

Statement of Authorship: RAF developed environmental data layers, developed and coded joint species distribution models, created figures and contributed to writing. ADW and NBF contributed extensive mussel location data and environmental data layers. RAF wrote the first draft of the manuscript but all authors contributed substantially to revisions specifically DJB specifically contributed substantially to the revision process.

Data Accessibility Statement: If this manuscript is accepted to Ecology Letters these data will be published in a public repository (Dryad) and the DOI for the data will be included in the final manuscript.

Title: Testing the Eltonian Noise Hypothesis in a Species-rich Community

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Short Title: Testing the Eltonian Noise Hypothesis

Keywords: Joint Species Distribution Model, Ecological Niche model, Community, Freshwater Mussels, Latent Variable Modeling, Hierarchical Modeling of Species Community

Type of Article: Letters

Word Count: Abstract:149, Main Text:3588, Textbox:0

References: 66 References

Figures, Tables, Text boxes: Figures: 4, Tables:1, Text boxes:0

Abstract:

Few ecological niche models (ENM) incorporate the Eltonian niche or examine a population's niche at multiple spatial scales. We used Bayesian Joint Species Distribution Models (JSDMs) across multiple spatial scales to examine whether freshwater mussel communities in east Texas adhered to the Eltonian Noise Hypothesis, which asserts that species interactions exert greater influence on conspecific species at finer spatial scales. For both abundance and presence data, we observed a statistically greater number of strong interactions at the finest spatial scale compared to larger spatial scales. While 34% of abundance interactions and 24% of presence interactions showed strong positive relationships, only 6% of abundance interactions and 0% of presence interactions showed strong negative relationships. We found that freshwater mussel communities conform to the Eltonian Noise Hypothesis. Inclusion of the Eltonian niche and consideration of spatial scale are necessary to accurately model niches and increase efficacy of ENMs as conservation tools.

Introduction:

The Eltonian niche, first defined in the early 20th century (Elton 1927), describes the functional roles of a species in a biological community. Such roles are based on the suite of interspecific interactions that influence the presence and/or abundance of a population in a specific location at a specific time (Soberón 2007). In contrast, the Grinnellian niche represents a set of scenopoetic, non-consumable environmental variables that dictate the distribution of a population (Soberón 2007; Soberón & Nakamura 2009). The Hutchinsonian niche, defined as the n-dimensional hypervolume in which a population has an intrinsic growth rate greater than one (Hutchinson 1957), is composed of the fundamental niche (akin to the Grinnellian niche) and the realized niche (akin to the Eltonian niche). These core conceptions of ecological niche affect numerous ecological sub-disciplines and have been revised and modified to better meet the growing understanding of niche (Holt 2009; Dehling & Stouffer 2018).

The Eltonian Noise Hypothesis (ENH) has been proposed to explain the importance of spatial scale for identifying the niche of a species (Soberón & Nakamura 2009). It posits that the impact of the Grinnellian and Eltonian niches on the presence or abundance of a population varies with spatial scale. This hypothesis predicts that at coarse spatial scales, environmental factors (i.e., the components of the Grinnellian niche) dictate species presence or abundance, while biotic interactions (components of the Eltonian niche) have greater influence on presence or abundance at finer spatial scales. Often the environmental and presence/abundance data used to model a population's niche is collected at disparate spatial scales, but little consideration is given to how this disparity of scales may impact understanding of the ecological niche (Ovaskainen *et al.* 2017). For example, Grinnellian niche dimensions have been examined at multiple spatial scales in many taxa, but many of these studies failed to examine the effects of species interactions when analyzing fine scale niche dimensions

or when comparing niche models between fine and coarse spatial scales (Graf *et al.* 2005; Cabeza *et al.* 2010; Razgour *et al.* 2011; Francis *et al.* 2017).

An ecological niche model (ENM) identifies ecosystem conditions suitable for the survival and persistence of populations. Many different dimensions of niche have been studied using ENM, including species distributions, habitat suitability, resource-use, functional diversity, and niche conservatism (James *et al.* 1984; Elith & Leathwick 2009; Novais *et al.* 2016; Francis *et al.* 2017; Dehling & Stouffer 2018). Yet until recently, many of the uses for ENM were relegated to specific ecological sub-disciplines such as foraging ecology, landscape ecology, and community ecology. The increase in open-source species occurrence databases and abiotic scenopoetic datasets have resulted in an increase in ENMs based on Grinnellian niches for numerous taxa (Soberón 2007). The same has not been true for understanding of species functions, leading to the “Eltonian Shortfall” or lack of knowledge concerning species interactions (Peterson *et al.* 2011, Hortal *et al.* 2015). Creating ENMs that incorporate both the Eltonian and Grinnellian niches should result in more realistic understanding of niche dimensions that control species distributions. Such ENMs that also account for variation in spatial scale have been shown to be more accurate than those that do not account for one or more of these niche dimensions (Soberon & Peterson 2005; Soberón & Nakamura 2009; Kissling *et al.* 2012; Araújo *et al.* 2014; Fraterrigo *et al.* 2014; Alvarez-Martínez *et al.* 2015; Inoue *et al.* 2017a).

Ecological niche models that include both Grinnellian and Eltonian dimensions are often referred to as joint species distribution models (JSDMs). Such models allow for a correlative analysis of the impacts of Grinnellian and Eltonian niche on the presence or abundance of a population (Warton *et al.* 2015; Ovaskainen *et al.* 2017). This approach has been used to increase the accuracy of single species distribution models (Araújo *et al.* 2014; Alvarez-Martínez *et al.* 2015), explain community responses

to environmental change (Ovaskainen *et al.* 2016; Abrego *et al.* 2017; Burgazzi *et al.* 2020), and understand the influence of community members on total community assemblage (Abrego *et al.* 2020; Mod *et al.* 2020). Multiple methodologies exist to generate JSDMs and the methodology depends greatly on the goals of specific studies. Traditionally, direct measurements of the impact of a given species on the presence or abundance of other species is assessed via an observed interaction such as predation or competition. Such approaches are labor intensive and not feasible over large spatial extents or in complex communities (Meier *et al.* 2010). Correlative methodologies, such as developing Grinnellian niche models for each species in a community and using these as predictors for other species, have increased in prevalence (Costa & Schlupp 2010; Araújo *et al.* 2014). More recently, latent variable modeling which relies on the residual variation after accounting for the Grinnellian niche has been used to incorporate the Eltonian niche into JSDMs (Wang *et al.* 2012; Warton *et al.* 2015). Because Grinnellian and Eltonian niche dimensions influence species presence or abundance at different spatial scales, this approach often results in a scalar mismatch when generating a JSDM. Accounting for such mismatches should result in more accurate JSDMs.

The freshwater mussels of the superfamily Unionoidea are both a speciose and critically threatened taxonomic group in North America (Strayer *et al.* 2004). They often occur in dense beds containing upwards of 60 species (Haag 2012). Freshwater mussels have complex life histories that include obligate use of fish hosts for growth and maturation of parasitic glochidia larvae, followed by sessile juvenile and adult stages. The combination of high species richness in mussel communities and the dependence on fish hosts suggests the importance of biotic interactions for persistence of mussel communities (Haag & Stoeckel 2015). The sessile nature of juvenile and adult mussels and their presence in diverse community assemblages make freshwater

mussels a model system for testing the Eltonian Noise Hypothesis. While several studies have developed ENMs for freshwater mussels, they primarily describe the Grinnellian niche (Pandolfo *et al.* 2016; Daniel *et al.* 2018; Walters *et al.* 2017) and tend to have low predictability between aquatic systems (Strayer 2008) which may result from missing crucial species interactions.

We investigated interactions among freshwater mussel species in species-rich communities across multiple spatial scales in east Texas, USA. Consistent with the Eltonian Noise Hypothesis, we predict that interaction magnitude between freshwater mussel species will decrease as spatial scales of predictor variables increase. We used JSDM techniques to examine the impacts of individual freshwater mussel abundance and presence on freshwater mussel community composition.

Methods:

Freshwater mussel abundance data were collected at 165 sites in east Texas between 2009–2012 (Fig 1). Abundance estimates were derived using both contemporary quantitative transect sampling (Dunithan 2012; Troia *et al.* 2015) and historic collections. We developed JSDMs across four nested spatial scales, ordered from finest to coarsest: site (n=165), HUC 8 (n=15), river drainage (n=5; Sulphur River, Big Cypress Creek, Sabine River, Neches River, and Trinity River), and drainage basin (n=2; Gulf of Mexico and Red River). Site, river drainage, and drainage basin represent ecologically relevant spatial scales, while HUC 8 is an arbitrary anthropogenic scale derived by the USGS in which a unit typically represents a subsection of a larger river drainage.

Six environmental covariates were used to assess the Grinnellian niche dimensions of mussel-mussel JSDMs. We used the State Soil Geographic Database (USDA 1994) to acquire soil measurements of percent calcium carbonate, average organic matter, percent clay, and pH. Soil environmental covariates were clipped to a

100m buffer around all rivers. The hydrologic environmental covariates river discharge (cfs) and mean annual groundwater recharge (mm/year; Wolock 2003) were obtained from the NHDFlowline dataset (USGS 2005). All environmental covariate rasters were projected UTM 15 N, WGS 84 and data were processed in ArcMap v10.5 (ESRI, Redlands CA). These environmental covariates have been shown to accurately represent the Grinnellian niches of freshwater mussel communities in east Texas (Walters *et al.* 2017).

To develop the mussel JSDM across multiple spatial scales, we employed the Hierarchical Modelling of Species Communities (HMSC) package in R v 3.5 (Ovaskainen & Soininen 2011; Oldén *et al.* 2014). This package uses a Bayesian approach via a Markov-chain Monte Carlo (MCMC) estimation (Ovaskainen *et al.* 2017) to create JSDMs that include both the contributions of environmental covariates and species-species associations. We set MCMC chains to run 100,000 iterations, with samples taken every 100th iteration following a burn-in of 1000 iterations. This methodology estimates both the direction (positive / negative) and magnitude (0 - 1) of each species interaction. To allow for a *post hoc* comparison of model accuracies, mussel data were randomly split into training (75%, 124 sites) and test (25%, 41 sites) datasets. Based on preliminary examinations of model residuals, we determined that an over-distributed Poisson distribution was the appropriate prior distribution. Hierarchical Modelling of Species Communities initially develops a Grinnellian niche model using a generalized linear regression with the six environmental covariates as independent variables. The remaining variation, described by latent variables, can then be attributed to the Eltonian niche (Warton *et al.* 2015; Ovaskainen *et al.* 2016). Latent variable modeling resulted in mussel-mussel coefficient matrices representing the interaction magnitude (0-1) and direction (i.e. the positivity or negativity of the interaction). Mussel-mussel interaction matrices were created for each spatial scale. A positive interaction

indicated that a pair of species occurred together more frequently than expected in posterior distributions at a user defined confidence interval (typically 95%), while negative interactions predicted them to co-occur less frequently.

We built one set of multi-scale JSDBMs for mussel-mussel interactions using abundance data and another set using presence data. The latter were generated by reducing the abundance data to a binary presence/absence format. The results of the abundance data for mussel-mussel interactions indicate the correlation between the abundance of one species as it relates to the abundance of another species in the community. For example if Species A has a strong positive interaction with Species B in the mussel-mussel abundance interaction matrix, it would indicate that when Species A is abundant, we would expect Species B to also be abundant. For the presence mussel-mussel JSDBM, the same interpretation is applied except that instead of the correlation between abundance, the mussel-mussel JSDBM assesses the correlation of presence between two species. The advantage of having both the abundance and the presence JSDBMs is that it gives separate resolutions to the effects of one species on another. For example, if there exists a strong negative relationship between Species A and Species B in the presence JSDBM this suggest that the presence of Species A excludes Species B, while if the same relationship existed for the abundance JSDBM then Species A may limit but not completely exclude Species B. Knowing whether these relationships are binary (i.e. presence JSDBM) or continuous (i.e. abundance JSDBM) allows for a nuanced understanding of the effects species exert in dense multi-species communities and has implications for developing conservation strategies.

To assess the differences in magnitude of interactions across spatial scales, we used linear mixed effect models (LME). The directions of interactions were compared using generalized linear mixed effect models (GLMEs) assuming a binomial distribution. Both GLME and LME were performed using the R package lme4 (Bates *et al.* 2007),

with magnitude value as the dependent variable and scale as the independent variable. Species-species interactions were not independent and were treated as random variables within both the GLME and LME. Potential variance in the mean magnitude and direction across spatial scales was assessed using an ANOVA on the results of the LME and GLME. In addition, we analyzed the difference in strong correlations (i.e. correlations ≥ 0.7 or ≤ -0.7 ; Ovaskainen *et al.* 2017) across spatial scales using a Chi-square test. We also examined whether variation in abundance or presence of each species was related to the environmental covariates and each spatial scale. Predictive power of each JSDM at each scale was calculated by comparing the Tjur R^2 (Tjur 2009) between the model and the test data. All analyses were considered significant at an alpha value ≤ 0.05 .

Results:

A total of 34 freshwater mussel species were found throughout the study area, with 28 species occurring in the Red River drainage and 27 species in the Gulf of Mexico drainage. At the river basin scale, we found 22 species in the Sulphur River, which is in the Red River drainage. In the Gulf of Mexico drainage, 21 species were in Big Cypress Creek, 18 in the Sabine River, 27 in the Neches River and 15 in the Trinity River. There was an average of 15 species per HUC 8, but values ranged from 1-24. The average abundance per site for an individual species was 101.5 mussels and ranged from 1-750. The mean abundance across all species was 492.8 per site and ranged between 1-3954 (Sup Fig 1). There was an average of 8.1 species present per site, but this ranged from 1-19 species. Average species occurrence was 39.2 sites, with individual species presence ranging from 1-107 sites (Sup Fig 2).

We developed abundance and presence JSDMs for four spatial scales (Site, HUC 8, Basin, Drainage) giving eight unique JSDMs. There was a total of 561 mussel-mussel interactions possible per spatial scale. There was a consistently greater number

of total predicted positive interactions compared to predicted negative interactions for both the abundance and presence JSDMs (Table 1; Fig 2). For the abundance JSDM, there were 189, 19, 1, and 1 predicted strong positive mussel-mussel interactions and 36, 9, 0, 1 predicted strong negative mussel-mussel interactions at the site, HUC 8, basin, and drainage spatial scales, respectively (Table 1; Fig 2). A similar predicted pattern was observed for the mussel-mussel presence JSDM with 136, 21, 0, and 0 predicted strong positive interactions and 0, 21, 0, 0 predicted strong negative interactions for the site, HUC 8, basin, and drainage scales, respectively (Table 1; Fig 2).

The results of the LME assessing magnitudes of interactions for both JSDMs were statistically different than their individual null models (abundance: $X^2=287.44$, $df=3$, $p<0.001$; presence: $X^2=462.31$, $df=3$, $p<0.001$). The results of the pairwise ANOVAs showed that site was the only statistically different spatial scale for magnitudes of interactions for both the abundance and presence JSDMs (Fig. 3). The results of the GLMEs which analyzed differences in directions of interaction were significantly different from their respective null models for both abundance and presence JSDMs (abundance: $X^2=42.936$, $df=3$, $p<0.001$; presence: $X^2=35.928$, $df=3$, $p<0.001$). Again, the result of the pairwise ANOVAs showed that site was the only statistically different spatial scale for both JSDMs (Fig 4). There was a statistically different number of strong correlations between the site and HUC 8 spatial scales for both the abundance and presence JSDMs (abundance: $X^2=227.23$, $df=1$, $p<0.001$; presence: $X^2=31.667$, $df=1$, $p<0.001$). The river basin and drainage basin spatial scales had too few strong interactions to be tested (Table 1). A majority of the variation across all species for abundance (57%) and presence (61%) was attributed to environmental covariates. The remaining variation across all species occurred at the site (abundance 28%, presence 24%), HUC 8 (abundance 6%, presence 7%), river

basin (abundance 5%, presence 4%), and drainage basin (abundance 5%, presence 4%) scales (Sup Fig 3). The predictive power of the HMSC abundance and presence JSDMs was lowest at the site scale and similar across the HUC 8, basin, and drainage scales (Sup Fig 4).

Discussion

Our results suggest that Eltonian niche dimensions decrease in importance as spatial scale increases for freshwater mussel communities in east Texas. The magnitudes of species interactions were statistically greater at the site scale than HUC 8, river basin, or drainage scales for both the abundance and presence JSDMs (Fig 2). Additionally, our results showed a greater number of predicted strong biotic interactions at the site scale compared to the larger HUC 8 scale. These results suggest that freshwater mussel communities in east Texas adhere to the Eltonian Noise Hypothesis. Our results may explain previous studies which suggest that local fine-scale environmental covariates fail to predict mussel community composition when applied to novel locations (Strayer 2008) and contrast with other studies reporting that landscape covariates, which typically occur at larger spatial scales, having the strongest influence on mussel community composition (Atkinson *et al.* 2012).

At the site scale, the directionality of the abundance and presence JSDMs show greater positive values than at any other spatial scale. These results indicate that when an individual freshwater mussel species occurs, it is likely that other community members will occur and when the target species is at high abundance, others will also be at higher abundances at that specific location. These results are consistent with common assemblage patterns of freshwater mussels in the Mississippian region, with several highly abundant and widely distributed species dominating beds and numerous rare species occurring at lower abundances (Haag 2012). Though we did not explicitly examine if these patterns of directionality were associated with environmental

gradients, it has been shown that freshwater mussel community assemblages are impacted by both abiotic (i.e., temperature, discharge) and biotic (i.e., food availability) gradients (Spooner & Vaughn 2012). Our results indicate that environmental factors are most important in determining the abundance or presence of species (Sup Fig 3). Extensively documented broad scale declines in freshwater mussel communities due to multiple stressors (Haag 2012) suggest that contemporary freshwater mussel community structure is explained by the Eltonian Noise Hypothesis and possibly the Stress-Gradient Hypothesis (Bertness & Callaway 1994). The latter states that in stressful environments, species interactions shift from competition to facilitation. Considering the numerous documented population declines of freshwater mussels throughout North America (Haag 2012), the Stress Gradient Hypothesis may account for the strong positive interactions we observed at the site scale, but further investigation is required to quantify possible stressors affecting freshwater mussel communities in east Texas. Additionally, there is evidence to suggest that the type of interaction between populations within a community might differ across scale with facultative interactions having effects at larger spatial scales than nonfacultative interactions (Mod *et al.* 2020), which may explain why there are observed strong interactions at the HUC 8 spatial scale for both the presence and abundance JSDMs.

While the average magnitude and directionality of interaction are consistent with the Eltonian Noise Hypothesis and observed biogeographical region assemblage patterns (Haag 2010), variation of the presence and abundance for individual populations was, on average, greatest at the site spatial scale. We also found that the ability of our JSDMs to accurately predict species abundance or presence was lowest at the site spatial scale regardless of the inclusion or exclusion of variation from environmental variables (Sup Fig 4). The low predictability of abundance and presence at the site scale and the previously accurate description of the Grinnellian niche of the

east Texas freshwater mussel community (Walters *et al* 2017), may suggest that there is a missing Eltonian niche dimension that could be affecting mussel abundance and presence at fine spatial scales. One possibility could be the relationships between freshwater mussels and their obligate fish hosts, which has been shown to affect the abundance and presence of freshwater mussels (Vaughn *et al.* 2008; Haag & Stoeckel 2015; Inoue *et al.* 2017b). JSDMs have potential as useful tools for investigating the obligate parasitic interactions between mussels and their hosts, but our results suggest that fish host and freshwater mussel data must be collected at very fine spatial scales to allow for ecologically relevant interpretations.

While ENMs have been repeatedly touted as powerful tools to aid in conservation planning for many taxa (Guisan *et al.* 2013; Levin *et al.* 2014) and many Grinnellian ENMs exist, many conservation plans forgo ENMs and instead utilize expert opinion to account for biotic interactions (Tulloch *et al.* 2016; Di Febbraro *et al.* 2018). Limited occurrence data, occurrence collection bias, scalar mismatch of ecological variables, poor understanding of the Eltonian niche, and lack of consideration of socio-economic factors are some of the many issues which have limited the use of ENMs as conservation tools (Lecours 2017; Mair *et al.* 2018). Developing ENMs that consider the Eltonian Noise Hypothesis and that incorporate both the Eltonian and Grinnellian niches should do a better job of accounting for scalar mismatch of niche space and environmental covariates. Having more complete and multi-scale ENMs will improve their usefulness as conservation tools.

Grinnellian ENMs have advanced substantially in the last 20 years, with a near-exponential growth in use, but the failure to consider biotic interactions has given rise to the “Eltonian Shortfall” (Dehling & Stouffer 2018). The extensive use of these ENMs has been a direct result of widely available occurrence data and easily accessible remotely sensed scenopoetic environmental data. Though the data to develop Eltonian ENMs is

more difficult to acquire, these data are becoming more readily accessible with increases in the number and extent of biodiversity databases. The added benefit of incorporating the Eltonian niche into ENMs is that it increases their usefulness as conservation tools by utilizing both abiotic and biotic factors to identify niches while also addressing factors that arise at different spatial scales. Both scale and the Eltonian niche are often omitted from consideration when conservation strategies are developed and implemented. This has been shown to reduce the effectiveness of conservation efforts (Boyd *et al.* 2008; Huber *et al.* 2010; Wiens *et al.* 2010; Zhu *et al.* 2013). The incorporation of biological interactions and scale into ENMs will not only increase the management and conservation efforts aimed at reducing loss of biodiversity in response to global climate change and other anthropogenic stressors (Seo *et al.* 2009; Ashraf *et al.* 2017).

Acknowledgments: We would like to thank the Miami University Aquatic Ecology Laboratory and anonymous reviewers for their assistance on this manuscript.

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Tables & Figures

Table 1. Result of the Hierarchical Modeling of Species Community model of freshwater mussel abundance and presence interactions across four separate spatial scales. There was a total of 561 potential interactions among the 34 freshwater mussel species in east Texas. Strong interactions have an interaction magnitude greater than or equal to 0.7 or less than or equal to -0.7 and can be considered substantial interactions. Strong interactions are more prevalent at finer spatial scales, supporting the Eltonian Noise Hypothesis.

	positive interactions	negative interactions	strong positive interactions	strong negative interactions	total strong interactions
site abundance	392	169	189	36	225
HUC 8 abundance	313	248	19	9	28
basin abundance	331	230	1	0	1
drainage abundance	292	269	1	1	2
site presence	371	190	136	0	136
HUC 8 presence	297	264	21	21	42
basin presence	314	247	0	0	0
drainage presence	286	275	0	0	0

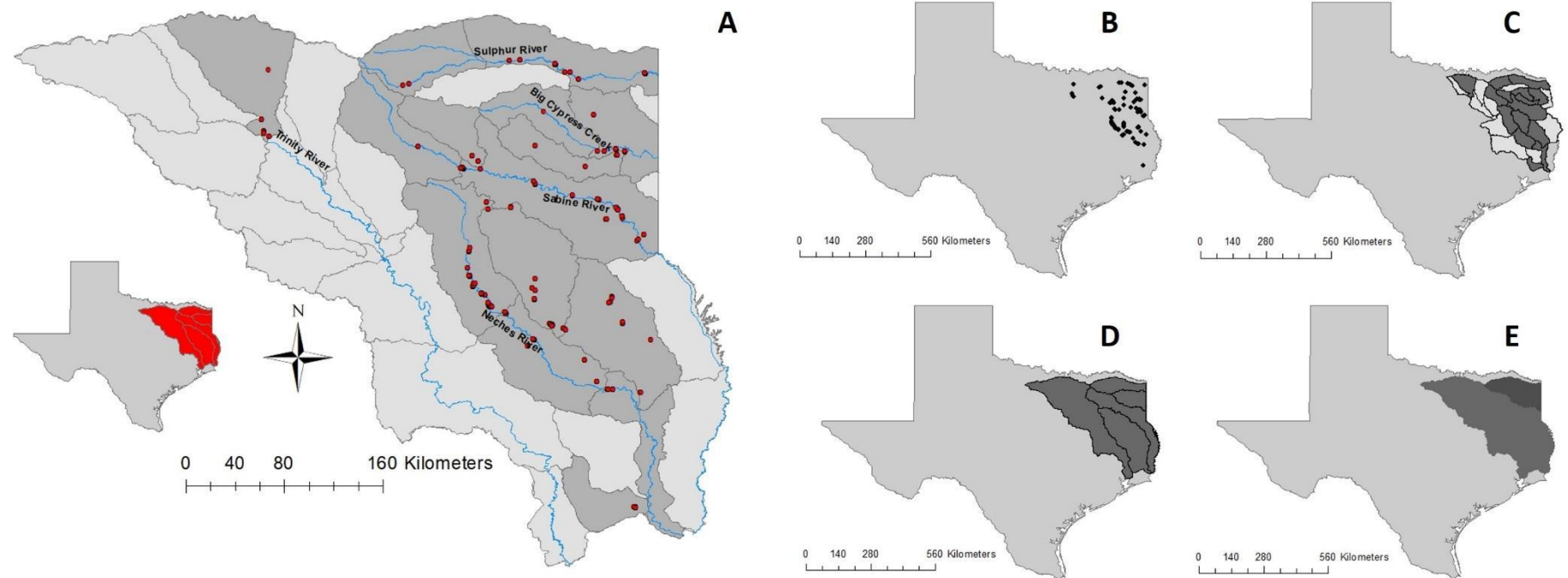


Figure 1. 165 sampling locations across east Texas. Dark grey shapes are HUC 8s with sampling locations indicated; light grey HUC 8 areas did not have any sampling sites (A). Four spatial scales used in the HMSC analysis: Site (B), HUC 8 (C), Basin (D), and Drainage (E). In panel C, darker areas indicate the 15 HUC 8s where collection sites occurred.

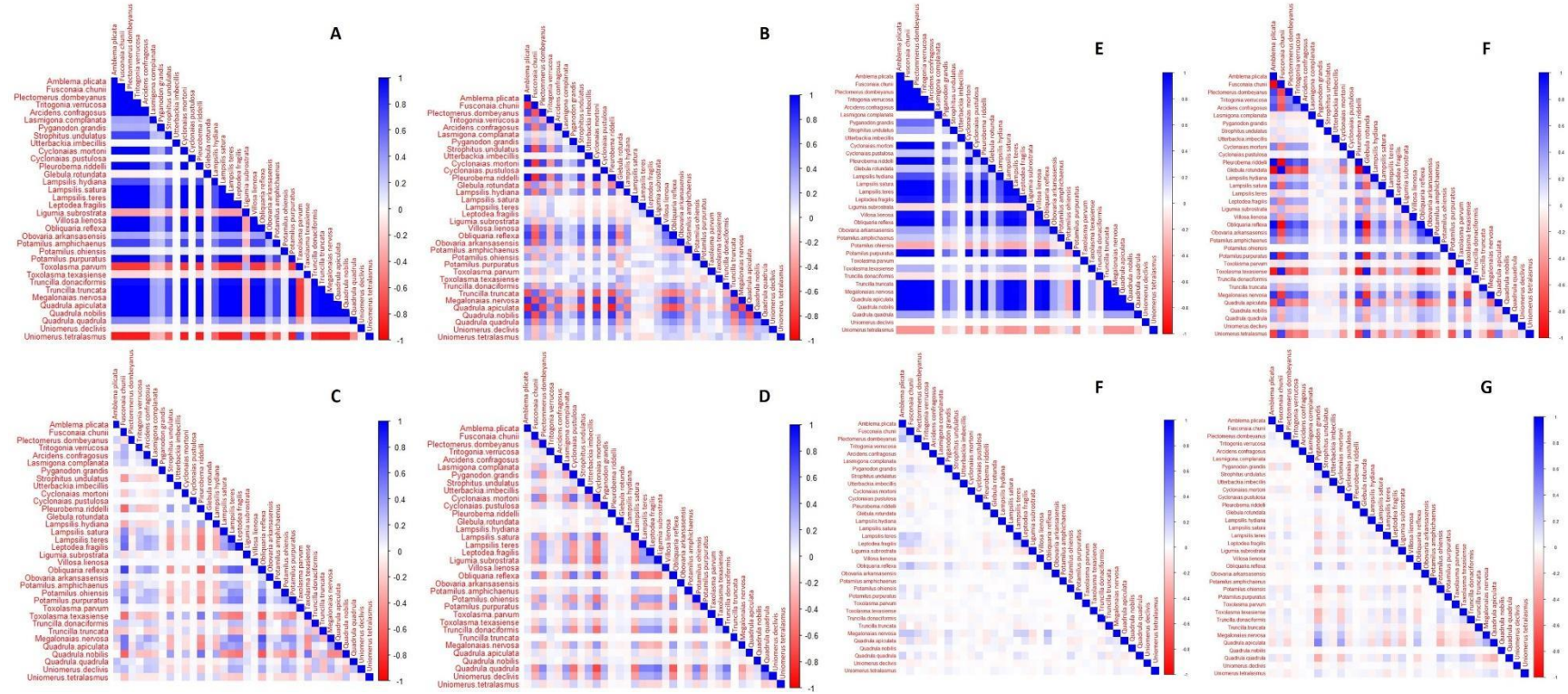


Figure 2. The results of the HMSC model for the abundance data across four spatial scales: site (A), HUC 8 (B), river basin (C), drainage basin (D). The results of the HMSC model for the presence data across four spatial scales: site (E), HUC 8 (F), river basin (G), drainage basin (H). Blue colors represent positive interactions and red colors negative interactions. The intensity of the hue indicates the magnitude of the interaction. There are substantially more positive interactions than negative interactions. Also, the number of strong interactions (i.e., interactions ≥ 0.7 or ≤ -0.7) are more prevalent at finer spatial scales.

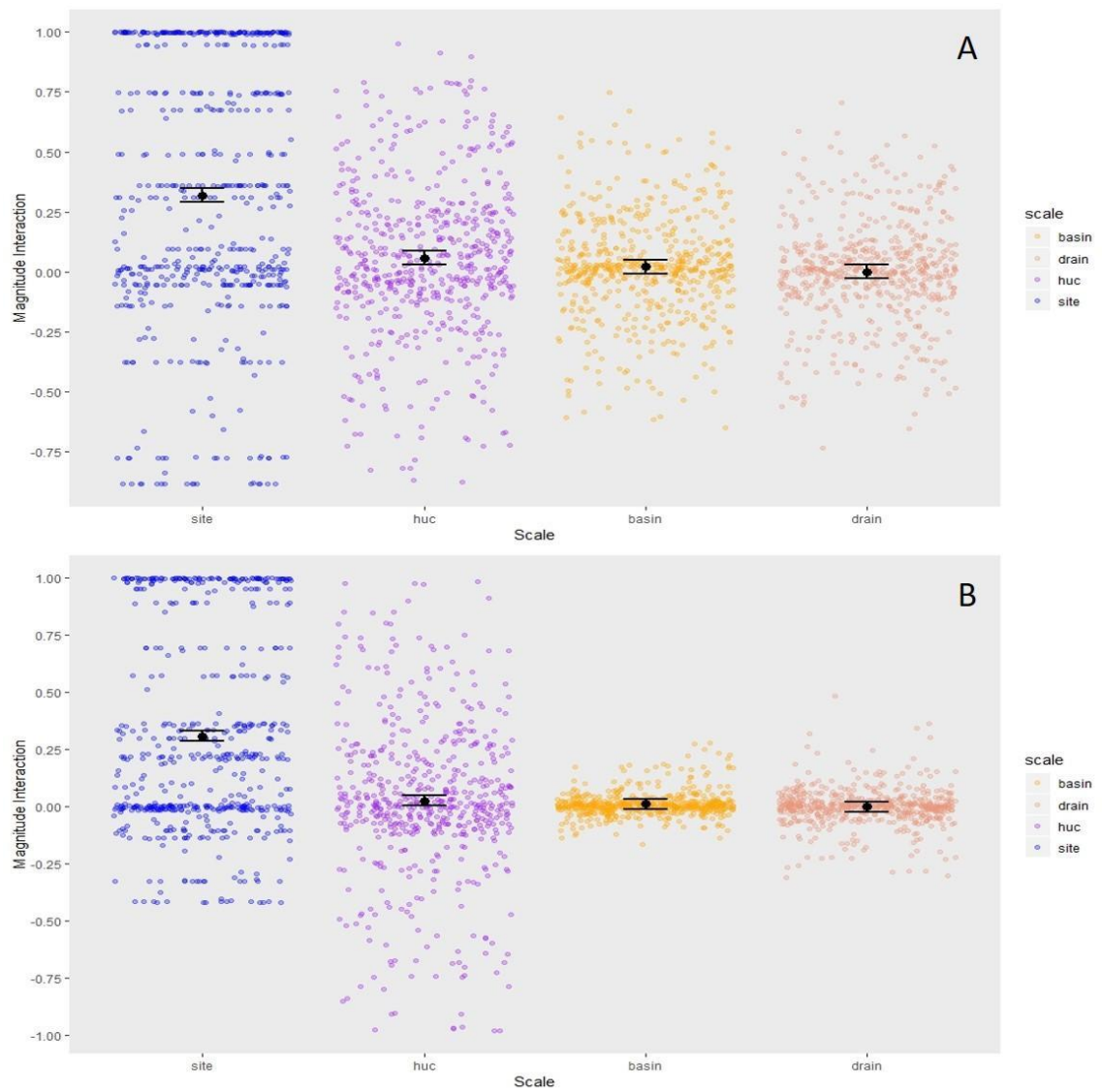


Figure 3. Comparison of average magnitude of interaction across four spatial scales for the abundance (A) and presence (B) data. These data show that the magnitude of interaction was statistically different at the site scale compared to all other spatial scales at an alpha of 0.05.

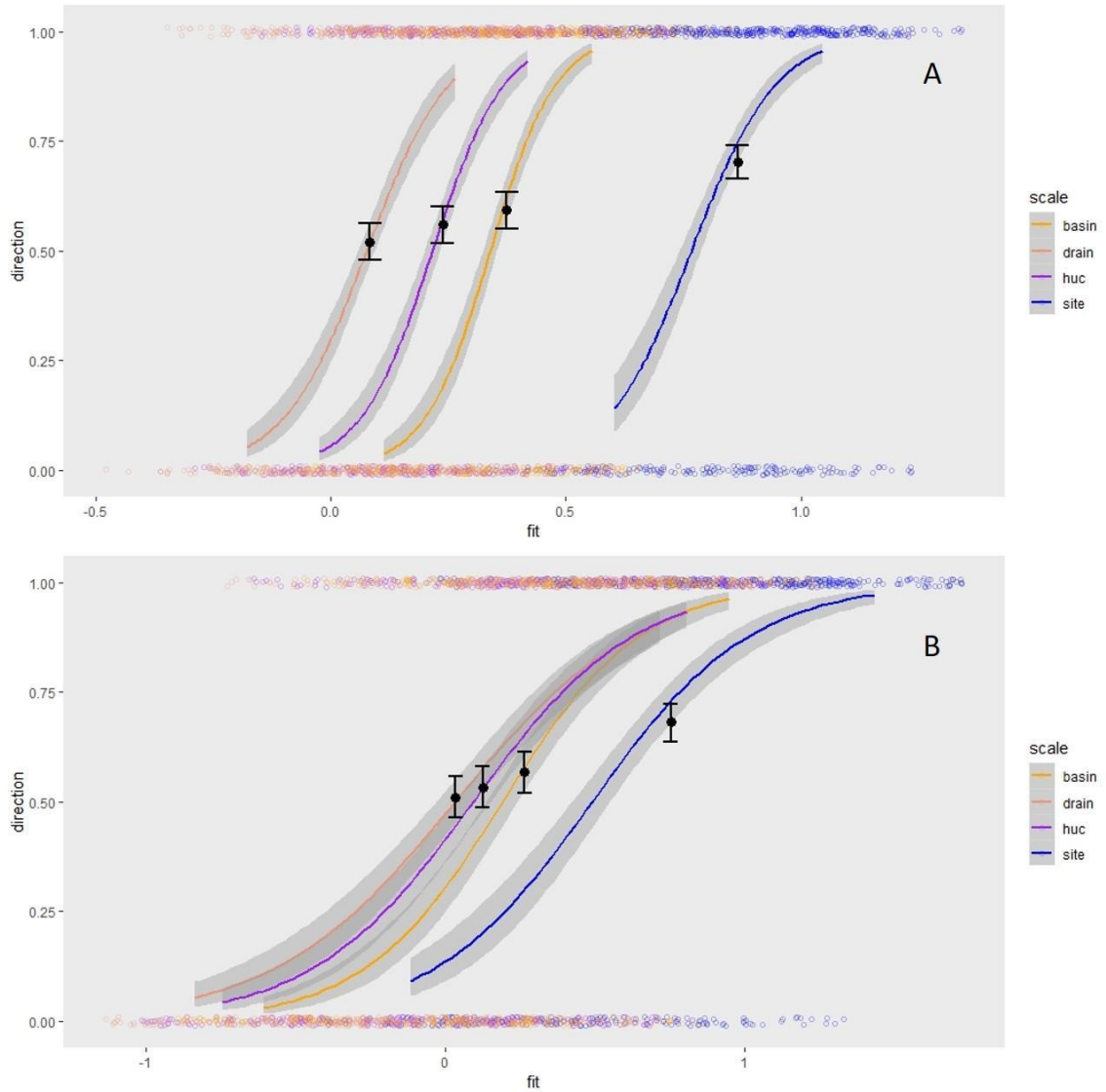


Figure 4. The results of the generalized linear mixed effect model for the direction of the abundance (A) and presence (B) data across spatial scales. The dots and error bars show the average direction of each data set at each spatial scale. Site is the only spatial scale that is significantly unique $\alpha = 0.05$.