

**FACTORS AFFECTING THE PROPORTION OF THREE-DIMENSIONAL SPIDER
WEBS ALONG A PRECIPITATION GRADIENT**

by

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Abstract

Our study considers how predation by ants and intense rainfall affect the proportion of three-dimensional (3D) versus two-dimensional (2D) spider webs along a precipitation gradient. We predicted that if predator protection benefits of 3D webs outweighed the costs of rain damage, the proportion of 3D webs would increase with annual rainfall, which is expected to correlate with predation intensity (the *predation* hypothesis). Alternatively, if the costs of rain damage were more significant, we expected a decrease in the proportion of 3D webs with annual precipitation (the *rain intensity* hypothesis). To assess how predation and rain intensity affect the proportion of 3D webs, we selected seven sites along a rain gradient in western Ecuador. First, we verified annual rainfall and January to April rain intensity data using geographic information systems (GIS). Second, we surveyed up to 120 webs along six separate transects at each site. In areas adjacent to the transects, we estimated ant predation intensity using tuna baits. Finally, using the same transects, we determined how vegetation lushness changed with rainfall. To do so, we measured leaf area, canopy cover, and the diameter at breast height of adjacent trees. We found that 3D webs increased in proportion with annual rainfall, which correlated positively with predatory ant abundance, consistent with the predation hypothesis, but counter to the rain intensity hypothesis. We found, however, that in areas of greater precipitation, lush vegetation provided greater shelter under which spiders built their webs. As such, we suggest that greater availability of immediate cover in lush and wetter habitats would mitigate the destructive power of intense rainfall, allowing the predator protection benefits of 3D webs to be realized despite the simultaneous occurrence of strong rains. Microhabitat factors may thus interact with broader-scale biotic and abiotic factors in structuring web-building spider communities.

Preface

Mark Robertson and Leticia Avilés designed this research project. Mark Robertson collected the field data with the assistance of Luis Camacho, Katrina Kaur, Tiffany Lutz and Leonardo Negrete. Analyses were conducted by Mark Robertson with supervision from Leticia Avilés. Specimen identification was done by Antonio Brescovit of Instituto Butantan, Sao Paulo, Brazil.

A version of chapters 1 and 2 has been submitted for publication, and is currently under review.

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Dedication

I dedicate this thesis to my late grandmother, Ellie Robertson. She had to leave school at age 12, and worked hard so that her children and grandchildren did not have to.

Chapter 1: Introduction

For decades, ecologists have attempted to understand the structure of natural communities by considering the relative importance of abiotic versus biotic factors, and how the two interact (Dunson and Travis, 1991). In the 1950s and 1960s, heavy emphasis was placed on abiotic factors. This was at least partially due to Andrewartha and Birch (1954), a textbook that was extremely popular in North American universities. By the 1970s and 1980s however, the emphasis had once again returned to biotic factors, which was possibly a reaction to the previous emphasis on abiotic ones (Dunson and Travis, 1991). Contemporary ecological research remains concerned with how natural communities are structured by abiotic and biotic factors. For example, the understory plant communities of ponderosa pine forests are structured by abiotic factors like soil nitrogen, soil pH and soil texture. However, biotic factors modify the structure of this community: Unpalatable understory plant species are found at higher abundance in ponderosa pine forests with more intense herbivory (Laughlin and Abela, 2007). In summary, although it has long been an area of research, the issue of how abiotic and biotic factors interact to structure natural communities is still poorly understood (Dunson and Travis, 1991; Santos, 1993, Duan et al., 2016; Marins et al., 2016).

Web building spider communities represent a vehicle to address this general problem. Spider webs may be categorized as either two-dimensional (2D) or three-dimensional (3D). 2D, or orb webs, are suspended mid-air by radiating frame threads, and use spirals of silk for prey capture (Blackledge et al., 2011). 3D webs, on the other hand, may take the form of substrate-bound sheet webs (Blackledge et al., 2009), chaotic cob webs (e.g. *Achaearanea tepidariorum*; Koch,

1841), tangle webs with globe-shaped refuges (e.g. *Theridion sisyphium*; Benjamin, 2003), and even complex sheet and tangle webs (e.g. *Anelosimus* spp.; Simon, 1891; see Benjamin and Zschokke, 2003).

In addition to serving as prey capture devices, 3D webs may provide predator protection benefits not found in 2D webs (Blackledge et al. 2003). One may expect, therefore, that 3D webs may increase in abundance relative to 2D webs where predation rates are greater. 3D webs, however, require relatively large amounts of silk and activity to be built and maintained (e.g. Ford, 1977) and thus likely represent a significant investment for individual spiders (Tanaka, 1989). As such, 3D webs are seldom abandoned. One might expect, therefore, that destructive events, such as intense rainfall, may reduce the proportion of 3D webs. 2D webs, in contrast, require relatively little silk (Janetos, 1982) and are often efficiently recycled (Peakall, 1971). 2D webs, therefore, are often relocated in the face of unfavorable conditions (e.g. low food availability; Chmiel et al., 2000, destructive wind and rain; Hodge, 1987). In summary, 3D webs appear costlier than 2D webs, but provide protection against predators not found in 2D webs. The question is thus how does the trade-off faced by 3D webs in terms of cost and protection play itself off in environments where intense rains, an abiotic factor, and high rates of predation, a biotic factor, both occur.

In order to address this question, we investigated the proportion of 3D vs. 2D webs in web building spider communities, along a precipitation gradient in Western Ecuador. Along this gradient we expected that the frequency of intense rainfall and of predation, in particular by ants, would increase along with annual precipitation. The frequency of intense rainfall events tends to

increase with annual precipitation (see Groisman et al., 1999). Predation intensity is also expected to increase with annual rainfall, as the latter will increase primary productivity (a well-documented relationship – see Lieth, 1975, Del Grosso et al., 2008), which, in turn, will increase numbers of primary consumers, which will then lead to an increase of secondary consumers, such as predatory ants. Previous data documenting predator-prey population dynamics (e.g. O’Donnell and Phillipson, 1996, Carvalho et al., 2015) have confirmed such relationships in other systems.

The possibility that 3D webs may serve as predator protection devices is explored by Blackledge and colleagues (2003). In 86 of 111 studies, these authors found that mud-dauber (Sphecidae) wasps captured proportionately more 2D weavers than 3D weavers. The authors argue that the predator defense value of 3D webs is two-fold: wasps must navigate tangles of silk to reach the spider, and silk thread vibrations give a spider early warning of a predator’s approach (Blackledge et al., 2003). In contrast, wasp predation on 2D webs is common, with Sphecidae and Pompelidae wasps responsible for 93% of predatory attacks on the 2D weaving *Metepeira incrassata* (Pickard-Cambridge, 1903; Rayor, 1996). Unfortunately, no one has directly tested the possibility 3D webs may also potentially confer predator protection against ants.

Further evidence that 3D webs are costly to produce and maintain comes from the observation that a 3D-web architecture is associated with sociality in spiders. All but one of eight spider genera where social species have originated build dense tri-dimensional webs (Avilés and Guevara 2017). Spiders may benefit from sharing the costs of web maintenance, in particular in environments where webs are frequently damaged by strong rains, as in the lowland tropical

rainforest where the majority of social spider species occur (Avilés and Guevara 2017). Web investment per adult of the social 3D web weaver *Agelena consociata* (Denis, 1965), for instance, decreased with the number of individuals in the group (Riechert et al. 1986). Colony extinction, which decreased with colony size in this social spider, was associated with nest destruction by intense rain (Riechert et al. 1986), further suggesting 3D webs are costly. Further evidence that spider sociality facilitates 3D web maintenance comes from eastern Ecuador: Solitary and subsocial spiders in the genus *Anelosimus* (which build dense 3D webs) are absent from lowland rainforests, being found only at higher elevations, where rain is not as intense, and in dry habitats (Avilés et al. 2007; Guevara and Avilés 2015). In contrast, only social *Anelosimus* species are found in lowland tropical rainforest. These distributions coincide with rainfall intensity patterns (Purcell and Avilés, 2008; Guevara and Avilés 2015).

When considering the proportion of 3D vs. 2D webs along a precipitation gradient, we predicted that if predator protection benefits of 3D webs outweighed the costs of rain damage, the proportion of 3D webs would increase with annual rainfall (the *predation* hypothesis). Alternatively, if the costs of rain damage were more significant, we expected a decrease in the proportion of 3D webs with annual precipitation (the *rain intensity* hypothesis). We found that 3D webs increased in proportion with annual rainfall, which correlated positively with the abundance of predatory ants, consistent with the predation hypothesis, but counter to the rain intensity hypothesis. We found, however, that in areas of greater precipitation lush vegetation provided greater shelter under which spiders built their webs. We thus suggest that greater availability of immediate cover in lush and wetter habitats would mitigate the destructive power of intense rainfall, allowing the predator protection benefits of 3D webs to be realized

despite the simultaneous occurrence of strong rains. Microhabitat factors may thus interact with broader-scale ecological factors in structuring web-building spider communities.

Chapter 2: Factors affecting the proportion of three-dimensional spider webs along a precipitation gradient

2.1: Synopsis:

To investigate the role of intense rainfall and predation in affecting the proportion of 3D webs, we selected seven sites in western Ecuador along a precipitation gradient. First, using GIS, we determined their average annual rainfall and rain intensity in the months of January through April. Next, using a minimum of six transects per site, we determined the proportion of 3D webs among the entire web-building spider community. We categorized the first 20 spider webs per transect as either 2D or 3D, giving a total of at least 120 webs per site. Along the same transects, we also investigated whether vegetation lushness changes with rainfall. To do so, we measured the length and width of leaves, estimated canopy cover, and measured the DBH of trees wider than 10 cm. Finally, we considered whether the abundance of predatory ants changed with rainfall. To do so, we distributed tuna baits near our transects, and recorded when, if at all, they were discovered by ants, and the amount of ant activity per bait.

If intense rainfall was more significant than predation in affecting the proportion of 3D webs, then we expected the proportion of 3D webs to decrease with annual rainfall (the *rain intensity* hypothesis). Conversely, if predation was more important than intense rainfall, we expected an increase in the proportion of 3D webs with annual rainfall (the *predation* hypothesis).

We found an increase the proportion of 3D webs with annual rainfall, which positively correlated with the increasing abundance of ants with annual rainfall. This matches the predictions of the predation hypothesis, but not the rain intensity hypothesis. However, we also found increasingly lush vegetation in areas of greater annual rainfall, providing spiders more vegetation shelter for their webs. We suggest this lush vegetation mitigates the importance of intense rainfall, and highlights the importance of interactions between microhabitat characteristics, and broader ecological factors, in structuring web-building spider communities

2.2: Methods

Study Sites

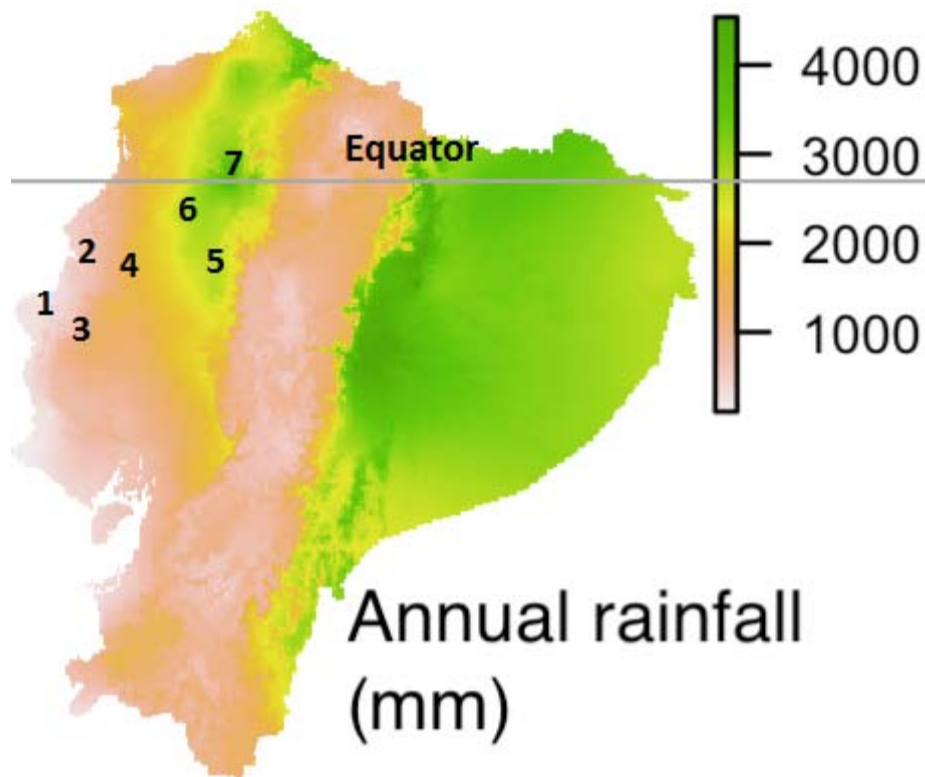


Figure 2.1. Location of study sites in western Ecuador. For more information about our study sites, refer to table 1

We selected seven study sites along a precipitation gradient of relatively uniform elevation in Western Ecuador (Figure 2.1. and Table 2.1.). For this we sought sites with minimal vegetation disturbance, which are unfortunately rare in western Ecuador. Therefore, the only site where primary forest remained was Rio Palenque. From May to July 2015, we visited these sites two separate times each in order to investigate the relationship between rain intensity, potential predator pressure, and the proportion of dense three dimensional (3D) spider webs

Table 2.1. Study sites, their annual rainfall and January-April rain intensity

Study Site	Elevation (metres)	Latitude	Longitude	Mean annual temperature (°C)	Annual rainfall (mm)	January – April Average rain intensity (mm/hr)
Crucita (1)	36.8	S0.873	W80.53	29.03	328	1.8
Bahia de Caraquez (2)	60.8	S0.659	W80.40	29.37	479	2.02
Portoviejo (3)	96.5	S1.03	W80.29	30.83	848	2.49
Chone (4)	89.4	S0.564	W80.04	28.26	1145	3.1
Rio Palenque (5)	157.8	S0.59	W79.36	26.75	2642	5.82
El Carmen (6)	259.7	S0.259	W79.43	27.84	2849	5.77
Pedro Vicente Maldonado (7)	545	N0.108	W79.20	26.4.0	3469	4.47

Annual rainfall and intensity

We used Geographic Information Systems data (GIS) to obtain the average annual rainfall and precipitation intensity for our study sites. We obtained annual rainfall from the WorldClim V1.4 database (Hijmans et al., 2005), by averaging annual rainfall data from 1960 to 1990. These data were read in R using the Raster package (Hijmans et al., 2014) and then cropped to include Ecuador only. The steps for processing the annual rain intensity data were the same as for annual rainfall, but obtained from NASA’s Tropical Rainfall Measuring Mission (TRMM,

<https://pmm.nasa.gov/data-access/downloads/trmm>). Using TRMM data from 2010-2014, we obtained the average rain intensity for the months of January through April. These months immediately preceded our study period, and are also the four wettest months of the year. For more detailed information regarding how the annual rainfall and rain intensity data were processed, see Guevara and Avilés (2015, appendix s2).

Proportion of 3D webs

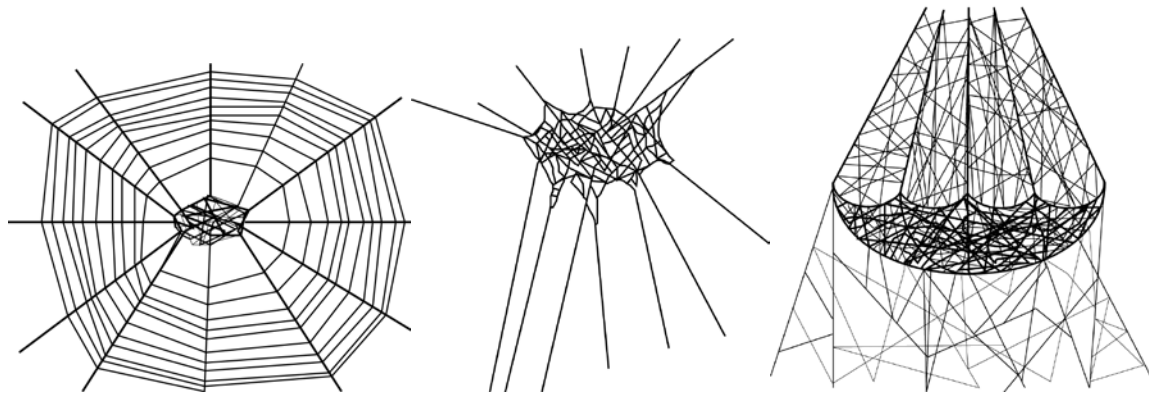


Figure 2.2. 2D (left) and 3D (centre and right) webs

At each of the six sites, we sampled up to 120 webs along six separate transects (20 webs per transect). Transects were 100 cm in width x 150 cm height (from 25 – 175 cm) and as long as it was required to encounter 20 webs. We categorized the first 20 encountered spider webs as either 2D or 3D. Orb webs were categorized as 2D, whereas tangle webs and sheet and tangle webs were coded as 3D (Figure 2.2.). In addition, we wrote brief descriptions of the spider webs' distinguishing features and preserved spiders in 95% ethanol for later identification.

Environmental parameters

Ant abundance

To estimate the abundance of predatory ants, we used as baits Eppendorf tubes filled with tuna. In an area adjacent to each spider web transect, we haphazardly distributed 15 Eppendorf tubes between 20 cm and 180 cm from the ground. We recorded when each individual Eppendorf tube was set, and checked every 10 minutes for up to three hours whether it was found by ants. This allowed us to determine how long ants took to discover each individual Eppendorf tube (a proxy for ant abundance). When (if at all) an Eppendorf tube was found by ants, we immediately estimated ant abundance using Philpott et al.'s 2008 ant activity index: 0 = no ants, 1 = 1–2 ants, 2 = 3–10 ants, 3 =>10 ants. Ant activity and the time they took to discover Eppendorf tubes were highly correlated ($F_{1,40} = 8.75$, $R^2 = 0.8471$, $p < 0.001^{***}$) with each other. As such, only the former metric is discussed in the results.

Vegetation lushness

To document how vegetation lushness changes with rainfall, we measured the extent of vascular plants every 3 m along the same transects as above, which we prolonged, if necessary, up to 50 m in length. We recorded canopy cover, diameter at breast height of trees >10cm (DBH), leaf length and width. We estimated percentage canopy cover using a 20-cm² gridded acetate sheet held upwards at arm's length. We measured the DBH of trees >10 cm within 3 m of either side of each transect. We took leaf length and width measurements from the three plants closest to the transect (one leaf from each plant, for a total of three leaves at each point). Finally, we estimated

the immediate vegetation cover (percentage cover of any vegetation 25 cm above the top of each spider web).

Analyses

Summary statistics

We produced all calculations, analyses and graphs in R (R Development Core Team, 2016) or JMP (v. 12.2.0, www.jmp.com). We calculated the density of spider webs per transect by calculating the distance in meters required to find 20 webs ($\text{web density}/\text{m}^3 = \text{transect length} * [20 \text{ webs} / 3 \text{ m}^3]/3$) and, of those, the proportion of 3D webs by dividing their count by 20. Finally, we calculated averages of our environmental variables. Per transect, we calculated average leaf area (using the formula for the area of an ellipse, $\pi/4 \times \text{leaf length} \times \text{leaf width}$), habitat cover, and the DBH of trees. We produced all graphs in ggplot2 (Wickham, 2009).

Model selection

We used linear or nonlinear models to explore the relationship between average annual rainfall and the other environmental variables. We used a mechanistic growth model for log-transformed mean leaf area and average canopy cover, as the two variables asymptote at the highest levels of rainfall. The equation for this model is $a * [1 - b * \exp[-c * \text{annual rainfall}]]$, where a = asymptote, b = scale and c = growth rate). We then considered how the proportion of 3D webs was affected by the subset of these variables that most related to the precipitation and predation hypotheses - rain intensity, average ant activity, and log transformed mean leaf area, as bigger leaves could provide shelter to webs against intense rain. For this purpose we used generalized linear models

(GLM) with binomial error structure and logit link function, with number of 3D webs considered successes. To reduce variance inflation factor (VIF) scores, we removed from consideration in these models variables that were redundant or highly correlated with those above listed, such as canopy cover, which correlated with leaf area, and time to bait discovery, which correlated with ant activity (Appendix table A.2.). We chose ant activity in preference to time to bait discovery because it was more reliable at predicting variation in the proportion of 3D webs. It appeared also more intuitive to use an index that increased with ant predation intensity, rather than an index that decreased. We did not consider DBH in the models, as it did not correlate with annual rainfall. To avoid pseudoreplication, in our analyses we aggregated results from the six transects into a single response variable for the number of 3D webs at a site and used the average of the environmental variables across the six transects as predictor factors.

We considered models with a variety of combinations of the potential explanatory variables—rain intensity, ant activity, and log-transformed average leaf area, including the variables on their own, in pairs, together, or with various combinations of their two way interactions (Appendix table A.4.). We then used Akaike Information Criterion (AIC) scores, corrected for finite sample sizes (AICc), to select the best candidate GLM. We note, however, that AICc scores do not assess a model's explanatory power. Rather, they assess its relative quality in comparison to other candidate models. We determined AIC scores using JMP (v. 12.2.0, www.jmp.com).

Using the `usdm` package (Naimi, 2015), we verified that the VIF scores of the explanatory variables in our GLM were non-problematic. High VIF scores (e.g. higher than 3; see Zuur et al., 2010) occur when explanatory variables are highly correlated with each other. High VIF scores

are problematic because they can mask effects of explanatory variables which may otherwise be significant. However, the VIF scores of our explanatory variables in the model investigated were less than 3. As such, they are not problematic (see appendix table A.3.). Finally, using the car package (Fox and Weisberg, 2011), we also show a matrix plot graphing every explanatory variable against each other (see appendix figure B.2.)

2.3: Results:

Table 2.2 Most common genera among 2D (left) and 3D (right) weavers, and the study site where they were found

3D web genera	Number of identified webs of that genus	Sites where found	2D web genera	Number of identified webs of that genus	Sites where found
<i>Coleosoma</i>	8	7	<i>Leucauge</i>	59	2,3,4,5,6,7
<i>Anelosimus</i>	7	1	<i>Cyclosa</i>	20	2,3,6,7
<i>Argyrodes</i>	6	1,2,3,4	<i>Micrathena</i>	11	3,4,6
<i>Architis</i>	5	4	<i>Araneus</i>	4	4,6
<i>Theridion</i>	3	1,2,3,4	<i>Alpaida</i>	3	3,4,7
<i>Moyosi</i>	2	4,6	<i>Mangora</i>	3	3,5,6
<i>Ero</i>	1	1	<i>Chrysometa</i>	2	6
<i>Scytodes</i>	1	2	<i>Argiope</i>	2	3,6
<i>Episinus</i>	1	3	<i>Uloborus</i>	2	2
<i>Achaereanea</i>	1	7	<i>Nephila</i>	1	3
<i>Tupigea</i>	1	4,5	<i>Epeirotypus</i>	1	4
<i>Dubiaranea</i>	1	7	<i>Pronous</i>	1	6
			<i>Eustala</i>	1	3

Across all transects, *Leucauge* (Tetragnathidae), *Cyclosa* (Araneidae), and *Micrathena* (Araneidae) were the most common 2D web-weaving genera, whereas *Coleosoma* (Theridiidae), *Anelosimus* (Theridiidae), and *Argirodes* (Theridiidae) were the three most common genera of 3D weavers(see table 2.2).

Proportion of 3D webs along the precipitation gradient

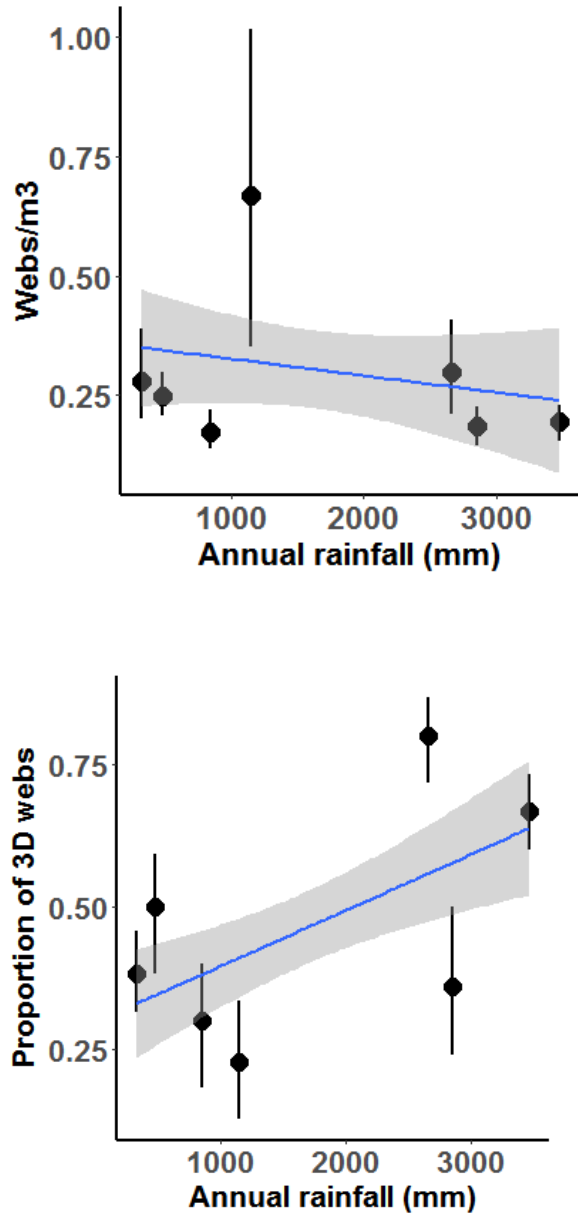


Figure 2.3. Spider density (webs/m³, top) and the proportion of 3D webs (bottom), as a function of annual rainfall.

Means \pm 95% confidence intervals for the proportions at each site shown

3D spider webs increased in abundance relative to 2D webs with annual rainfall (GLM L-R $X^2_{1,4} = 36.6$, $p < 0.001^{***}$, deviance $X^2 = 102.7$ see figure 2.3.). On the other hand, no pattern in the response of spider density (both 2D and 3D webs) to annual rainfall ($F_{1,5}=0.55$, $R^2 = 0.10$, $p = 0.49$) was found, as web building spiders were not more abundant in areas of greater precipitation.

Environmental Variables

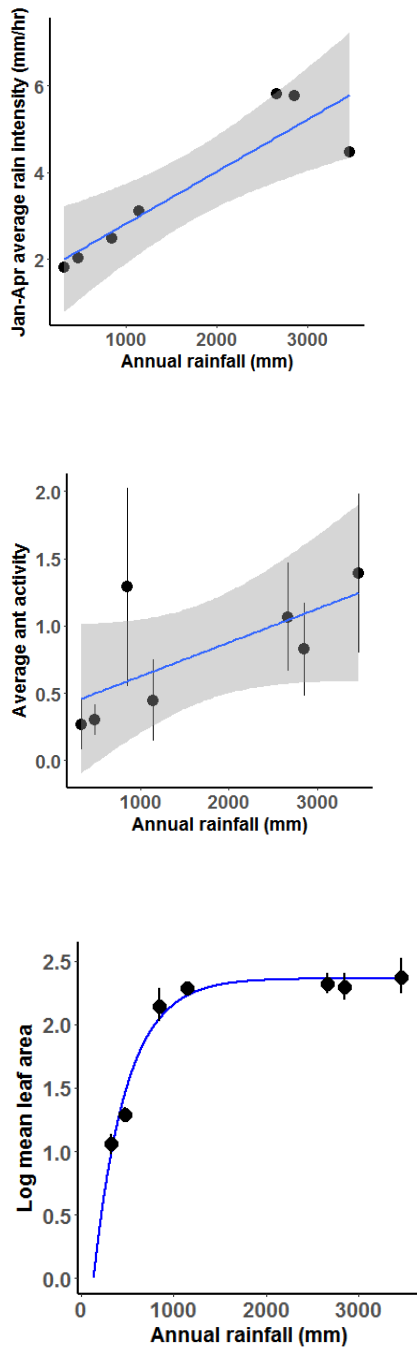


Figure 2.4. Rain intensity per locale, ant activity and log mean leaf area, per locale, as a function of annual rainfall.

Error bars represent 95% confidence intervals

Rain intensity, expected to influence the frequency of 3D webs, correlated positively with annual rainfall ($F_{1,5} = 21.1$, $p = 0.006$, $R^2 = 0.80$; see figure 2.4.). The abundance of predatory ants, as assessed by the activity index (figure. 2.4.), also increased with annual rainfall ($F_{1,5} = 5.43$, $p = 0.067$, $R^2 = 0.52$, when site 3, a likely outlier, is included in the model, and $F_{1,5} = 137.5$, $p = 0.0003$, $R^2 = 0.97$, when it is not), consistent with the expectation of more exposure to predation in rainier areas (see Appendix, figure B.1., for parallel results with time to bait discovery). Likewise, the log of mean leaf area per transect increased with annual rainfall ($F_{1,5} = 7.473$, pseudo $R^2 = 0.9636$, $p < 0.05^*$), but the relationship was asymptotic, as vegetation lushness increased with precipitation but leveled off after ~1000 mm of rain (see figure 2.4.). As shown in the appendix, canopy cover also increased asymptotically with annual rainfall (see appendix figure B.1.). There was no effect of annual rainfall on DBH (appendix figure B.1.). To simplify analyses, as well as to reduce variance inflation due to highly correlated factors, we removed from further consideration DBH, canopy cover, and time to bait discovery in models to predict the proportion of 3D webs along the precipitation gradient (see Methods).

Environmental variables vs. proportion of 3D webs

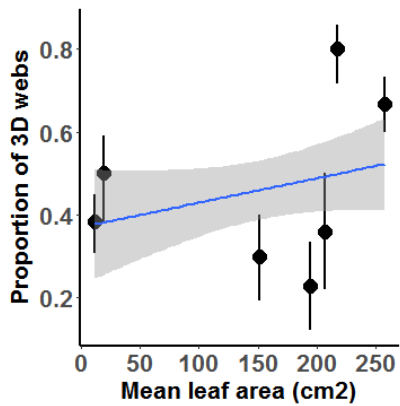
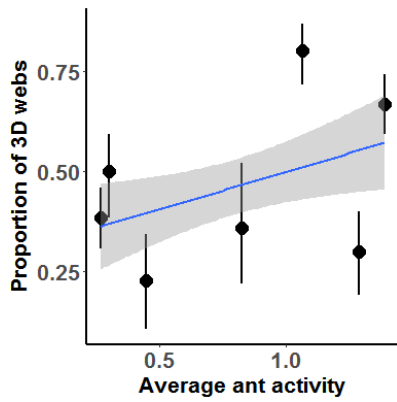
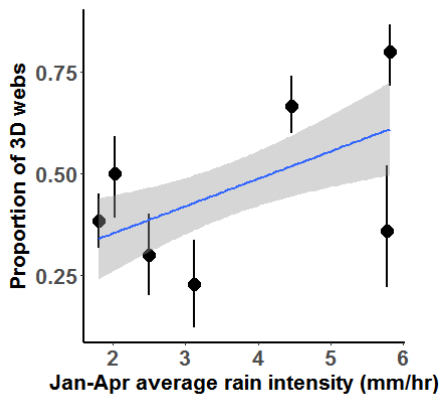


Figure 2.5. Average rain intensity (top), average ant activity (middle), and average leaf area (bottom), per locale, vs. the proportion of 3D webs. Error bars represent 95% confidence intervals

Table 2.3.Parameter values for most parsimonious model

Explanatory variable	Estimate	Standard error	L-R X^2	P-values	95% confidence interval
Intercept	-2.35	0.25	101.74	<0.0001	-2.85 to -1.87
Ant activity	1.78	0.21	76.13	<0.0001	1.37 to 2.21
Rain intensity:ant activity	1.72	0.2	78.42	<0.0001	1.32 to 2.12

The candidate model with the lowest AICc score contained ant activity and a significant interaction between ant activity and rain intensity (AICc = 92.1), but not rain intensity, per se (delta-AIC = 14, for the model that also contained rain intensity as a predictor variable. See Appendix, Table A.4.). The second most parsimonious model (delta-AIC = 4.9), contained, in addition to these two factors, an interaction between rain rate and mean leaf area, but not leaf area, per se (Appendix, Table A.4.). All other models had a difference in AIC scores close to 10 or above (Appendix, table A.4.).

Based on the candidate GLM with the lowest AICc score, the proportion of 3D webs was positively correlated with ant abundance (GLM: L-R $X^2_{1,4} = 76.1$, $p < 0.0001^{***}$, see Appendix Table A.4.), but with a significant interaction with rain intensity (GLM: L-R $X^2_{1,4} = 78.4$, $p < 0.0001^{***}$, see Appendix Table A.4.). Thus, the slope of the relationship between the proportion of 3D webs and ant abundance was relatively flat at dry areas and steepest at the rainiest areas. Table 2.3 (above) lists more information about the parameter values of this GLM. These data

match the predictions of the predation hypothesis, suggesting that ant abundance may play an important role in influencing the proportion of 3D webs.

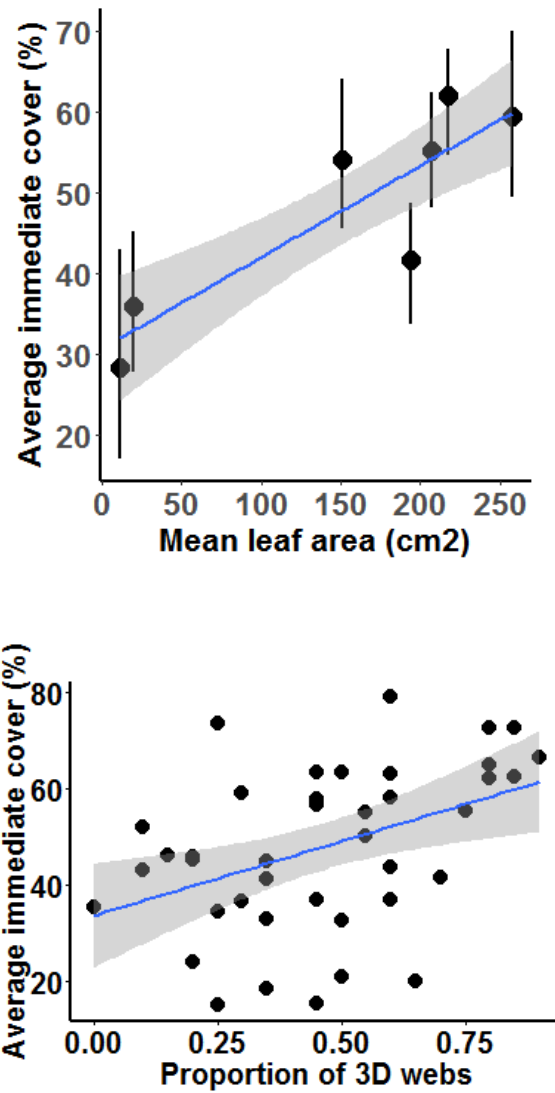


Figure 2.6. Mean leaf area vs. average cover immediately above 3D webs (top), and proportion of 3D webs vs. average immediate cover (bottom)

That the proportion of 3D webs was positively correlated with rain intensity is puzzling given the expected web damaging effect of intense rains. We found, however, that 3D webs had greater access to immediate cover at wetter locales ($F_{1,40} = 8.75$, $R^2 = 0.159$, $p < 0.001$), given the correlation between log mean leaf area and average immediate cover ($F_{1,5} = 10.3$, $p < 0.05$, $R^2 = 0.67$).

2.4: Discussion:

We found that the density of web-building spiders showed no response to variation in annual rainfall. The proportion of 3D webs, however, increased with annual rainfall. This was contrary to the rain intensity hypothesis, which predicted that the proportion of 3D webs would decline with rain intensity. Instead, our findings match the prediction of the predation hypothesis.

Indeed, predatory ant abundance increased with annual rainfall and significantly correlated with the proportion of 3D webs. The fact that the proportion of 3D webs increased with precipitation, which is contrary to the rain intensity hypothesis, may be possible due to lush vegetation in wetter locales mitigating the destructive effect of intense rainfall. In fact, the amount of vegetation cover immediately above webs (within 25 cm) increased as the proportion of 3D webs increased (figure. 2.6.). Overall, the most parsimonious model based on AICc scores suggests that the proportion of 3D webs is best explained by variation in ant activity, as well as an interaction between rain intensity and ant activity. The implications of these findings are further discussed below.

Environmental variables

We confirmed that rain intensity for the months of January through April increased with annual rainfall (Figure 2.4.). While these findings are not surprising, the relationship between rainfall and rain intensity is modified by elevation. For example, three habitats in eastern Ecuador, cloud forest (2100 m elevation), lower montane rainforest (1000 m elevation), and lowland tropical rainforest (400 m elevation), have roughly the same average daily rainfall. Average daily rain intensity, however, significantly increased with decreasing elevation (Purcell and Avilés, 2008;

Hofmann and Avilés 2017). Our two wettest locales, El Carmen (2849 mm average annual rainfall, 259.7 m elevation) and Pedro Vicente Maldonado (3469 mm average annual rainfall, 545 m elevation), were at slightly higher elevation than Rio Palenque, and had less intense rain (4.47-5.77 mm/hr) than Rio Palenque did (2642 mm average annual rainfall, 5.82 mm/hr average January-April rain intensity), which is a lowland (157 m, see table 2.1.) tropical Chocó rainforest (Ministerio del Ambiente del Ecuador, 2013).

The increased ant predation activity as rainfall increased along our precipitation gradient likely reflects the increased productivity expected of wetter locales (Del Grosso et al., 2008).

Elsewhere, increasing productivity has been linked to increasing ant abundance (Kaspari et al., 2000). Disturbance may have also affected our data, since ant abundance seems to increase in highly disturbed habitats (e.g. Graham et al., 2004; Graham et al., 2009). Two of our wetter sites, El Carmen and Pedro Vicente Maldonado, consisted of small forest fragments, surrounded by highly modified landscapes. Moreover, Portoviejo, which appears as an outlier in our ant data, was a regenerating forest regularly disturbed by cattle, and surrounded by plantations and pasture (*pers. obs*). Unfortunately, we have no data on the relative degree of disturbance of individual transects. It is worth considering that increased ant activity does not always correlate directly with predator abundance. For example, data from an Israeli rain gradient suggest generalist ant foraging activity increases with annual rainfall. Yet the same research shows generalist ant colony density actually decreases with rain. This is thought to be because with increased foraging activity, individual ant colonies can effectively defend resources, excluding workers from other colonies. The authors suggest that in wetter locales, competition is not necessarily more intense. Rather, it has greater relative importance (versus processes such as predation and

disturbance; Segev et al., 2015). Therefore, ant predation intensity may be independent of ant abundance, but future work is needed to determine whether this is so.

Not surprisingly, vegetation was more extensive in wetter sites. While diameter at breast height of trees showed only a marginal increase with annual rainfall, average canopy cover per transect significantly increased with annual rainfall. This is important, as dense canopy cover may mitigate the impact of intense rain. The canopy in Ecuadorian lower montane forests intercepts 25-52% of rainfall (Fleischbein et al., 2005). Similarly, ~50% of rainfall is intercepted by the canopy in northeast Puerto Rican lowland rainforest (Schellekens et al., 1999). Canopy interception, the difference between gross annual rainfall and the rain that actually reaches the forest floor (throughfall), has ecological consequences. Data from northern Wisconsin pine forests suggest greater throughfall leads to increased understory leaf cover (Anderson et al., 1969). In the same vein, we find a strong positive relationship between annual rainfall and average leaf area per transect. In South America's lowland tropics, average leaf width increases with the logarithm of annual rainfall, provided soils are well-drained and reasonably fertile (Givnish, 1984). Indeed, the positive relationship between mean annual precipitation and leaf area applies across continents and precipitation regimes (see Wilf et al., 1998)

We have demonstrated that 3D webs increase in proportion with annual rainfall, as do many environmental variables of interest. Next we explore how these variables correlate with the proportion of 3D webs.

Environmental variables vs. proportion of 3D webs

Rain intensity

That the proportion of 3D webs was positively correlated with annual precipitation, which is the opposite of what is expected under the rain intensity hypothesis, suggests factors besides rain intensity may affect the proportion of 3D webs. Intense rain certainly decreases survivorship of some invertebrates. For example, the gorse thrip *Sericothrips staphylinus* (Haliday, 1836) decreases in survivorship with greater rain intensity (Norris et al., 2002). This makes sense, given that gorse thrips are poor flyers, and gorse (*Ulex europaeus*) bushes have very small leaves. Similarly, colonies of two subsocial spider species in the genus *Anelosimus*, which build dense 3D webs and naturally occur in cloud forest habitats where rains are mild, were shown to have much diminished survival when transplanted to the lowland tropical rainforest, where rains are intense (Purcell and Avilés 2008; Hoffman and Aviles, 2017). Interestingly, experimentally sheltering the transplanted webs from the rain improved their survival (Purcell and Avilés 2008; Hoffman and Aviles, 2017). These findings beg the question of whether vegetation cover could mitigate the importance of intense rain to 3D web-building spiders.

Leaf area

Whereas overall log-transformed mean leaf area did not correlate with the proportion of 3D webs, according to the second most parsimonious model (Appendix, Table A.4.), at the wetter sites, transects with larger mean leaf area appeared to have a smaller proportion of 3D webs. A possible explanation for this pattern is that particularly large leaves may be an inappropriate

substrate for most 3D webs. Numerous vegetation characteristics are shown to influence the species assemblage of spider communities, (e.g. Zheng et al., 2017), as well as the abundance of 3D web-building spiders (e.g. Schmidt and Tschardt, 2005). Overall, however, larger leaves should provide greater opportunity for spiders to seek sites with greater immediate cover. We thus found that as the proportion of 3D webs increased, the amount of cover immediately above webs increased (Figure 2.6.). As we only measured vegetation cover directly above spider webs, rather than at random points, however, we cannot confirm that availability of immediate vegetation cover, per se, is greater at sites with larger leaves, although it is reasonable to suspect that it would be. In any case, however, our data suggest that spiders that build 3D webs preferentially built webs in sites with greater immediate cover. This inference is supported by the work of Samu et al. (1996), who found that the 3D web-weaving *Lepthyphantes tenuis* (synonym of *Tenuiphantes tenuis*; Blackwall, 1852) relocates its webs to sheltered microhabitats protected against intense rain (Samu et al., 1996).

Predation intensity

Overall, we found that as ant abundance increased, so did the proportion of 3D webs, suggesting that greater predation intensity may favor 3D over 2D webs. According to the most parsimonious model (Appendix, Table A.4.), this relationship appeared to be strongest at the wettest sites, where we found potential predation by ants to be strongest. Some 3D web-building spiders use silk to stop ants reaching their web. For example, the social spider *Stegodyphus dumicola* (Pocock, 1898) uses bands of silk below its nest to prevent attacks by the ant *Anoplolepis steingroeveri* (Henschel, 1998). Moreover, the jumping spider *Phintella piatensis*

(Barrion and Litsinger, 1995) uses its tough, densely woven 3D nest to avoid ant predation (Nelson and Jackson, 2014). Few studies, however, consider the protective function of dense 3D webs themselves. *Zodarion* (Walckenaer, 1826) and *Diores* (Simon, 1893) spp., both genera within the ant-mimicking Zodariidae, seem to use igloo-shaped retreats when near ants' nests (Cloudsley-Thompson, 1995). Furthermore, *Achaearanea globispira* (Henschel and Jocqué, 1994) build globular retreats of silk detritus as a refuge against wasps and other spiders. Intriguingly, whereas *A. globispira* preys on ants, the authors suggest the spiders' ability to sever suspension threads leading to the retreat protects them from attacks by bellicose ants (Henschel and Jocqué, 1994). Densely woven spider cocoons also appear to offer protection against specialist egg parasites (Hieber, 1992). In contrast with the findings of Henschel and Jocqué (1994), Hieber suggests silk suspension systems ward off predatory ants, as ants are reluctant to venture on to silk. The protective value of silk suspension threads is beyond the scope of the present study, but should be investigated in the future.

Model results, limitations, and alternative explanations

Link functions in GLMs automatically consider the additive effect of explanatory variables on the response variable. However, specifying interaction effects is important, as the effect of interactions are often not simply additive (Tsai and Gill, 2013). Our model suggests a significant interaction between predation and rain intensity in their effect on the proportion of 3D webs, with the relationship between ant abundance and the proportion of 3D webs apparently becoming steeper at wetter sites. Nonetheless, we must consider other factors that may influence the proportion of 3D webs.

Other predators may have affected the proportion of 3D webs. Wasps, for example, are significant spider predators (e.g. Colville et al, 2015). However, they usually target 2D web weaving spiders (Rayor, 1996; Kurczewski, 2010), a likely consequence of 3D webs' predator defence function (see Blackledge et al., 2003). Birds also may have been significant predators in our system. Two 3D web-weaving species, *Pityohyphantes phrygianus* (Koch, 1836) and *Achaearanea cf. riparia* (Blackwall, 1834), are found at higher mean densities when bird predation is removed (Gunnarson, 2008). Perhaps bird predation is intense in our study system, and negates the significance of predation by ants. Lizard predation on spiders is also significant in some ecosystems (e.g. Pacala and Roughgarden, 1984; Spiller and Schoener, 1988), but their effect on 3D web-weaving spiders is uncertain. Ideally, future work in this system will survey the abundance of all potential spider predators, both vertebrate and invertebrate. Assessing the relative importance of different predation types should give a clearer picture of the 3D web's utility in our system.

Chapter 3: Conclusion

Spiders are an ancient and ubiquitous predator (Turnbull, 1973), as well as a motif in many cultures (e.g. Davis, 1996; Sanan and Loveren, 1999). Clearly, they have been a source of fear and fascination for millennia. Here, we have provided insight into the trade-off between maintaining webs that provide predator protection, versus their vulnerability to destruction by intense rain. In addition, we demonstrate the importance of microhabitat characteristics in modifying the role of broader-scale ecological processes.

Increased diversity of microhabitats allows more spider species to co-exist than would otherwise be possible (Duffey, 2012; Carvalho et al., 2015). Moreover, humid, structurally complex vegetation appears to facilitate successful prey capture by Linyphiid spiders (Harwood et al., 2001). Conversely, microhabitat characteristics may allow spiders to avoid becoming prey themselves. For example, increasing density of Norway spruce needles provides spiders with more areas to escape predation by birds (Askenmo et al. 1977). In addition, spiders that build their webs in sheltered microhabitats are less vulnerable to predation by lizards than spiders which do not (Manicom et al., 2008). Appropriate microhabitat characteristics also help spiders escape stressful conditions. For example, wandering spider species which are vulnerable to desiccation seem to select relatively humid microclimates (Lapinski and Tschapka, 2014). Furthermore, *Oecobius navus* (Blackwall, 1859) an abundant, cosmopolitan small (~10 mm) 3D web weaver, builds its webs in sheltered microhabitats, affording it protection from intense rain and sunlight (Voss et al., 2007).

Despite our study's strengths, there are several limitations. First, we estimated ant abundance using tuna baits. While tuna baits attract predatory ants, they also attract scavenging ants (Bito et al., 2011). As such, our estimate of predation pressure may be inflated. Future work may benefit from using live baits (e.g. termites, see Novotny et al., 1999), as this would presumably allow one to isolate the effect of predatory ants from scavenging ones. Second, we do not have independent measurements to estimate the availability of immediate vegetation cover. While it seems reasonable to assume that there will be more immediate vegetation cover in areas with lush vegetation, future workers should measure immediate vegetation cover at standardized points, independent from spider webs. Finally, while 3D webs do seem relatively costly (Ford, 1977), no research has experimentally verified that 3D webs are relatively more costly than 2D ones. Such research would strengthen the assumptions of our research.

Spider webs exhibit a dazzling range of shapes and sizes, but all can be categorised as 2D or 3D. 3D webs cost more material and activity than a 2D web, but provide benefits not found in the latter category. With our data from a western Ecuador rain gradient, we suggest that the proportion of 3D webs may be greater in wetter areas as a result of the greater protection this type of web offers against predation by ants and potentially other predators. That 3D webs can still be common despite intense rains, on the other hand, may be the result of lush vegetation in those areas providing greater opportunity for the spiders to select sites where webs are sheltered. This may allow 3D web-building spiders to enjoy the predator protection benefits of their webs, without constantly losing them to intense rainfall.

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Appendix

Appendix A. Additional information about spider taxonomy, explanatory models and candidate models

Table A.1. Spider genera per locale

Study Site(name and #)	Annual rainfall (mm)	2D web genera	Number of individual web IDs of that genus	3D web genera	Number of individual web IDs of that genus
Crucita (1)	328	NA	NA	<i>Anelosimus</i>	7
				<i>Ero</i>	1
				<i>Argyrodes</i>	3
Bahia de Caraquez (2)	479	<i>Leucauge</i>	21	<i>Scytodes</i>	1
		<i>Micrathena</i>	1	<i>Theridion</i>	1
		<i>Uloborus</i>	2	<i>Argyrodes</i>	1
		<i>Cyclosa</i>	5		
Portoviejo (3)	848	<i>Micrathena</i>	3	<i>Episinus</i>	1
		<i>Leucauge</i>	2	<i>Theridion</i>	1
		<i>Cyclosa</i>	7	<i>Cyclosa</i>	1
		<i>Eustala</i>	1	<i>Argyrodes</i>	1
		<i>Argiope</i>	1	<i>Mangora</i>	1
		<i>Nephila</i>	1		
		<i>Alpaida</i>	1		
		<i>Mangora</i>	1		
Chone (4)	1145	<i>Micrathena</i>	4	<i>Moyosi</i>	1
		<i>Leucauge</i>	13	<i>Theridion</i>	1
		<i>Epeirotypus</i>	1	<i>Leucauge</i>	1
		<i>Alpaida</i>	1	<i>Architis</i>	5
		<i>Araneus</i>	1		
Rio Palenque (5)	2642	<i>Leucauge</i>	1	<i>Argyrodes</i>	1
		<i>Pronous</i>	1	<i>Tupigea</i>	1
El Carmen (6)	2849	<i>Leucauge</i>	19	<i>Leucauge</i>	1
		<i>Mangora</i>	1		
		<i>Chrysometa</i>	2	<i>Micrathena</i>	1
		<i>Araneus</i>	2		
		<i>Cyclosa</i>	2	<i>Moyosi</i>	1
		<i>Micrathena</i>	2		
		<i>Argiope</i>	1		
Pedro Vicente Maldonado (7)	3469	<i>Cyclosa</i>	5	<i>Achaearanea</i>	1
		<i>Alpaida</i>	1	<i>Dubiaranea</i>	1
				<i>Leucauge</i>	1
				<i>Coleosoma</i>	8

Table A.2. VIF scores of all potential explanatory variables

Explanatory variable	VIF score
Annual rainfall	8.3
Rain intensity	9.54
Average diameter at breast height	1.35
Average immediate cover	1.85
Habitat cover	6.61
Log mean leaf area	6.85
Average time ants took to discover Eppendorf tubes	8.38
Ant activity	9.32

Table A.3. VIF Scores of explanatory variables in final explanatory model.

Explanatory variable	VIF score
Rain intensity	2.07
Ant activity	1.39

VIF values considered to be problematic are greater than 3 (Zuur et al., 2010) or 10

(Montgomery et al., 2012),

Table A.4. Comparison of candidate explanatory models based on AICc scores. RI = rain intensity. AA = ant activity, LA = log leaf area

MODEL	FACTORS	AICc
single factor	RI	154.7
	AA	163.6
	LA	179.3
two factor	RI + AA	159.3
	RI + LA	129.8
	AA + LA	166.0
three factor	AA + LA + RI	112.5
fully factorial	fully factorial	loses DF
two-way interactions	AA + LA + RI + RIxAA + RIxLA + AAxLA	no AIC provided
removing least significant factors	AA + LA + RI + RIxAA + RIxLA	no AIC provided
	AA + LA + RIxAA + RIxLA	133.2
	AA + LA + RIxLA	170.2
	AA + RI + RIxAA	106.1
	AA + RIxAA + AAxLA	103.7
	AA + LA + RIxAA	101.6
	AA + RIxAA + RIxLA	96.99
most parsimonious	AA + RRxAA	92.1

Appendix B. Additional relationships between environmental parameters

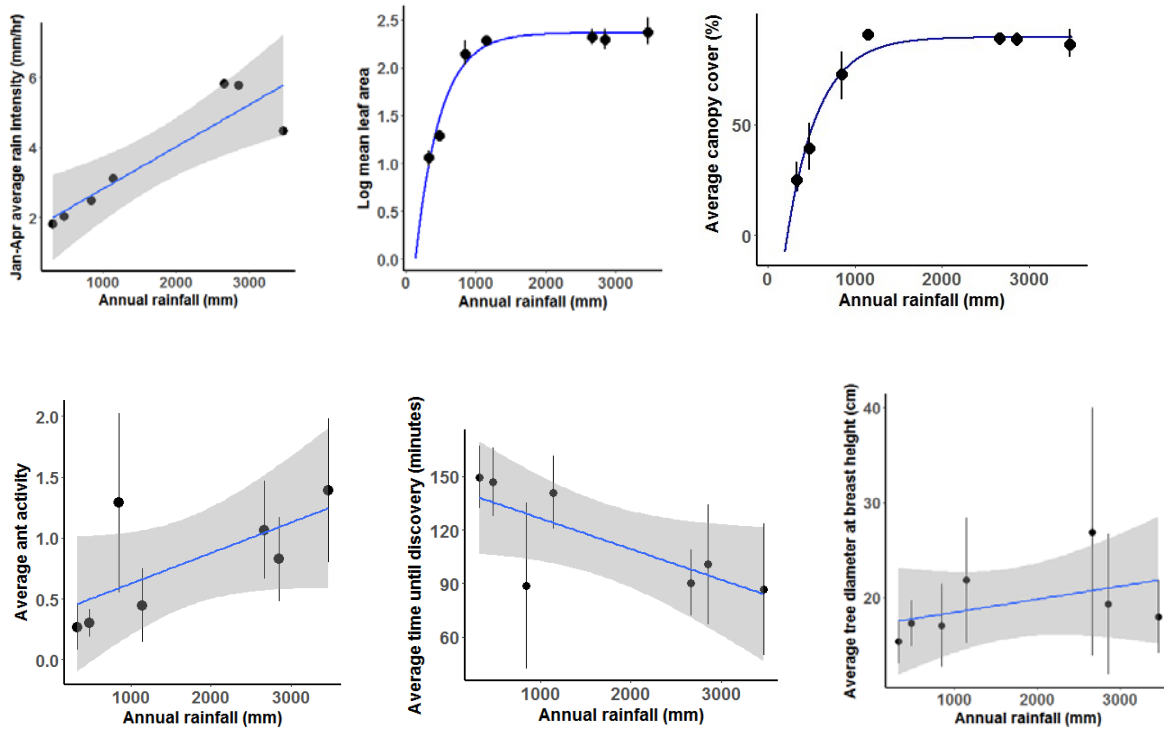


Figure B.1. Annual rainfall (mm), versus Jan-Apr average rain intensity ($F_{1,5} = 21.06$, $R^2 = 0.77$, $p < 0.01^{**}$), log mean leaf area ($F_{1,5} = 7.47$, pseudo $R^2 = 0.9636$, $p < 0.05^*$), average tree diameter at breast height ($F_{1,5} = 7.47$, $R^2 = 0.22$, $p = 0.1618$), average time ants took discover Eppendorf tubes per locale ($F_{1,5} = 7.21$, $R^2 = 0.5084$, $p < 0.05^*$), and average ant activity, ($F_{1,5} = 5.45$, $R^2 = 0.7698$, $p < 0.001^{***}$). Graphs listed clockwise from top-left.

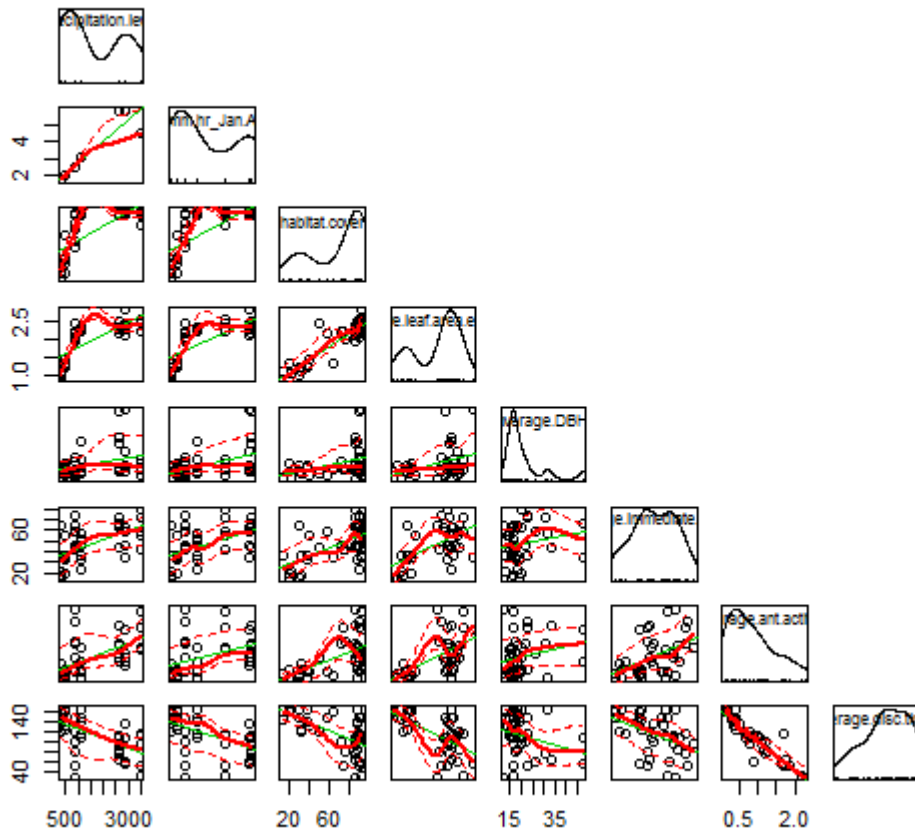


Figure B.2. Each explanatory variable plotted against every other explanatory variable