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Canopy and litter ant assemblages share similar climate-species density relationships.

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SUMMARY

Tropical forest canopies house most of the globe's diversity, yet little is known about global patterns and drivers of canopy diversity. Here we present models of ant species density, using climate, abundance and habitat (i.e., canopy v. litter) as predictors. Ant species density is positively associated with temperature and precipitation, and negatively (or non-significantly) associated with two metrics of seasonality, precipitation seasonality and temperature range. Ant species density was significantly higher in canopy samples, but this difference disappeared once abundance was considered. Thus, the apparent differences in species density between canopy and litter samples are likely due to differences in abundance-diversity relationships, not differences in climate-diversity relationships. Thus it appears that canopy and litter ant assemblages share a common abundance-diversity relationship influenced by similar but not identical climatic drivers.

KEYWORDS: Formicidae, species richness, global diversity gradients

1. INTRODUCTION

Tropical forest canopies may house more than half of the world's animal species (Erwin 1982; Stork 1993; Ødegaard 2000; Novotny *et al.* 2002), but little is known about how canopy diversity varies at global scales (but see Majer *et al.* 2001; Kitching *et al*. 1993). If the patterns and the climatic correlates of canopy diversity are different from ground-dwelling taxa, current models (which are largely based on ground-dwelling taxa) may not apply for a striking majority of Earth's biodiversity. Alternatively, if similar factors drive canopy and ground-dwelling species diversity, then understanding the factors that shape the diversity of ground-dwelling taxa will be useful for understanding canopy diversity as well.

Ants can comprise more than half of the arthropod abundance and biomass of tropical forest canopies (e.g., Fittkau and Klinge 1973; Floren & Linsenmair 1997; Tobin 1995; Davidson 2003). It is clear that climate is correlated with ant diversity, with the combination of temperature and precipitation often representing the best two climatic predictors for the diversity of litter-dwelling ants (Kaspari, *et al*. 2004; Sanders, *et al*. 2007; Dunn, *et al.* 2009). However, different factors may limit the diversity of litter and canopy ants. Canopy ants tend to feed at lower trophic levels than litter ants (Yanoviak & Kaspari 2000; Blüthgen *et al* 2003; Davidson *et al*. 2007) and therefore may depend more directly on plant production. As plant productivity is highest in warm, wet and aseasonal environments (e.g., Schuur 2003), canopy ant diversity may be more strongly associated with precipitation and temperature than litter ant diversity. Additionally, if canopy ants maintain large colony sizes relative to litter ants (Davidson, 2007), then a given number of workers may be distributed among fewer canopy species, leading to different abundance-diversity relationships. Finally, canopy ants potentially face greater exposure to climatic variability (e.g., Hood and Tschinkel, 1990) than litter ants, which may lead to greater dependence of canopy diversity on climatic seasonality.

Here we generate models of ant species density (i.e., *S*=the number of species in a sample; Gotelli and Colwell, 2001) that use climate, abundance and stratum (i.e., 23 canopy v. 192 litter collections) to understand how and how well these variables predict ant species density.

2. Data

We compiled data on canopy ant species density from the literature using studies that sampled arboreal assemblages by canopy fogging. Fogging studies attempt to sample only ants present in the canopy, but this does not necessarily exclude ground-nesting, canopy-foraging species. We recorded species density (*S*), and abundance (*N*= the number of individual ants), and for studies that did not differentiate spatially between locations, we used the mean of each variable. Twenty-three localities met the above criteria (see Table S1). To compare canopy patterns with better-understood patterns of litter ants (e.g., Kaspari *et al*., 2000, 2004; Sanders, *et al*. 2007, Dunn *et al*. 2009), we extracted similar data from 192 litter samples (i.e., the subset of Winkler extractions from forested areas from Dunn *et al*. 2009 that reported abundance, see Table S2). For each location, we extracted mean annual temperature, annual precipitation (hereafter, “temperature” and “precipitation”), annual temperature range, and precipitation seasonality (i.e., the coefficient of variation of monthly precipitation) from WorldClim (Hijmans *et al.* 2005). All climatic predictor variables were converted to z-scores.

3. ANALYSES AND RESULTS

We combined canopy and litter samples and made three nested generalized linear models to predict *S,* using 1) climatic variables; 2) climate plus canopy/litter; and 3) climate, canopy/litter, and abundance. Climate contributed significantly (all but one climatic effect test was significant, see Table 1) and similarly (i.e., the confidence intervals of the parameter estimates overlapped, Table 1) to all three models. Temperature, precipitation and abundance were all positively correlated with species density in all 3 models, while temperature range and precipitation seasonality were either negatively correlated with or were not significant predictors of ant species density (Table 1). Both of the more complex models performed better, based on AIC scores than the simpler models (Table 1). Model predictions of species density accounted for 52% of the variation in the combined observed data and 73% of the variation in canopy species density (Figure 1).

To investigate whether the effects of the predictor variables differed between canopy and litter samples, we created three (non-nested) generalized linear models separately, adding the interaction term for canopy/litter*temperature, canopy/litter*precipitation and canopy/litter*abundance. All three interaction terms were significant (Table 2) and the confidence intervals for most parameter estimates overlapped (excepting precipitation in the precipitation-interaction model, Table 2) with the "+Abundance" model (i.e., the best model without interaction terms). Of the six models presented here, the "best" model (i.e., the lowest AIC score) includes the effects of temperature, precipitation, precipitation seasonality, abundance and the abundance-canopy/litter interaction.

4. DISCUSSION

As would be expected (Kaspari, *et al*. 2004; Sanders, *et al*. 2007; Dunn, *et al.* 2009), ant species density was highest in warmer, wetter and relatively stable forests. More important to our goals, three details of the models presented here indicate that species density of canopy and litter ant share similar climatic drivers. First, when considering only climate and habitat, Canopy/Litter was a significant predictor of species density, but adding abundance to the model made Canopy/Litter non-significant. Thus, the apparent differences in species density between canopy and litter samples are probably due to differences in abundance-species density relationships, not differences in the relationships between climate and species density. Second, the climatic parameter estimates were generally consistent across models that incorporated climate, canopy/litter and abundance, as well as across models with the interactions of temperature, precipitation and abundance with canopy/litter. Lastly, the overall model (i.e., the "+Abundance" model in Table 1), which was generated with disproportionately more litter assemblages, shows a better match between predicted and observed species density for the canopy assemblages (r^2=0.73, n=23, see Figure 1) than it does for the overall data set (r^2=0.52, n=192).

The interaction models indicate differences between canopy and litter species density, but these differences appear relatively minor. The addition of terms for the interactions of canopy/litter and temperature, precipitation and abundance all yielded models that were statistically better than the non-interaction models (based on AIC scores, see Table 2), but the addition of interaction terms did little to increase the match between predicted and observed species density (i.e., compare the r^2 observed ~ predicted in Tables 1 &2). Our results suggest that these modest differences are a function of differences in the number of individuals sampled. Once abundance was included in the model, the effect of canopy/litter was not a significant predictor of species density. Thus, differences between canopy and litter are likely due to differences in how climate affects the abundance of canopy vs. litter ants and/or how collection methods sample a single abundance-diversity relationship shared by the canopy and litter habitats.

While we argue that the differences in the climate-species density relationships between canopy and ground ant are minor, the models which include interaction terms indicate that canopy species density may be more sensitive to the positive effects of temperature and precipitation (i.e., the interaction terms for both predicted higher species density for canopy samples). Additionally, the interaction of canopy/litter and abundance indicates that for a given abundance, canopy samples have fewer species than litter samples (underscoring the potential differences in abundance-species density relationships and supporting the suggestions of Davidson, *et al.* 2007).

While the forest canopy is of great interest to biologists, it remains difficult to study and relatively poorly known. Consequently, canopy biodiversity has played a relatively minor role in understanding and conserving biodiversity. The tendency to date has been to emphasize the differences between canopy and forest floor faunas (e.g., Yanoviak and Kaspari 2000), but here we highlight their similarities. Both faunas increase in species density with increasing temperature, precipitation and climatic stability (Kaspari, *et al*. 2004; Sanders, *et al*. 2007; Dunn, *et al.* 2009) and the differences in their diversity for a given set of climatic conditions appear to be primarily due to differences in abundances (whether in abundances in samples or abundances per some area or volume). A key remaining question is how best to determine the relevant area or volume over which such abundances should best be considered. If, despite their differences in life history and diet, canopy and litter ants have similar species-abundance distributions, it would suggest broad generalities among ant assemblages regardless of whether the ants are walking overhead or underfoot.

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Table One: Three nested Generalized Linear Models of species density with all samples combined. The first model (“Climate”) includes the climatic parameters. “+ Canopy/Litter” adds the classification variable (whether the samples are from the Canopy or Litter). “+Abundance” adds abundance (*N*) as a measure of sampling effort. All climatic variables have been converted to z-scores. The two more complex models are significant given AIC minimization. Note that the effect of canopy/litter is significant, unless the number of individuals is included. Parameter estimates and AIC values do not include non-significant terms. **p<0.0001, *p<0.01, ns=not significant at p=0.05

	Climate			**Canopy/Litter**			**Abundance**		
	Estimates	**84%CI**		**Estimates**	**84%CI**		**Estimates**	**84%CI**	
Intercept	3.075**	3.050	3.100	3.056**	3.029	3.082	3.063**	3.039	3.088
Mean Annual Temperature	0.514**	0.468	0.561	0.513**	0.466	0.556	0.565**	0.535	0.595
Annual Precipitation	0.208**	0.182	0.234	0.217**	0.192	0.243	0.246**	0.224	0.268
Temperature Range	-0.130**	-0.181	-0.079	-0.105**	-0.157	-0.054	ns	ns	ns
Precipitation Seasonality	-0.115**	-0.141	-0.089	-0.096**	-0.123	-0.070	-0.095**	-0.120	-0.070
Canopy/Litter [Canopy]	------			0.169*	0.115	0.222	ns	ns	ns
Number of Individuals	------			------			0.135**	0.125	0.144
AIC	-28,259			-28,278			-28,528		
r^2 observed ~ predicted	0.452			0.465			0.522		

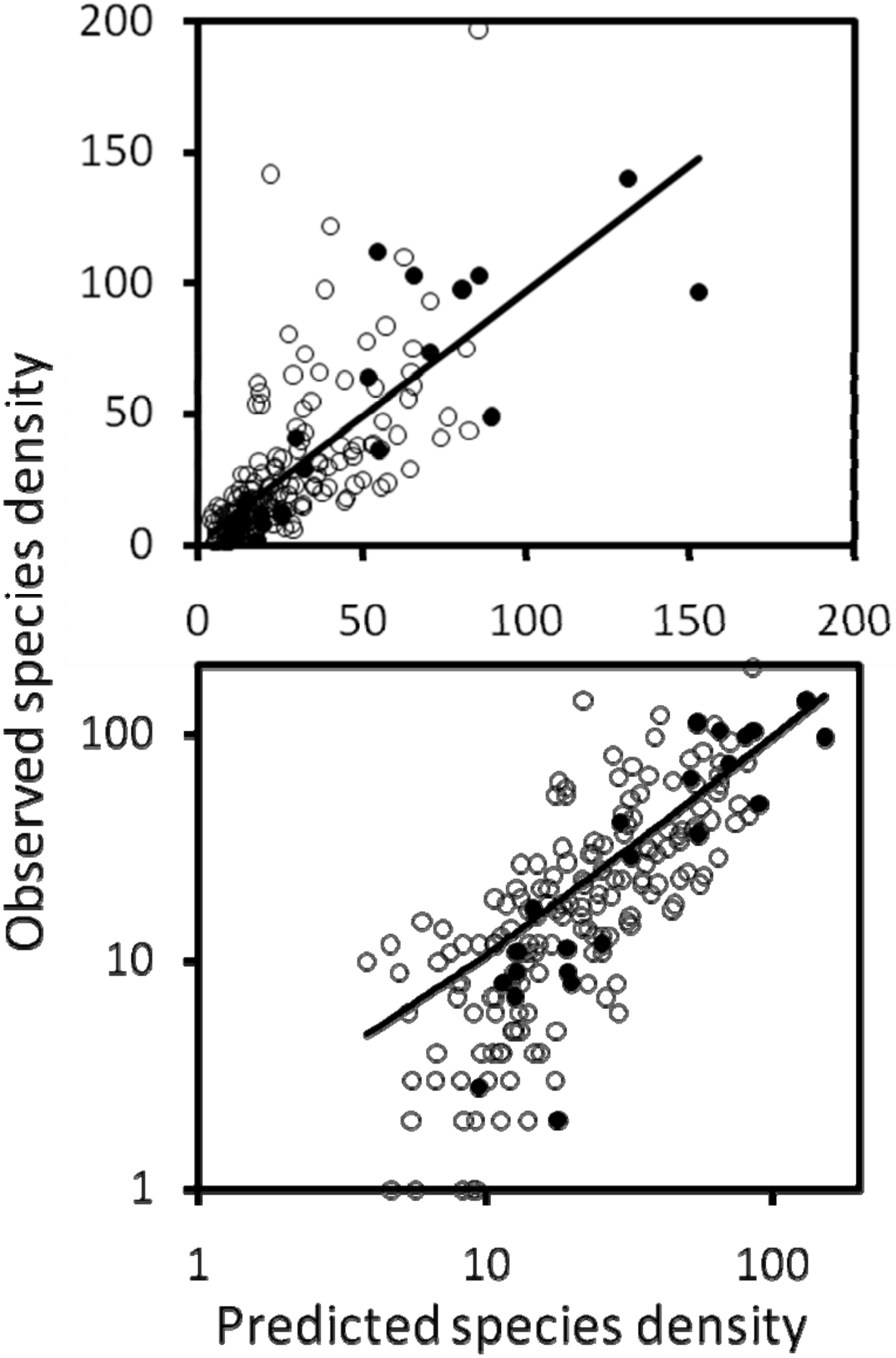
Table Two: Three (non-nested) Generalized Linear Models of species density with all samples combined. All three models include climatic variables, canopy/litter, abundance and the interaction of Canopy/Litter and Temperature, Precipitation and Abundance respectively. The effect sizes for the interaction terms are for Canopy samples (with Litter samples being that value*-1). Thus the effects of Mean Annual Temperature, Annual Precipitation, and Abundance differ between Canopy and Litter samples. Parameter estimates and AIC values do not include non-significant terms (i.e., for the abundance model). **p<0.0001, *p<0.01, ns=not significant at p=0.05

	Interaction of Canopy/Litter and:								
	Temperature			**Precipitation**			**Abundance**		
	Estimates	**84%CI**		**Estimates**	**84%CI**		**Estimates**	**84%CI**	
Intercept	3.088**	3.062	3.115	3.084**	3.058	3.109	3.076**	3.034	3.118
Mean Annual Temperature	0.489**	0.441	0.537	0.512**	0.467	0.558	0.556**	0.504	0.607
Annual Precipitation	0.209**	0.182	0.236	0.193**	0.165	0.221	0.243**	0.205	0.281
Temperature Range	-0.084*	-0.136	-0.031	-0.088*	-0.138	-0.037	ns	ns	ns
Precipitation Seasonality	-0.106**	-0.133	-0.079	-0.110**	-0.136	-0.084	-0.094**	-0.137	-0.051
Canopy/Litter [Canopy]	-1.514**	-1.894	-1.133	-0.283**	-0.283	-0.133	ns	ns	ns
Number of Individuals	0.140**	0.126	0.149	0.143**	0.132	0.154	0.361**	0.316	0.407
Interaction of Canopy/Litter and focal variable	0.006**	0.006	0.008	0.148**	0.104	0.191	-0.251**	-0.299	-0.203
AIC	-28,565			-28,549			-28,657		
r^2 observed ~ predicted	0.526			0.521			0.539		

FIGURE LEGENDS

Figure 1. Ant species density predicted by our model (i.e., the “+Abundance” model in Table 1) compared to observed ant species density. Open circles represent litter samples, closed circles represent canopy fogging samples. Both panels present the same information, with the bottom panel scaled with $\log_{10}$-transformed axes (to allow visualization). The line represents the ordinary least squares regression on the combined data set with observed=1.1+ (0.96*predicted), $p<0.0001$, $r^2=0.52$, n=192. The relationship for the canopy data is observed=1.8+ (0.93*predicted), $p<0.0001$, $r^2=0.73$, n=23.

Figure 1



200
150
100
50
0
0
50
100
150
200
100
10
1
1
10
100
Observed species density
Predicted species density