Species interactions across space and climate:
A statistical analysis

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This paper is a term project for the course *PBL Data Science in Ecology* with the Berry Institute, completed during the Spring and early Summer of 2019. It represents a short, independent research project developed and carried out by the student under the supervision and collaboration with the instructor.

Table of Contents

1. INTRODUCTION

The nature of the relationships between species has long fascinated scientists. In the environment around us, all species interact with each other. All the interactions collectively create a network. Analysis of these networks can help us not only better understand the interactions between specific species but also how the properties of the network affect how the ecosystem functions. For the former, it can help to protect endangered species (or manage invasive ones) and predict future species population change. The latter has long been a focus of study in ecology (McCann, 2012).

The literature on species interactions and food webs is vast (Pimm, 1982; McCann, 2012). One of the key topics is to understand how the properties or complexity of the network of interactions changes the stability of the system (May, 1969; Pimm et al., 1991; Landi et al., 2018). While some general trends have been discovered, there is hardly a consensus (Galiana et al., 2019).

In this study, I focus specifically on network properties and climate. I use species interaction data of Galiana et al. (2019) to analyze how properties of species interaction networks change along current and past climate gradients, and how these relationships vary across small and large spatial scales. My results have implications for the management of species interaction networks in the face of climate change.

2. MATERIALS AND METHODS

I use global host-parasitoid data from Galiana et al. (2019) to analyze how the properties of species interaction networks change across annual temperature ranges, historical climate change gradients, and local (small) and regional (large) spatial scales. The data set is a collection of data from 171 study sites distributed across all continents except Antarctica. All networks are the interactions between insect parasitoids and their insect hosts. Each network is a matrix of ones and zeros that represent the interaction (or not) of parasitoids and their hosts at each study site.

2.1. Data description

Annual temperature range is defined as the difference between the warmest and the coldest temperature within the year. Historical climate change is calculated as the difference between the mean present-day annual temperature and the estimated past annual temperature in 21000 B.C.E. Spatial scale is a variable which describes the extent or size the study experiment: small-scale (local, <1000 km^2) or large-scale (regional, ≥ 1000 km^2).

Specifically, I focus on four properties of each species interaction network: generality, connectance, vulnerability and resource overlap. Generality is taken as the mean number of hosts per parasitoid. Connectance is the number of actual interactions (links) divided by the total number of possible interactions. Vulnerability is defined as the mean number of parasitoids per host species. Resource overlap is the average number of hosts that parasitoids share.

The data includes 171 observations obtained from 74 small-scale (local) study sites and 99 large-scale (regional) sites. A summary of data subset can be found in Table 1.

Table 1. List of variables and summary statistics

	Mean	*Variance*	*Min*	*Max*
Climate variables				
Annual temperature range	25.720	79.562	9.30	50.60
Past climate change	6.415	45.774	-5.370	29.170
Network properties				
Spatial scale	1.572	0.246	1.000	2.000
Connectance	0.438	0.042	0.061	1.000
Generality	2.642	2.987	1.111	12.148
Vulnerability	8.743	20.597	1.769	28.036
Overlap	0.642	0.047	0.139	1.000

2.2. Hypotheses and predictions

Specifically, I will ask the following research questions. First, how does generality change along annual temperature range and historical climate change gradients, and is this relationship different at local and regional spatial scales? Second, how does annual temperature range affect network connectance, consumer diet overlap and resource vulnerability across spatial scales?

For the first, I predict that generality will decrease as annual temperature range and historical climate change increase. We would expect regions close to the equator to have lower annual temperature ranges and historically more stable temperatures, areas frequently found to be "biodiversity hotspots" (Myers et al., 2000). As we move away from the equator to the poles we expect greater annual temperature and historical climate ranges, with lower numbers of species in the extreme environments near the poles. Higher biodiversity increases the number of possible hosts can a parasitoid can feed upon. I predict that the relationship between generality and climate is stronger at local scales. Larger studies increase the chances of including endemic species, which by definition are more specialized.

For the second, I predict that the connectance, vulnerability and consumer diet overlap will change with annual temperature range. Variable environments place additional pressure on species, which likely changes the structure of the network. However, the nature of these changes depend on a complex relation between species and their environment (Loreau, 2010; McCann, 2012). I predict that my network properties will rise with annual temperature range at the local scale and will decrease at regional scale.

2.3. Statistical analyses

To address my research questions, I visually inspected the data using scatter and box plots. I used t-statistics to test for differences across local and spatial scales, and conducted linear regressions on my dependent (temperature and climate) and explanatory (network properties) data to statistically measure the effect of one on the other. I used the ten percent level as the tolerance threshold to determine statistical significance. Finally, I calculated R-squared values to approximate model fit.

3. RESULTS

3.1. How does generality change along annual temperature range and historical climate change gradients, and is this relationship different at local and regional spatial scales?

Aggregating the data by local and regional scales - ignoring climate gradients - gives no clear indication of a difference between spatial scales (Figure 1c), a result which is confirmed by a t-test ($p<0.269$).

However, when we take into account changes in climate we find different results. I find that generality decreases with annual temperature range across spatial scales ($slope=-0.019$, $p<0.208$), decreases with annual temperature range at local scales ($slope=-0.052$, $p<0.086$), and increases slightly at regional scales ($slope=0.003$, $p<0.846$) (Figure 1a). The R-squared values for each model are very low (local: $R^2=0.040$; regional: $R^2=0.0004$; all: $R^2=0.009$), demonstrating that the model does not explain or fit the data well. Note that the relationship between generality and annual temperature range is statistically significant only at the local scale.

For the relationship between past climate change and generality, as past climate change increases generality decreases across spatial scales ($slope=-0.038$, $p<0.054$) (Figure 1b). Generality decreases more quickly with past climate change at local than at regional scales (local: $slope=-0.065$, $p<0.107$; regional: $slope=-0.023$ $p<0.246$). As before our R-squared values are far from one (local: $R^2=0.037$; regional: $R^2=0.014$; all: $R^2=0.022$), so the fit between the model and the data is not ideal. Notice that the regression coefficient is statistically significant across spatial scales, and is quite close to the ten percent tolerance threshold at the local scale.

How does annual temperature range affect network connectance, consumer diet overlap and resource vulnerability across spatial scales?

Visualizing the data by spatial scale gives no indication of a difference between local and regional spatial scales (Figure 2d-f). These results are confirmed by a student's t-test (connectance: $p\text{-}value<0.126$; consumer diet overlap: $p\text{-}value=0.185$; vulnerability: $p\text{-}value<0.962$).

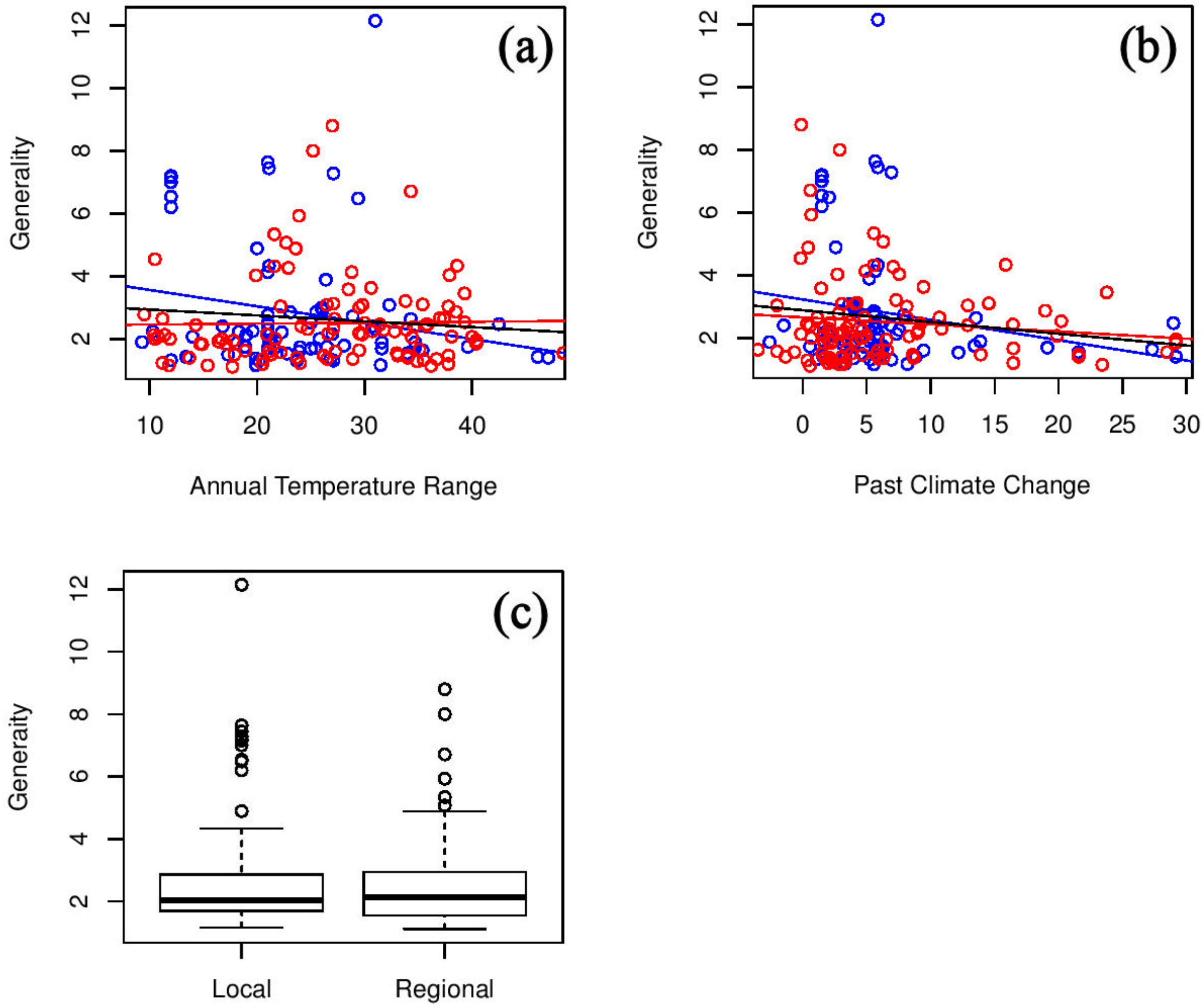

Figure 1. Generality and (a) annual temperature range, (b) past climate change, and (c) across spatial scales. In (a, b) color indicates the spatial scale of the data: local (blue) and regional (red). Linear best-fit lines have been added to show trends in the data, where the black line indicates the fit across both spatial scales. In (c), the dark lines correspond to the median values, boxes the 25% and 75% quantiles, and whiskers the minima and maxima of the data. Individual markers show the presence of outliers.

Taking into account the relationship with annual temperature range, we observe large differences between local and regional scales (Figure 2a-c). For network connectance, at the local scale as annual temperature range increases, connectance slightly increases as well (*slope=0.007*, *p-value<0.037*, R^2*=0.059*). On the contrary, at regional scales, network connectance decreases as annual temperature range increases (*slope=-0.004*, *p-value<0.070*, R^2*=0.033*). This leads to little or no trend in the data across spatial scales (*slope=-0.0004*, *p-value<0.811*, R^2*=0.0003*).

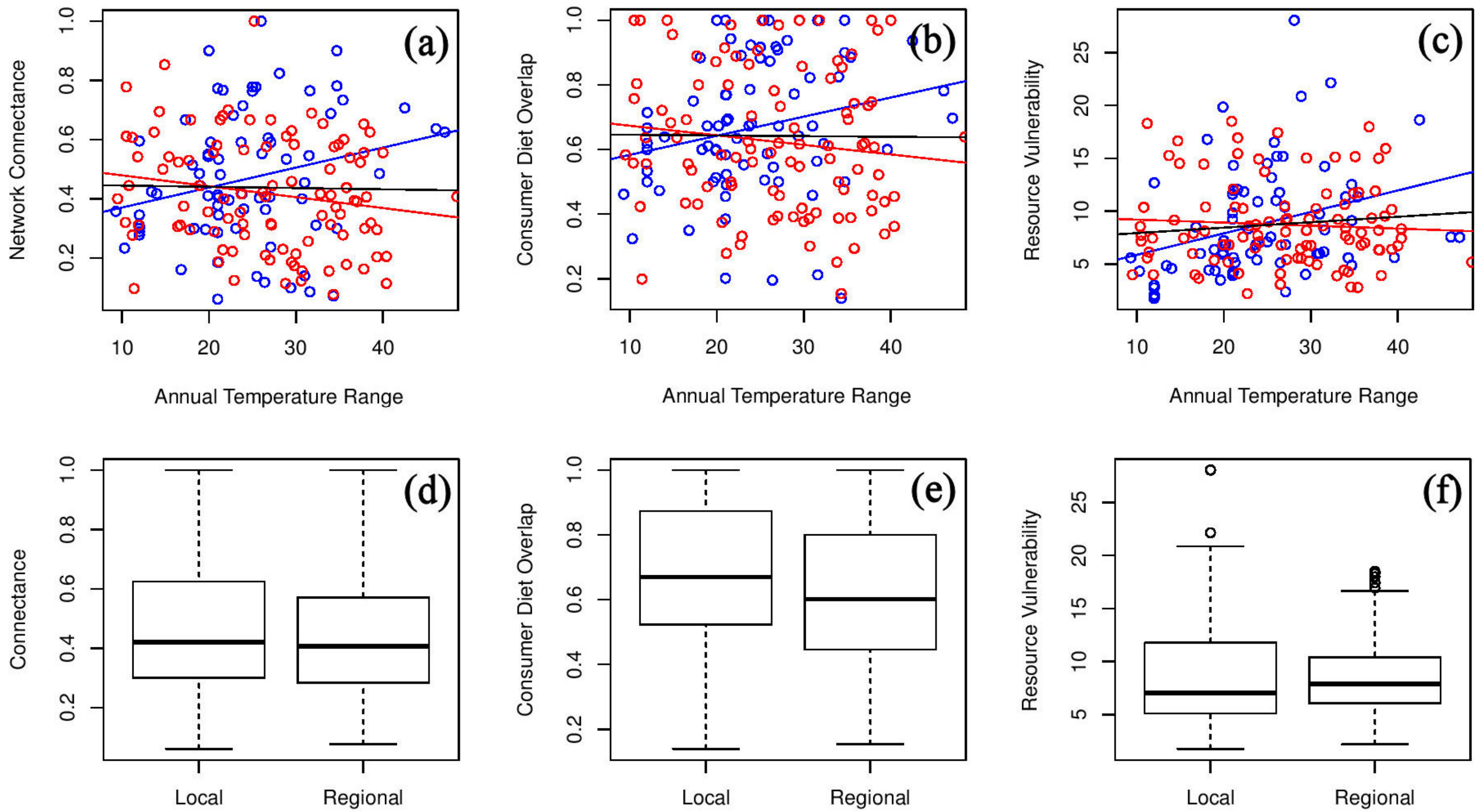

Figure 2. Network properties and annual temperature range across spatial scales. In (a-c) color indicates the spatial scale of the data: local (blue) and regional (red). Linear best-fit lines have been added to show trends in the data, where the black line indicates the fit across both spatial scales. In (d-f), solid dark lines correspond to the median values, boxes the 25% and 75% quantiles, and whiskers the minima and maxima of the data. Individual markers show the presence of outliers.

Consumer diet overlap shows a similar trend. At the local scale, as the annual temperature range increases, consumer diet overlap increases (*slope=0.006*, *p-value<0.054*, R^2*=0.051*). On the other hand, at the regional scale, as the annual temperature range increases, consumer diet overlap declines (*slope=-0.003*, *p-value<0.213*, R^2*=0.016*). We find a slight decreasing trend with annual temperature range across spatial scales (*slope=-0.0002*, *p-value<0.912*, R^2*=0.714E-6*). These trends also applies to the relationship between annual temperature range and resource vulnerability (local: *slope=0.203*, *p-value<0.007*, R^2*=0.097*; regional: *slope=-0.028*, *p-value<0.508*, R^2*=0.005*), though the trend across spatial scales is positive (*slope=0.051*, *p-value<0.186*, R^2*=0.010*). Our R-squared values are still well below one, but slightly higher than our previous analysis.

4. DISCUSSION

Focusing on statistically significant results, I found that generality decreased with annual temperature range and historical climate change (local and across spatial scales, respectively). Connectance increased with annual temperature range at the local scale and decreased with it at the regional scale. Both consumer diet overlap and resource vulnerability increased with annual temperature range at the local scale.

Our results imply less specialization on a single host as we move to more variable climates. The number of hosts per parasitoid decreases (generality), but parasitoids parasitize the same hosts (consumer diet overlap and vulnerability). As the number of hosts slightly decreases and the number of parasitoids remains more-or-less constant on average (Figure 3), this results in a slight increase in connectance. Future analyses could measure the effect of this change in network structure on ecosystem stability (Pimm et al., 1991).

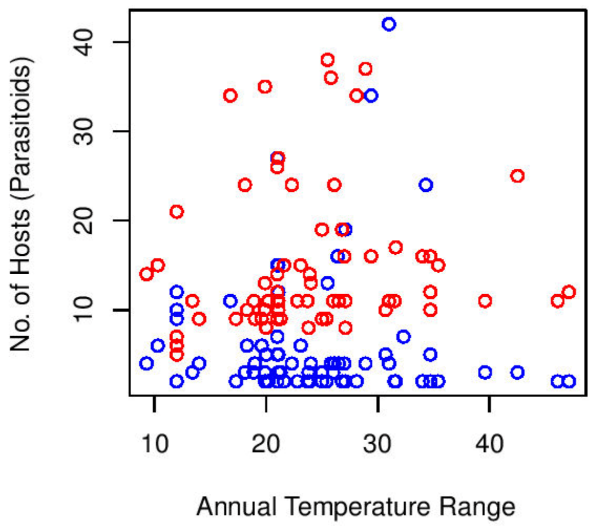

Figure 3. Number of hosts (blue) and parasitoids (red) across all study sites in the data.

It is interesting that often the trend is opposite or not statistically significant at the regional scale. I speculate that this is because of ecosystem stability at high spatial scales. Recently ecologists have found a stability-area relationship (StAR) in which ecosystem stability increases with the size of a study area (Wang et al., 2017). As we increase annual temperature range and move towards harsher environmental conditions, changes in the species interaction network at the local scale are “averaged out” across the larger landscape.

My study offers an example of the tradeoffs of aggregating data. Grouping the data by spatial scale gives little indication that there are differences between local and regional scales, yet I found large differences in the relationship between network properties and annual temperature range over local and regional scales (Figures 1 and 2). Aggregating data is a useful way to explore data and can be required when data is scarce. However, it is important to consider all relevant variables and how they might interact with each other. Indeed, a deeper analysis of the driving factors of network properties would need to carefully consider all the relevant variables and their interactions (Gelman and Hill, 2007).

My results can aid in understanding how the structure of host-parasitoid networks will change with climate change. We expect greater variation in temperatures and extreme weather events in the future (IPCC, 2013), which is in part captured by annual temperature range. Our results predict greater vulnerability as changes in network structure will put more “predation” pressure on host species.

5. REFERENCES

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