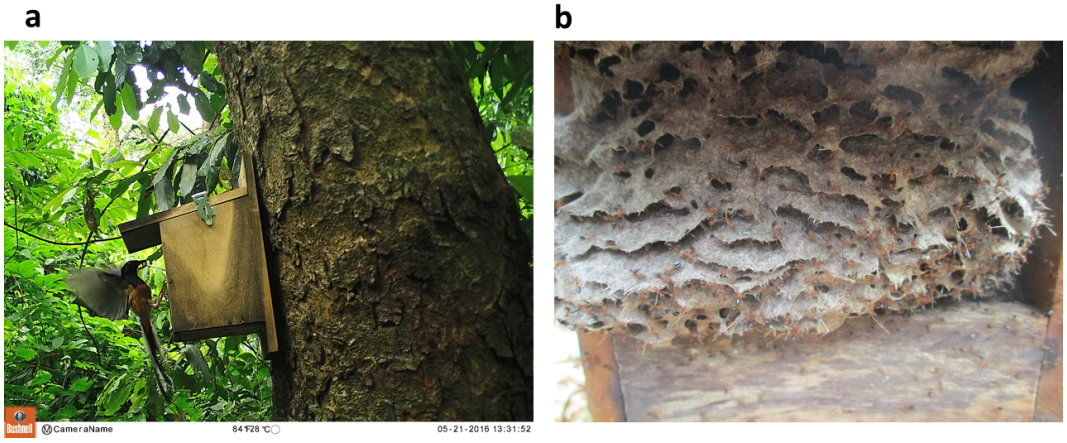
occupants at weekly intervals at the more accessible low elevations from mid-April - June and biweekly intervals at the 1200m elevation from early May - June. In 2017, when we had all three kinds of nest boxes, we continued checking nest boxes at weekly intervals at low elevations and checked them on two occasions at 1200m elevation, once in mid-May and then at the end of May. We were unable to continue checking nest boxes at 1200m elevation at biweekly intervals in June due to political unrest in the region. We assembled our data from the 11 visits to nest boxes at 200m elevation in April-June 2017 with columns for nest box ID, week of visit, state of a nest box at a given visit and state of the same nest box at a previous visit.

All the nest boxes used by birds at low elevations were used by a single species, the white-rumped Shama (*Kittacincla malabarica*), hereafter called the Shama (Fig. 3.1a). To evaluate the effect of ants on the use of a nest box by Shama at the low elevations, we coded presence of nesting birds at a visit (i.e. "Shama") as a binary outcome and removed rows where the state at the previous visit was "Shama". We also removed rows where the states transitioned from "ant" to "other" and vice versa. "Other" state usually comprised of nest boxes that were unoccupied at the moment but might have an old Shama nest inside. On some occasions, "Other" state included nest boxes with other arthropods such as a wasp, spider or termites. We fit a generalized linear mixed model with the state of the nest box at the previous visit (i.e. "Ant" or "Other") as the fixed effect and week of visit and nest ID as crossed random effects. We compared the fit and AICc values for this model to a model with no fixed effect. We noticed that ants from the genus *Crematogaster* tend to create more nesting structures in the boxes and are therefore more likely to be able to exclude birds from the nest boxes (Lambrechts et al., 2008). Therefore, we repeated these analyses with "*Crematogaster*" and "Other" as the previous state. For these analyses, we pruned our dataset to remove rows where the previous state was ants that did not belong to the genus *Crematogaster*.

Finally, we asked whether presence of a bird nest in a nest box increases the probability of use of the nest box by ants at low elevations. We coded ant presence in a nest box at each visit as a binary outcome and removed rows where ants were present in the nest

box at the previous visit. We fit a GLMM with nest box status at previous visit (i.e. "Shama", "Old nest", "Empty") as the fixed effect and week of nest box visit and nest box ID as crossed random effects. We compared the fit and AICc values of this model to a model with no fixed effects. We used the R package lme4 (Bates et al., 2015)for all GLMMs and the package MuMIN (Bartoń, 2016) for all AICc values.

Figure 3.1.: a. Open-fronted nest box with a White-rumped Shama (*Kittacincla malabarica*) feeding the chicks **b.** Ants of *Crematogaster sp.* nesting in one of the open-fronted nest boxes.



3.3.4. Evaluating the role of substrate in determining the probability of nest box use by ants

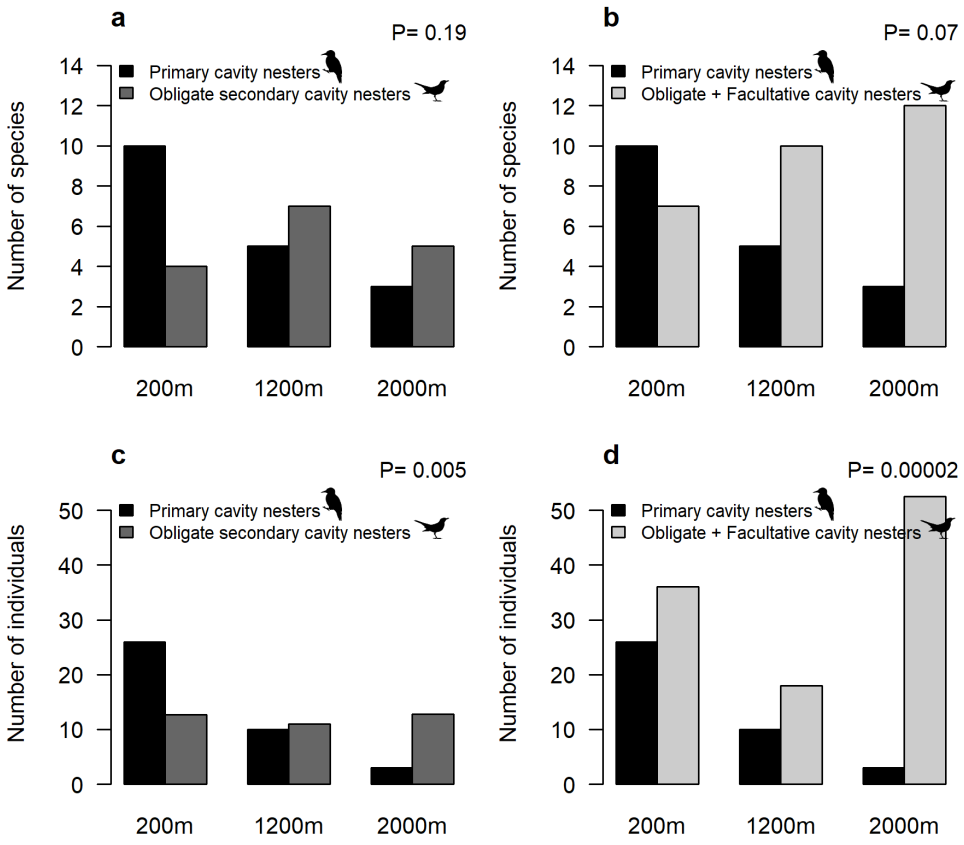
Using the hole-type nest boxes added in 2017, we carried out an experiment to assess if ants prefer using nest boxes with some leafy substrate added to it. We added leaves from the forest floor in half of the nest boxes of each hole-size at both 200 and 1200m elevations. We used chi-square tests to assess if presence of substrate in the nest boxes affects the probability of nest box use by ants at 200 and 1200m elevation. Because we had data from more visits at 200m elevation leading to more observations of ants in the nest boxes there, we repeated the chi-square tests for both elevations with data from a

single visit about 40-50 days after putting up the nest boxes.

3.4. Results

3.4.1. Comparison of primary & secondary cavity-nesters at low and mid-elevations

Figure 3.2.: a. Number of species of primary and obligate secondary cavity nesting species at different elevations. **b.** Number of species of primary and all secondary (i.e. obligate + facultative) cavity nesting species at the same sites **c.** Abundances (i.e. average numbers/5 ha grid) of primary and obligate secondary cavity nesting species at the same sites **d.** Abundances (i.e. average numbers/5 ha grid) of primary and all secondary cavity nesting species at the same sites. All data based on surveys of breeding birds in 5 hectare grids at 200, 1200 and 2000m elevations in eastern Himalaya from Price et al. (2014). P-values were obtained from chi-square tests. Animal silhouettes taken from phylopic (http://phylopic.org/) and incorporated in the figure using the package rphylopic (https://github.com/sckott/rphylopic)



The number of obligate secondary cavity nesting species is very similar across the three elevations (Fig. 3.2a & Fig. C.4). However, when facultative secondary cavity nesting species are included, there are 1.3- 1.7x more secondary cavity nesting species at 2000m elevation than at 200m (Fig. 3.2b & Fig. C.4). Based on the species lists from grid surveys, there are more primary cavity nesting species at low elevations and the ratio of primary to secondary cavity nesters is almost significantly different ($\chi^2 = 5.31$, df = 2, P = 0.07, Fig. 3.2a). However, the range interpolation data shows a similar number of primary cavity nesters across all elevations (Fig. C.4).

In terms of individual abundances, the ratio of primary cavity nesting birds to both obligate and all secondary cavity nesters was significantly different between the three elevations (Fig. 3.2). There were more primary cavity nesters compared to obligate secondary cavity nesters at 200m elevation and more obligate secondary cavity nesters than primary cavity nesters at 2000m (χ^2= 10.6, df = 2, P = 0.005). When facultative secondary cavity nesters are included, secondary cavity nesters outnumber primary cavity nesters at all elevations, but the difference in their abundance increased sharply with elevation ($\chi^2 = 21.3$, df =2, P = 0.00002). Thus, we did not find any evidence for lower cavity production at low elevations and suggest that there should be more cavities at low elevations.

3.4.2. Effect of weaver ant presence on nest box use

The models with frequency of weaver ant presence on the tree as a fixed effect, nest box use by a bird as the binary dependent outcome and year or nest box identity as a random effect had slightly higher AICc values compared to models with no fixed effect (ΔAICc = 0.4). This indicates that frequency of weaver ant presence on trees does not explain any variation in nest box use by these birds (Fig. C.5, GLMM results: Mean $\pm$ SE= -0.29 $\pm$ 0.49, P = 0.55).

3.4.3. Use of nest boxes by ants and birds at low and mid-elevation

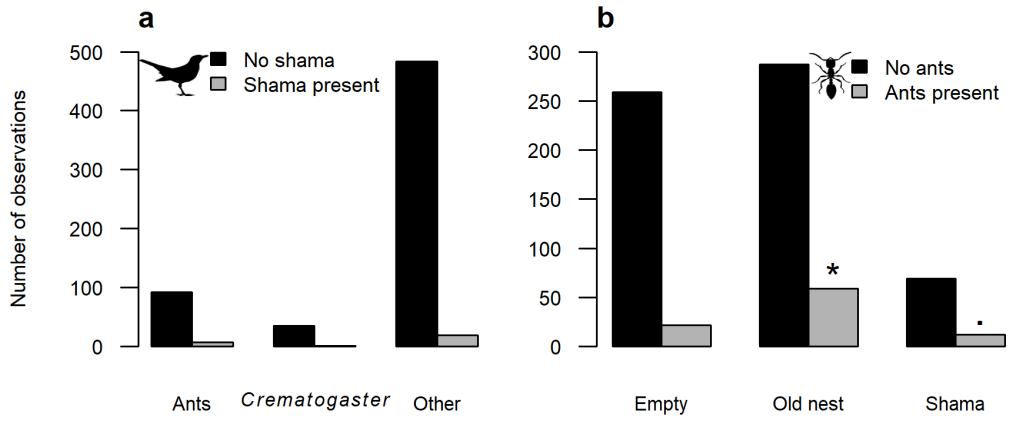
In 2016, 58 of 124 (46.8%) nest boxes were used by the Shama at the 200m elevation site. We also found Shama nests in 41 out of 84 (50.6%) open-fronted nest boxes in 2017. However, not a single nest box of either open-fronted or hole-type design was used by any bird species at 1200m elevation in either 2016 or 2017. In 2017, when we recorded ants systematically, we found ants at least once over 11-13 visits in 61 out of 84 (72.6%) open-fronted nest boxes at the 200m elevation. 53 out of 61 of these nest boxes (90.2%) contained ants belonging to the genera *Camponotus*, *Crematogaster*, *Dolichoderus*, *Pheidole*, *Polyrhachis* and *Tapinoma* (see Supplementary table S3.1 for the identity of nest box occupants at each of the visits at 200m elevation). At 1200m elevations, we found ants in 3 out of 23 (13%) open-fronted nest boxes over two visits in 2017. All of these belonged to the genera *Camponotus* or *Polyrhachis*.

Our nest box monitoring at the 200m elevation site from 2017 shows that presence of ants in a nest box at the previous visit did not affect the likelihood of finding a nesting bird at the following weekly visit (Fig. 3.3a). In fact, a GLMM with nesting bird, i.e. Shama as a binary response, nest box status as fixed effect, week and nest box ID as random effects had a higher AICc value (ΔAICc = 2.02) compared to a similar model with no fixed effect. 17 out of 84 (20.2%) open-fronted nest boxes monitored in 2017 had *Crematogaster* ants in them at least once over 11-13 visits, but the ants completely obstructed the nest box entrance in only 3 nest boxes (3.6%). Presence of *Crematogaster* did not have a significant effect on the likelihood of finding a nesting bird at the following visit, even though we only recorded one instance of transition from *Crematogaster* to Shama (Fig. 3.3a). A model with no fixed effects had a lower AICc value compared to a model with nest box status at the previous visit (i.e. *Crematogaster* or other) as a fixed effect (ΔAICc = 2.03).

On the other hand, nesting by Shamas facilitated the use of a nest box by ants. Ants used a nest box more often when there was an old bird nest (GLMM, Mean $\pm$ SE= 0.89 $\pm$ 0.3, P = 0.003) or a nesting bird (GLMM, Mean $\pm$ SE= 0.8 $\pm$ 0.43, P = 0.06) observed at the

previous visit (Fig. 3.3b). The GLMM model with nest box status ("Old nest", "Shama" or "Empty") as a fixed effect performed better than a random-effects only model (ΔAICc = 5.32).

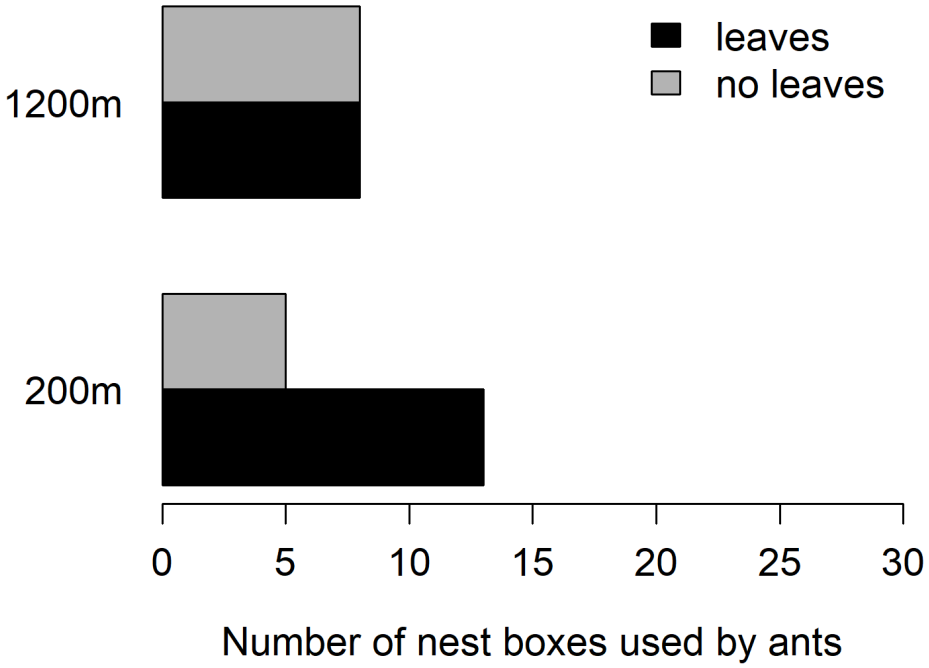
Figure 3.3.: a. Likelihood of use of nest boxes by shama does not depend on the previous state of the nest box (i.e. ants, Crematogaster or "other") **b.** Likelihood of use of nest boxes by ants depends on the previous state of the nest box (i.e. shama, old nest or empty). Animal silhouettes taken from phylopic (http://phylopic.org/) and incorporated in the figure using the package rphylopic (https://github.com/sckott/rphylopic)



3.4.4. Role of leafy substrate in determining the probability of nest box use by ants

At the 200m elevation site, at least once over the course of 8-12 visits, 26 of the 31 hole-type nest boxes with leaves in them were colonized by ants compared to only 14 of 29 nest boxes without any leaves (χ^2= 7.02, df = 1, P = 0.008). We found a similar pattern at 200m elevation when we analyzed the data from a single visit with ants in 13 out of 27 nest boxes with leaves compared to only 5 out of 29 of empty boxes (Fig. 3.4, χ^2 = 4.79, df = 1, P = 0.029). However, at 1200m elevation, the number of nest boxes used by ants was identical irrespective of the addition of leaves (Fig. 3.4).

Figure 3.4.: Number of nest boxes with ants at a single visit at 200 and 1200m elevations with two nest box treatments: leaves added or no leaves added.



3.5. Discussion

Overall, our observation of high use of nest boxes by birds at low elevations compared to no use at mid- elevations suggests that nesting cavities might be a limiting resource at low elevations. Despite being densely placed, almost 50% of our open-fronted nest boxes at low elevations were occupied by breeding birds. This is on the higher end of nest box occupancy reported by other studies, including studies in the tropics and subtropics. For example, in sub-tropical Atlantic forests, Cockle et al. (2010) found birds in only 1 or 2 out of 15 nest boxes per year. Similarly, only 2% of nest boxes were occupied by birds in a study in lowland Peru (Brightsmith, 2005), 2.6% in New Guinea (Warakai et al., 2013) and 20% in a study in savannahs and forests in Kenya Veiga et al. (2013a). In contrast, we tried nest boxes of three different designs at the mid-elevations around 1200m and none of those were used by birds.

All our nest boxes at low elevations were occupied by a single species of bird, the White-

rumped Shama, which is known to use a high percentage of nest boxes offered in other studies as well (Palko and Kalyakin, 2011; Chotprasertkoon et al., 2017; Angkaew et al., 2019). Therefore, an alternate explanation for the stark difference in nest box use at low and mid-elevations might be that Shamas merely prefer these boxes over natural cavities and that there are no understory secondary cavity nesting species at the 1200m elevations. This is unlikely because many of our nest boxes were occupied within a week, even though they were placed after the breeding season had started. This suggests that many of our nest boxes were occupied by pairs that were unable to find natural nesting cavities. Additionally, there are many understory secondary cavity-nesting species at the 1200m elevation such as the small Niltava (*Niltava macgrigoriae*), large Niltava (*Niltava grandis*) and the pale blue flycatcher (*Cyornis unicolor*) that did not occupy the nest boxes. We argue that our nest boxes were only occupied by the Shama at low elevations because it is the most abundant bird in the understory and might be behaviorally dominant over other understory birds. This view is supported by our observation of a black-naped monarch (*Hypothymis azurea*) nest in one of our nest boxes that did not proceed to egg-laying for unknown reasons. Extensive use of nest boxes by Shamas at our field site and elsewhere might indicate nesting cavity limitation for understory birds across moist lowland forests in south and south-east Asia.

Nesting cavity limitation at the low elevations is unlikely to arise from a low cavity production rate, given the extremely high abundance of primary cavity nesters at these elevations (Fig.3.2). We recognize that non-excavated cavities constitute a large percentage of the cavities used by birds (Bai et al., 2003; Wesołowski, 2007; Cornelius et al., 2008). For example, in the Sal forests of Nepal, which are similar to the forests at our low elevation site, only 27.9% of cavities were excavated by birds (Baral et al., 2018). However, we do not have any evidence that decay processes leading to such cavities are slower or that cavity loss through treefall is higher at the low elevations. Moreover, cavities created by excavating birds such as woodpeckers might be preferred by some secondary cavity nesters (Politi et al., 2009; Sandoval and Barrantes, 2009; van der Hoek et al., 2017). Thus, our results suggest that nesting cavity limitation at low elevations derives

not from lower cavity production, but from interactions with other taxa, including ants. We did not find any evidence that birds preferentially choose nest boxes on trees with weaver ants. However, we recorded many instances of other arboreal ant species breeding in the nest boxes. Other studies have also reported ants colonizing and breeding in nest boxes (Palko and Kalyakin, 2011; Veiga et al., 2013b; Lambrechts and Schatz, 2014), and artificial nests with entrance diameters large enough to be used by birds, have been colonized in studies of arboreal ants (Powell et al., 2011; Jiménez-Soto and Philpott, 2015). We observed three instances of ants belonging to the genus *Crematogaster* completely blocking the entrance to nest boxes with their carton nests in 2017 (Fig. 3.1b). Consistent with our field observations, Lambrechts et al. (2008) reported blocking of nest box entrances by *Crematogaster scutellaris* in the Mediterranean. Moreover, a study on the nesting of Shamas in Vietnam found many of the same ant genera occupying nest boxes as we did, and suggested that the ant *Polyrhachis armata* might compete with Shamas for cavities (Palko and Kalyakin, 2011). Thus, occupation of a nest box by ants might preclude birds from using it. However, contrary to our expectations, birds occupied nest boxes with or without ants at similar proportions at low elevations (Fig. 3.3a), although not the nest boxes where the entrance was completely blocked by *Crematogaster* species. One explanation for this might be that we added so many nest boxes to the area that we removed any nest box limitation. We suggest that future studies should employ nest boxes at different densities on multiple sites in a similar habitat to better examine competition between birds and ants for nest boxes. Moreover, setting up video recorders inside nest boxes or natural nesting cavities would reveal more details on cavity turnover between species.

We found that ants use nest boxes with some leaves inside more often than empty nest boxes (Fig. 3.4). Natural cavities are unlikely to be as empty and smooth as new nest boxes and therefore, nest boxes with some leaves might better resemble natural cavities and might indicate that it is a good nesting site. Therefore, natural cavities might be more often occupied by ants compared to nest boxes. Some surveys of natural cavities have reported use of cavities by ants (Walker et al., 2005; Mitrus et al., 2016). It is

difficult to assess if ants were actually not present in other studies of natural cavities or merely not recorded because they were not the subject of study. Interactions between cavity nesting birds and ants are not limited to competition. For example, Mitrus et al. (2016) suggest that ants belonging to the species *Lasius brunneus* preferentially cohabit cavities with great tits *Parus major* and marsh tits *Poecile palustris* for thermal benefits. Future studies should examine natural cavities for interactions between birds and ants in tropical and subtropical low-elevation forests where arboreal ants are abundant.

While ants might play an important role in moist tropical and subtropical forests, other taxa may be major competitors for cavity nesting birds in other sites (Gibbons and Lindenmayer, 2002; Jablonski et al., 2013; Veiga et al., 2013a; Bonaparte and Cockle, 2017). We recorded instances of use of nest boxes by spiders, large caterpillars, potter wasps and cockroaches. Based on our study and literature review, we recommend that future studies should examine interactions between different taxa for use of nesting cavities in different habitats to gain insights into the diversity and distribution of cavity-nesting bird species. Combined with our findings of competition between Asian weaver ants and birds for arthropod prey, our results suggest that near-absence of ants at mid-elevations plays an important role in shaping the mid-elevational peak in bird species richness. More generally, our work shows that use of resources such as food and nesting or roosting space by distantly related species can play an important role in shaping patterns of species diversity.

A. Supplementary figures, chapter 1

Figure A.1.: Pattern of non-ant arthropod abundance along elevational gradients. Latitude, location and Study ID (see Table S1) are indicated on top of each panel. Elevation in meters is indicated on the bottom of each panel and ranges from 0-4000m for all the plots. The curves show loess smooth fits to the data. Abundance data were standardized to have a mean of zero and standard deviation of one before plotting.

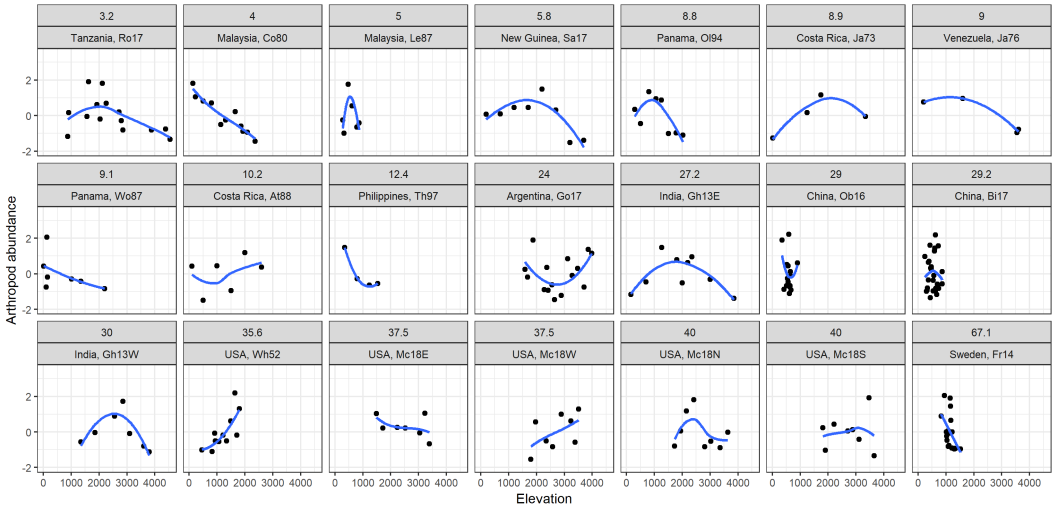


Figure A.2.: Pattern of non-ant arthropod abundance (black filled circles) and ant abundance (red filled circles) along elevational gradients. Latitude, location and Study ID are indicated on top of each panel. Elevation in meters is indicated on the bottom of each panel. The curves show loess smooth fits to the non-ant arthropod abundance data. Abundance data were standardized to have a mean of zero and standard deviation of one before plotting.

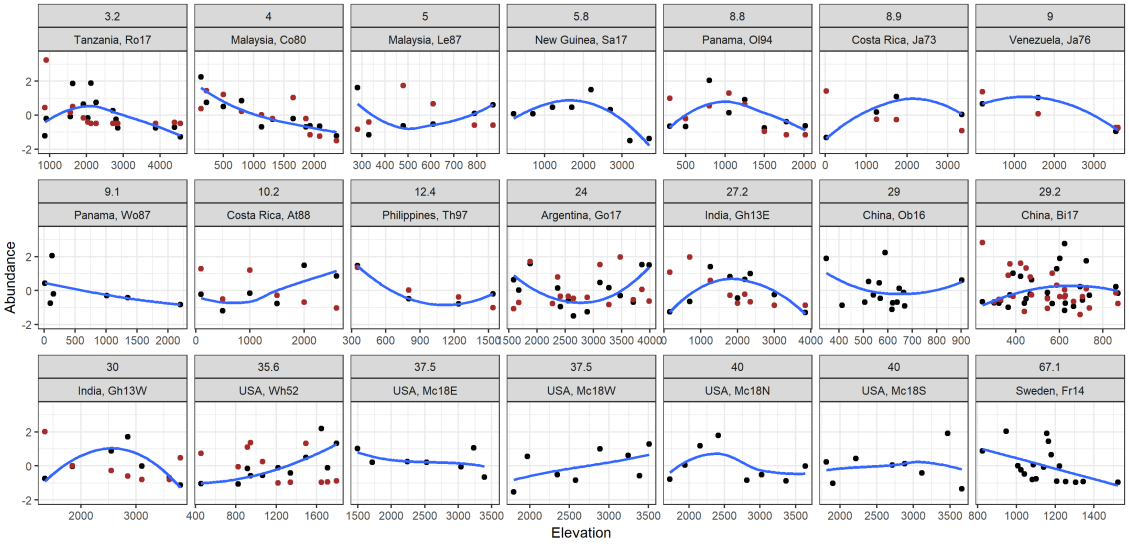
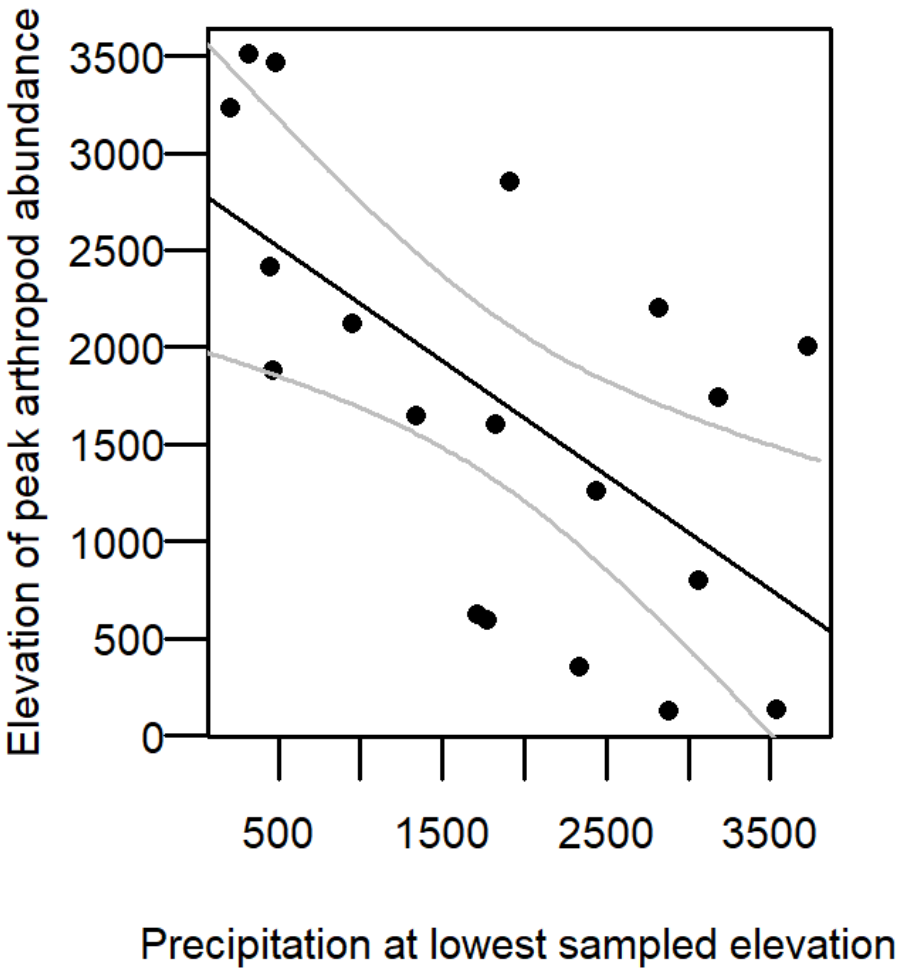


Figure A.3.: Elevation of peak arthropod abundance is negatively correlated to the amount of precipitation at the lowest sampled site. Grey lines indicate 95% confidence interval.



B. Supplementary figures, chapter 2

Figure B.1.: Leaf damage on each pair of control and treatment trees before (a,d), one month after (b,e) and one year after (c,f) weaver ant removal and exclusion. The grey line shows a slope of 1.0, i.e. points on this line indicate pairs that do not differ in arthropod abundance. (a-c) leaf damage estimated using either 16 leaves from different parts of the tree (d-f) leaf damage estimated on a clipped branch (all P> 0.05)

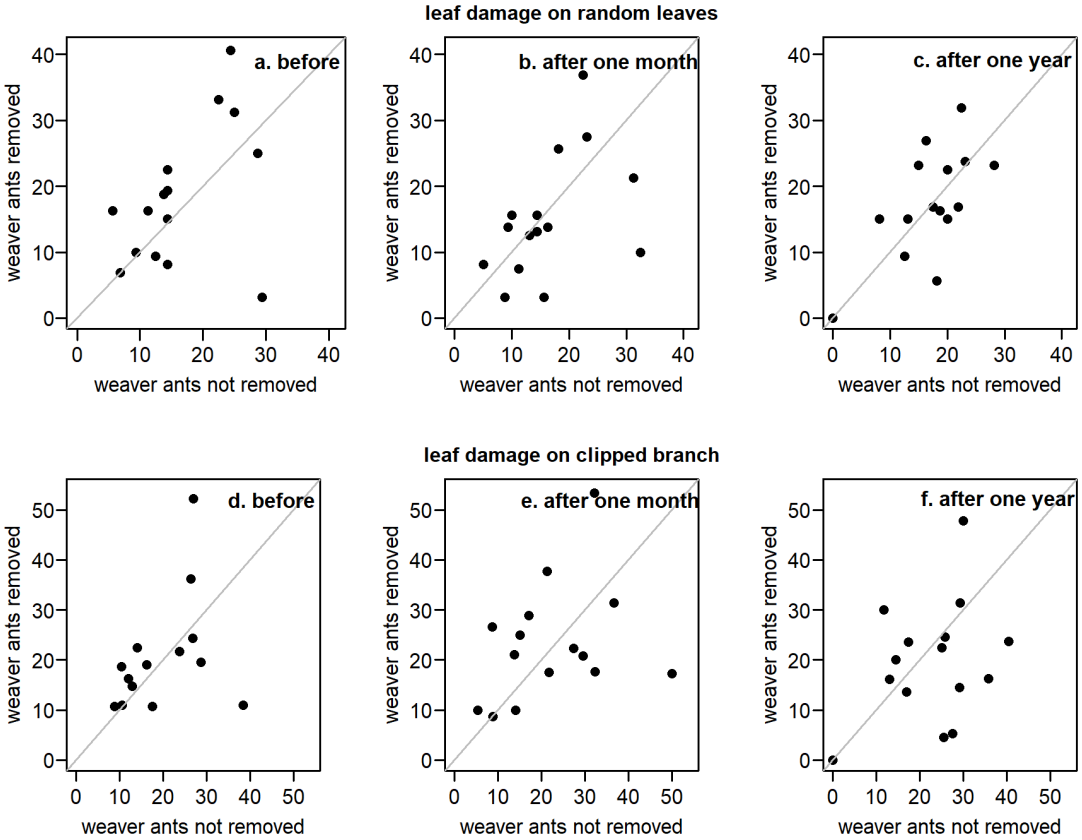
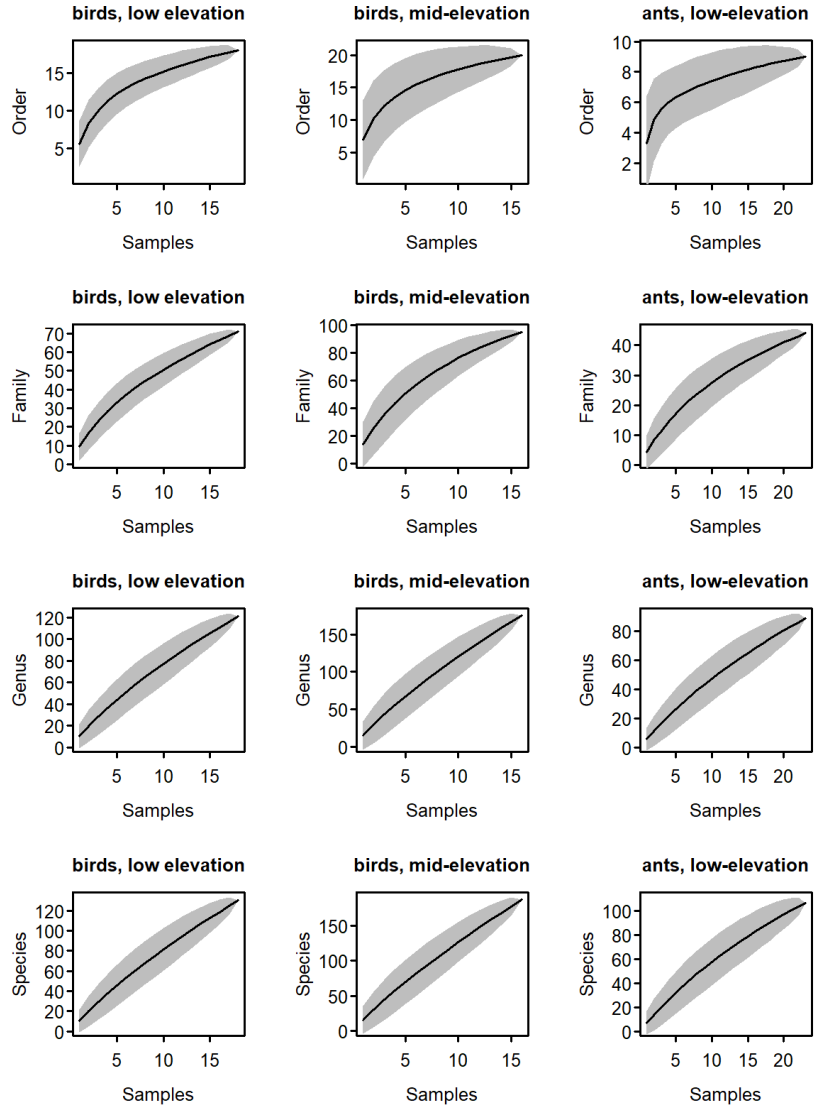


Figure B.2.: Taxa accumulation curves at order, family, genus and species levels for the diets of birds at low and mid-elevations and Asian weaver ants.



C. Supplementary figures, chapter 3

Figure C.1.: Diagram of an open-fronted nest box with the dimensions used in our study. This design was derived from the robin nest box plan provided by the British Trust for Ornithology (https://www.bto.org/about-birds/nnbw/make-a-nest-box)

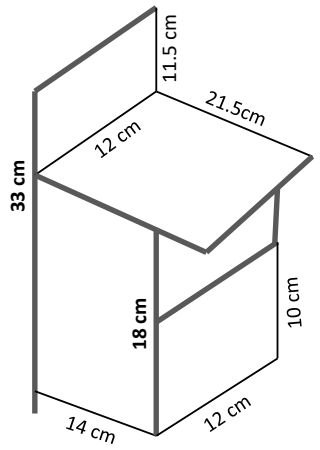


Figure C.2.: Map showing location of the open-fronted nest boxes at 200m elevation in Chapramari Wildlife Sanctuary.

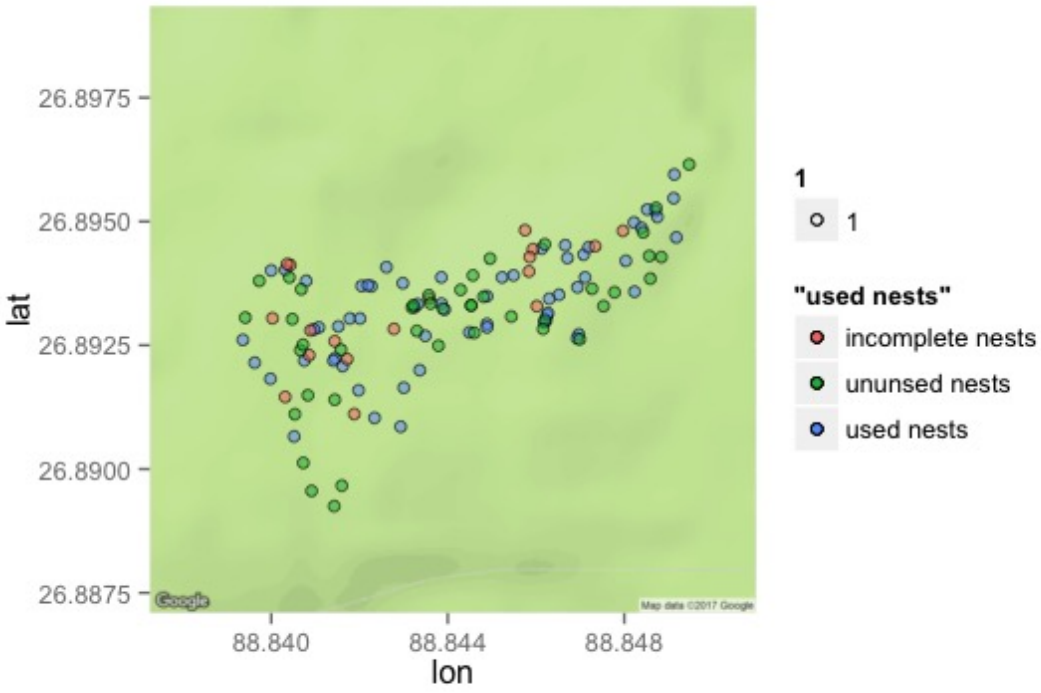


Figure C.3.: Map showing location of open-fronted nest boxes at 1200m elevation around Mouchaki camp in Neora Valley National Park.

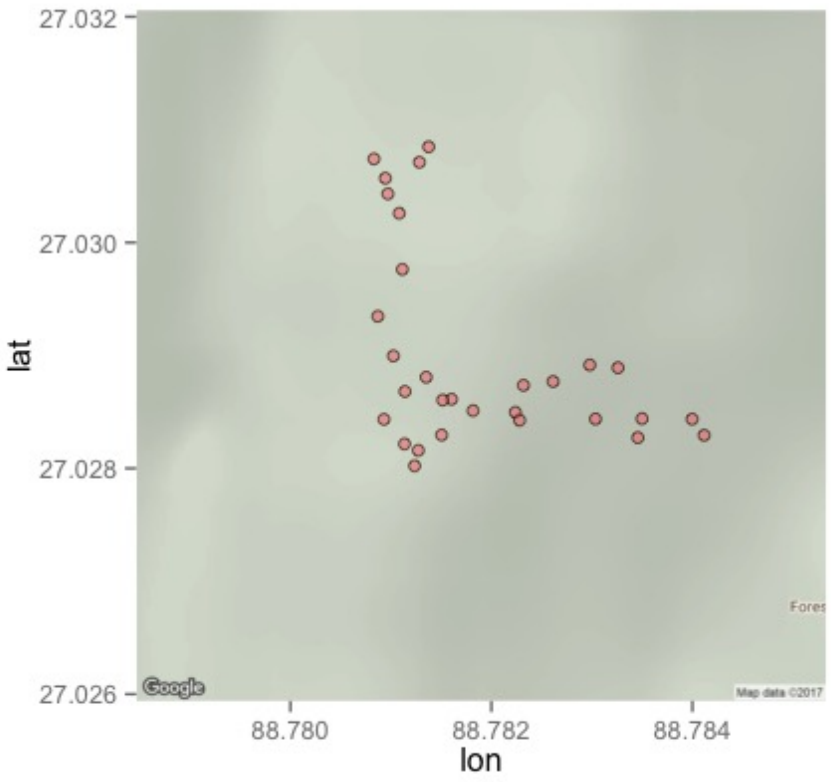


Figure C.4.: Number of species of primary, obligate secondary and all secondary (obligate + facultative) cavity nesting species at different elevations based on range interpolation data.

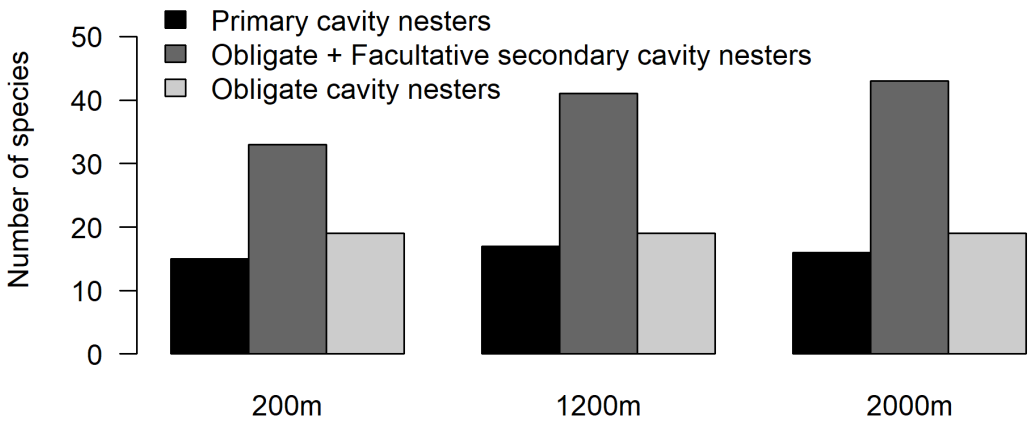
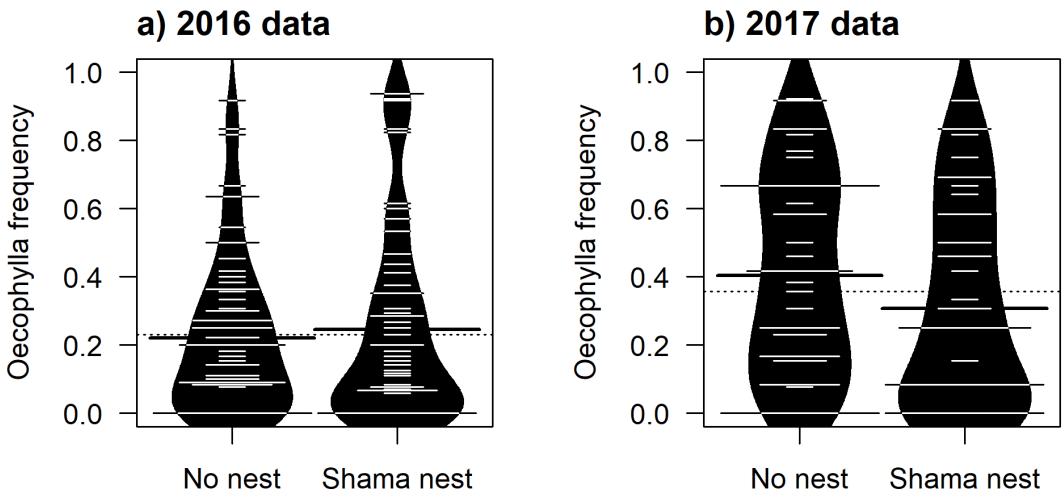


Figure C.5.: Bean plot showing frequency of weaver ant presence on trees with nest boxes used by Shamas versus trees with nest boxes not used by Shamas.



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