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# Resource Partitioning and Habitat Selection in Southern Appalachian *Macromia* Species

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## Abstract

Odonate nymphs are considered bioindicators of lotic ecosystem health due to their sensitivity to factors including hydrology, substrate composition, and water quality. Species in the genus *Macromia* are regarded as an indicator of lotic ecosystem health, yet species-specific distribution and habitat associations in the Southern Appalachian region have been poorly described. This study aimed to characterize the distribution and resource partitioning of the three co-occurring *Macromia* nymph species present in the Southern Appalachian region: *Macromia alleghaniensis, Macromia illinoiensis,* and *Macromia margarita*. Nineteen sites were selected that represented a variety of lotic habitats, ranging in stream size and environmental conditions. The environmental variables considered included drainage area, maximum elevation, slope, and watershed land coverage. *Macromia* nymphs were sampled from these sites to identify species-environment and species-species relationships as well as potential niche differentiation. Resource partitioning was evident among the three species, with drainage area being the largest contributing factor to species distribution. *M. margarita* was associated with low drainage area systems, while *M. illinoiensis* was associated with high drainage area systems; *M. alleghaniensis* showed no clear association with drainage area. No co-occurrence was observed between *M. illinoiensis* and *M. margarita,* indicating resource partitioning between these two species. These findings improve the understanding of habitat partitioning in *Macromia species* and enhance their ability to serve as bioindicators and aid in conservation efforts in southern Appalachian lotic ecosystems.

# Introduction

Dragonflies in the genus *Macromia* (river cruisers) consist of several medium to large bodied species that are predominantly river inhabitants with a few species occurring in lakes and ponds (Tennessen 2019). Adults within this genus are typically characterized by elongated bodies, rapid flight, and a strong association with medium to large flowing waters. Due to the genus' reliance on well-oxygenated rivers and streams, *Macromia* species often exhibit relatively narrow habitat requirements and limited dispersal among river systems, making them sensitive indicators of aquatic ecosystem integrity (Paulson 2011). In eastern North America, several species of *Macromia* including *Macromia illinoiensis*, *Macromia alleghaniensis,* and *Macromia margarita* (Westfall 1947) have garnered attention for their unique biogeographic distributions, morphological characteristics, and conservation profiles.

*Macromia margarita,* commonly known as the Mountain River Cruiser, is endemically restricted to the southeastern United States, particularly the Appalachian mountain region. This narrow distribution combined with relatively few documented occurrences has led to the perception that *M. margarita* is both uncommon and potentially vulnerable to habitat alteration. Whether its apparent rarity reflects true population scarcity, specialized habitat requirements, or limited sampling remains unclear, but its restricted range makes the species of particular interest from both conservation and biogeographic perspectives. *Macromia illinoiensis*, commonly known as the Illinois River Cruiser, is a widely distributed species ranging from the Great Lakes region to the Gulf Coastal plain and westward into the Mississippi River basin (Needham 2014). *Macromia alleghaniensis*, known as the Allegheny River Cruiser, are associated with small to medium slow flowing streams (Craves 2017). The species has a wide range across Eastern North America with distribution centered on the Appalachian region and extensions into the Ohio River and upper Mississippi River basins (Needham 2014).

Research has been conducted in other countries and regions on *Macromia* species' populations and nymph habitat (Rivera 2000 ; Leipelt 2005). However, this information is limited for the Southeastern United States. *Macromia* has been documented in Western North Carolina, but the mapping of species' distribution and research into preferred habitat is incomplete. Establishing baseline ecological and distributional information for this understudied genus would provide a foundation for future research, conservation, and management efforts in southern Appalachian stream ecosystems.

Resource partitioning is a fundamental ecological process of the divergence of resource use between species that once had greater overlap in their environmental requirements (Walter 1991). Such partitioning may occur through spatial segregation, dietary differentiation, or micro habitat preferences including substrate, water depth, cover, and bank characteristics. These mechanisms have been documented in Odonate communities where closely related species exhibit distinct microhabitat preferences or foraging strategies despite morphological similarities (Khelifa 2013). Although multiple *Macromia* species have been documented inhabiting similar riverine environments, little is known about the resource partitioning where their ranges overlap. Understanding patterns of habitat use and resource partitioning among *Macromia* species in the Southern Appalachian region is essential for understanding the mechanisms that allow coexistence in lotic ecosystems and for informing conservation strategies.

The goal of this study was to characterize the distribution and resource partitioning of the *Macromia* nymphs present in Southern Appalachia. Nineteen sites that represent diverse lotic environments ranging in stream size and environmental characteristics, were surveyed for *Macromia alleghaniensis, Macromia illinoiensis,* and *Macromia margarita*. This information was used along with existing data from previous collections to identify environmental characteristics associated with species presence, abundance, and co-occurrence. We hypothesized that there would be significant differences in resource partitioning and habitat preferences between the *Macromia* species.

# Methods

Nineteen sites were surveyed for *Macromia alleghaniensis, Macromia illinoiensis,* and *Macromia margarita* from September 2025 to November 2025 (Table 1). Sites were selected to represent a range of riverine habitats within the southern Appalachian region. In addition to the sites surveyed, *Macromia* records from previous collections were used to determine the presence of each species at each site. Analysis of the geographical data of each location was used to understand the environmental characteristics that influence resource partitioning and habitat preferences among different *Macromia* species.

## Data collection

The 4x2 survey method was utilized at each of the sites to ensure a consistent measurement of sampling effort. The 4x2 survey method consists of four scoops using a D net in 2 different stream habitat types: pools and root overhangs. Root overhangs were defined as submerged root structures along stream banks, while pools were characterized as areas of deep, slow-moving water, which are the environments where *Macromia* are most likely to be found (Rivera 2000). Pools with high amounts of leaf litter build up were target areas for sampling. The contents of the dip nets were then put into a sifter, and the nymphs were picked from there. The sifter was made from a 16-quart drain pan that had the bottom replaced with a screen that had 1cm$^2$ holes. This method of sampling was utilized at fourteen of the nineteen sites. Only those sites were used to analyze the abundance of *Macromia* nymphs. The other five sites were sampled before the 4x2 method was established. Any site that was not sampled using the 4x2 method could not be included in the abundance data due to the lack of a standard unit of effort. This avoided sites having artificially increased abundance due to being more sampling than other locations. All sites were used for the presence/absence analysis.

All *Macromia* species found were documented and collected. After collection, the *Macromia* nymphs were identified to species using published taxonomic keys (Tennessen 2019, Westfall 1947). Primary diagnostic features used to identify the nymphs include the height, width and curvature of the middorsal hook of abdominal segment 6 and the length of the posterolateral spines on segment 10 compared to the anal pyramid. Nymphs were photographed under a dissecting scope using a phone camera. Some of the nymphs were measured than released after identification while others remained in collection for additional research.

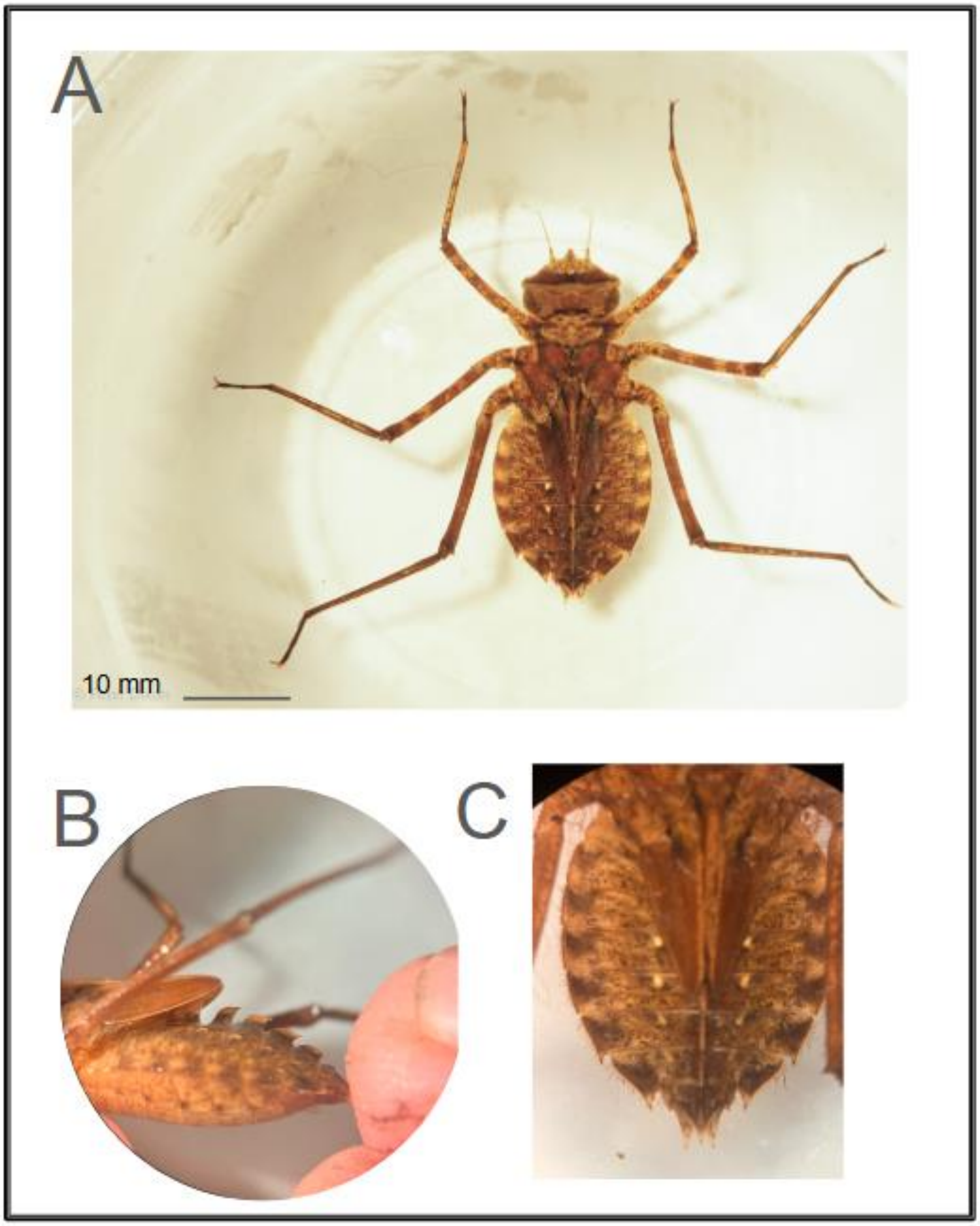

**Figure 1.** Representative morphology of a *Macromia Margarita* nymph. (A) A full body view of a *M. margarita* nymph. (B) A close up on the abdomen highlighting the S6 middorsal hook. (C) A close up of the abdomen highlighting the S9 posterolateral spines.

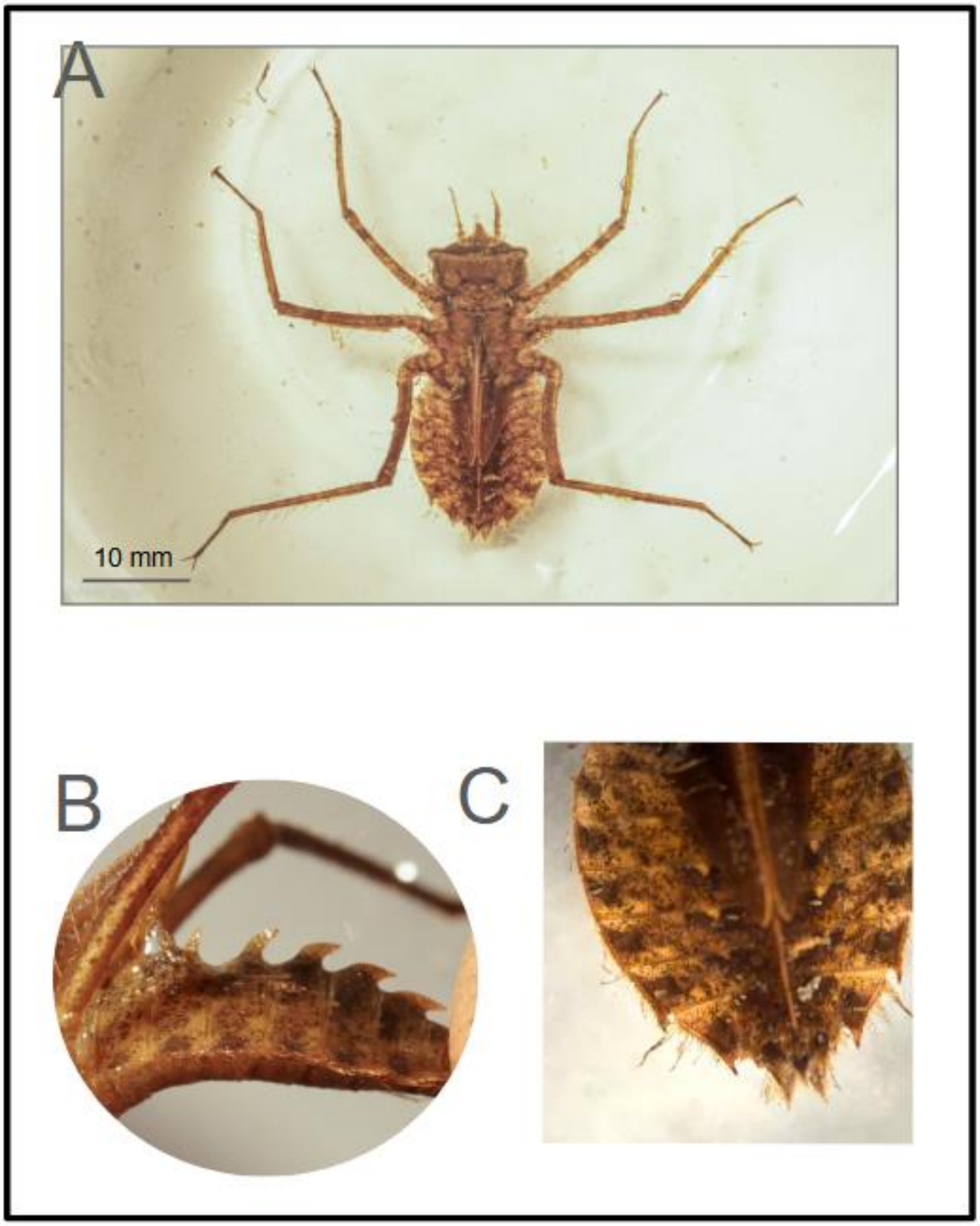

**Figure 2.** Representative morphology of a *Macromia alleghaniensis* nymph. (A) A full body view of a *M. alleghaniensis* nymph. (B). A close up on the abdomen highlighting the S6 middorsal hook. (C) A close up of the abdomen highlighting the S9 posterolateral spines.

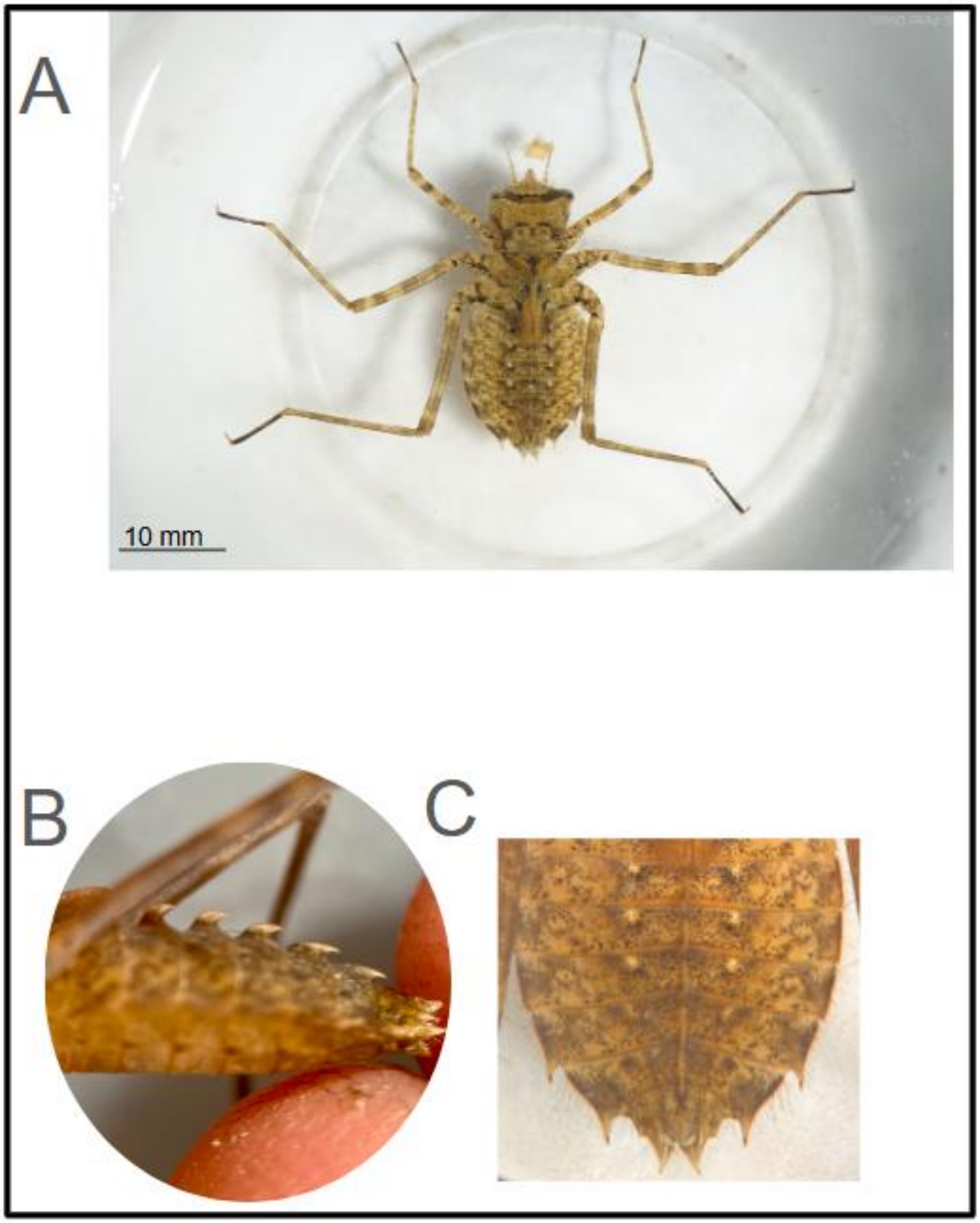

**Figure 3.** Representative morphology of a *Macromia illinoiensis* nymph. (A) A full body view of a *M. illinoiensis* nymph. (B). A close up on the abdomen highlighting the S6 middorsal hook. (C) A close up of the abdomen highlighting the S9 posterolateral spines.

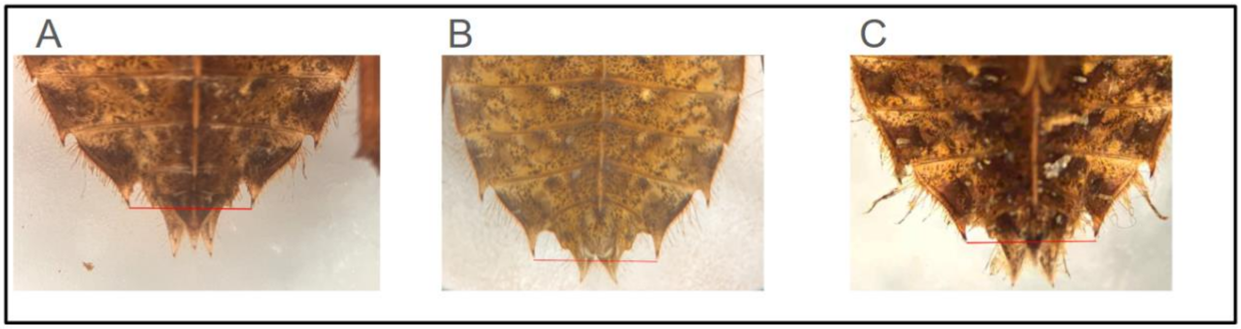

**Figure 4.** Images highlighting the morphological differences of the S9 posterolateral spines between *Macromia* species. (A). *M. margarita* typically has a S9 posterolateral spine to paraproct midventral length of < .5. (B) *M. illinoiensis* typically has a S9 posterolateral spine to paraproct midventral length of between .6-.7. (C) *M. alleghaniensis* typically has S9 posterolateral spines shorter than *M. illinoiensis* (Tennessen 2019).

**Figure 5.** Images highlighting the morphological differences of the middorsal hook of abdominal segment 6. A. *M. margarita* typically has a S6 middorsal hook with distal margin straight and an apex of the hook not projecting over anterior portion of the S7 segment. *B. M. illinoiensis* typically has a S6 hook that is pointed dorsoposteriorly. *C. M. alleghaniensis* has a s6 hook with a ratio of width to height of .036-.52 (Tennessen 2019)

## Environmental Variables

Environmental variables were selected to represent hydrological, geomorphic, and land-cover gradients hypothesized to influence species distribution. Drainage area, elevation max, mean elevation, mean basin slope and land-coverage information were obtained for each site using the StreamStats web application (U.S. Geological Survey 2019). Drainage area is the area of land that drains into the stream. Elevation is the average elevation of a stream and elevation max is the maximum elevation at that stream. Mean basin slope is the average total slope percent of the stream. Land cover variables included percent barren land, cultivated crops, developed land, forest, grassland/herbaceous cover, impervious surface, shrubland, open water, and wetlands. All environmental (Table 1) and land cover (Table 2) data were derived using the StreamStats web application, which incorporates classifications from the National Land Cover Database. StreamStats uses data from the U.S Geological Surveys, National Water Information System, and the National Streamflow Statistics database.

## Data analysis

Land-cover variables were summarized using principal component analysis using the Vegan package in R (R Core Team 2025 4.5.3) to reduce dimensionality and account for collinearity among predictors. Species abundance was modeled using Poisson generalized linear models using the dplyr R package(R Core Team 2025 5.1.513). Pairwise associations were used to evaluate co-occurrence among *Macromia* species across sites. Relationships between species composition and environmental variables were further examined using redundancy analysis using the Vegan package in R (R Core Team 2025 5.1.513).

**Table 1.** The sites surveyed and the drainage area, elevation, max elevation, and slope of each location.

| Site name | Latitude | Longitude | Drainage area ($mi^2$) | Elevation average (Feet) | Max elevation (Feet) | Slope (%) |
|---|---|---|---|---|---|---|
| McDowell Creek | 35.423809 | -82.550961 | 4.7 | 2330 | 3300 | 20.64 |
| Brush Creek | 35.840195 | -82.714156 | 4.86 | 2450 | 3670 | 43.17 |
| Elisha Creek | 35.918347 | -80.547801 | 6.77 | 783 | 891 | 30.13 |
| Bent Creek | 35.792107 | -82.538709 | 10.9 | 2570 | 4000 | 36.60 |
| Flat Creek | 35.729451, | -82.596196 | 16.5 | 2510 | 4240 | 25.41 |
| Laurel River | 35.953908 | -82.706802 | 36.1 | 2990 | 2991 | 47.1691 |
| Forks of Ivy | 35.792107, | -82.538709 | 46.5 | 2670 | 4260 | 31.309 |
| Little River | 35.255340, | -82.640587 | 59.7 | 2740 | 3780 | 22.856 |
| Spring Creek | 35.889178, | -82.828140 | 71.5 | 3100 | 5160 | 43.922 |
| Cane Creek | 35.426907, | -82.492451 | 79.7 | 2610 | 4410 | 47.169 |
| Swannanoa river | 35.607976, | -82.443084 | 80.5 | 3260 | 6370 | 43.736 |
| Laurel River | 35.913928, | -82.757195 | 129 | 2960 | 4930 | 37.213 |
| Cane River Yancey County | 36.025649 | -82.328269 | 158 | 3510 | 6680 | 42 |
| French broad in Marshall | 35.793351 | -82.677820 | 1340 | 2665 | 6370 | 29.094 |
| French broad in Hot springs | 35.894683 | -82.823001 | 1570 | 2670 | 6370 | 31.90 |
| French Broad Near Tn | 35.923777, | -82.868370 | 1650 | 2690 | 6370 | 26.8 |
| French Broad near airport | 35.421769, | -82.542125 | 634 | 2680 | 6000 | 37.9 |
| Mills river | 35.391275, | -82.568904 | 70.5 | 3070 | 5320 | 27.70 |
| Dingle Creek | 35.507588, | -82.518374 | 0.84 | 2540 | 3490 | 27.70 |

**Table 2.** The bank characteristics of each of the sites surveyed. The bank characteristics include barren, hay and other cultivated crops, developed, forested, grassland, impervious, shrubland, open water and wetland.

| Site name | Barren | Hay and cultivated | Developed | Forest | Grass | Impervious | Shrub | Open water | Wetland |
|---|---|---|---|---|---|---|---|---|---|
| McDowell Creek | 0 | 25.7 | 27.6 | 42.7 | 2.4 | 3.3 | 1.44 | 0 | 0 |
| Brush Creek | 0 | 13.8 | 3.4 | 80.1 | 1.6 | .2 | 1.1 | 0 | 0 |
| Elisha Creek | 0 | 22.7 | 18.2 | 49.3 | 5.9 | 4.1 | 3.6 | .2 | .1 |
| Bent Creek | .1 | 17 | 7.9 | 72.1 | 1.8 | 1.7 | 1 | .1 | .1 |
| Flat Creek | .1 | 18.9 | 13.2 | 64.8 | 2.3 | 1.6 | .7 | 0 | 0 |
| Laurel River | .1 | 4.5 | 3.9 | 90 | .8 | .3 | .8 | 0 | 0 |
| Forks of Ivy | .1 | 17 | 7.9 | 72.1 | 1.8 | 1 | 1.1 | 0 | 0 |
| Little River | 0 | 5.6 | 6.7 | 85.8 | .6 | .5 | .4 | .8 | .2 |
| Spring Creek | 0 | 4.4 | 3.5 | 90 | .6 | .1 | 1.1 | 0 | 0 |
| Cane Creek | .1 | 14.8 | 14.2 | 68 | 1.8 | 1.7 | 1 | .1 | .1 |
| Swannanoa river | 0 | 2.6 | 16.2 | 79.2 | .5 | 2.5 | .6 | .8 | .2 |
| Laurel River | .1 | 5 | 2.3 | 91.8 | .5 | .1 | .3 | 0 | 0 |
| Cane River | 0 | 7.5 | 5.7 | 85.2 | .7 | .5 | .7 | 0 | 0 |
| French broad in Marshall | .1 | 13.5 | 16.8 | 67.4 | 1.2 | 2.6 | .6 | .3 | .2 |
| French broad in Hot springs | .1 | 12.6 | 14.9 | 70.1 | 1.1 | 2.3 | .7 | .3 | .1 |
| French Broad Near Tn | .1 | 11.8 | 15.4 | 70.7 | 1 | 2.2 | .6 | .3 | .2 |
| French Broad near airport | .1 | 11.8 | 15.4 | 70.7 | 1.1 | 2.2 | .7 | .33 | .1 |
| Mills river | 0 | 3.4 | 2.7 | 92.9 | .4 | .1 | .3 | 0 | .2 |
| Dingle Creek | .8 | .7 | 47.5 | 50.4 | .6 | 10.1 | 0 | 0 | 0 |

# Results

## Species to Species relationships

Pairwise associations among species were assessed using Fisher's exact tests on the presence data of each of the species (Figure 6). There were no significant pairwise associations between *M. illinoiensis* and *M. alleghaniensis* (*p= .6563*) or between *M. alleghaniensis* and *M. margarita* (p =.1409). There was a significant negative association between *M. margarita and M. illinoiensis* (p = .01, odds ratio: 0), reflecting that these species do not cooccur in these streams.

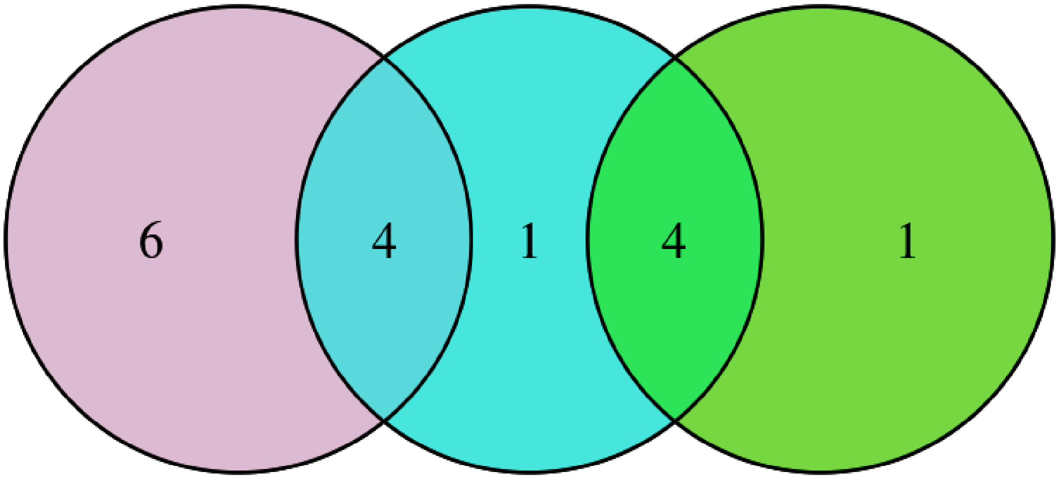

**Figure 6**. A Venn Diagram showing the co-occurrence among *Macromia* Species based on binary presence-absence data. Each of the numbers represents the amount of sites where those species were found. Of the 19 sites sampled, 6 sites contained only M. margarita (Pink), 1 site contains *M. alleghaniensis* (Cyan), 1 site contains only *M. illinoiensis* (Green), 4 sites contain *M. margarita* and *M. alleghaniensis*, and 4 sites contain *M. alleghaniensis* and *M. Illinoiensis*. *M. margarita* and *M. illinoiensis* were never found at the same site.

## Drainage area range by species

*M. Margarita* was observed at the lowest range of drainage areas of the three species (Table 3), having only been found at the lower 8% of the total range of drainage areas of the sampled sites. Both *M. alleghaniensis* and *M. illinoiensis* were observed across the full range of drainage areas sampled.

Table 3. The ranges of drainage area in which a species was found.

| Species | Range of Drainage area (mi$^2$) |
|---|---|
| *M. margarita* | 4.7-129 |
| *M. alleghaniensis* | 16.5-1650 |
| *M. illinoiensis* | 10.9-1650 |

## Redundancy analysis

Redundancy analysis (RDA) was used to relate species presence-absence to drainage area, maximum elevation, and slope (Figure 7). Mean elevation was not included, as it covaried with maximum elevation. The significance of individual environmental predictors was assessed using permutation-based ANOVA. The drainage area showed a significant influence on species composition ($F_{1,15}$=7.8335, p= 0.0012). The maximum elevation of a site had a significant impact on species composition ($F_{1,15}$=2.9049, p= 0.0472). Slope did not significantly influence species composition ($F_{1,15}$=0.415, p >0.5672). *M. alleghaniensis* was more likely to be found at sites that loaded positively with RDA1 (coefficient =3.781.73SE, $^{2}_{1}$ =9.73, p=0.002) *M. margarita* was more likely to be found at sites that loaded negatively with RDA1 (coefficient = -6.083.22SE, $^{2}_{1}$ =17.43, p=0.00003).

## Principal Component analysis

The first three principal components of the analysis explained 90% of the variance (table 4). The first principal component describing a forest–development gradient explained 40 percent of the variance, with positive loadings for forest cover and negative loadings for developed areas (table 5). The second principal component explained 30 percent of the variance and described a gradient between barren and developed areas to vegetated but non forested land (grass, crops, shrubs). The tertiary gradient explained 19 percent of the variance and described open water and wetland coverage (table 5). Species presence or absence was modeled using generalized linear models with binomial error distribution and logit link function. *M. margarita* was not significantly associated with the first three principal components (PC1, p=.136, PC2, p=.819, PC3=.575). *M. illinoiensis* was not significantly associated with the first three principal components (PC1, p=.175, PC2, p=.262, PC3=.729). *M. alleghaniensis* was not significantly associated with the first three principal components (PC1, p=.239, PC2, p=.137, PC3=.831).

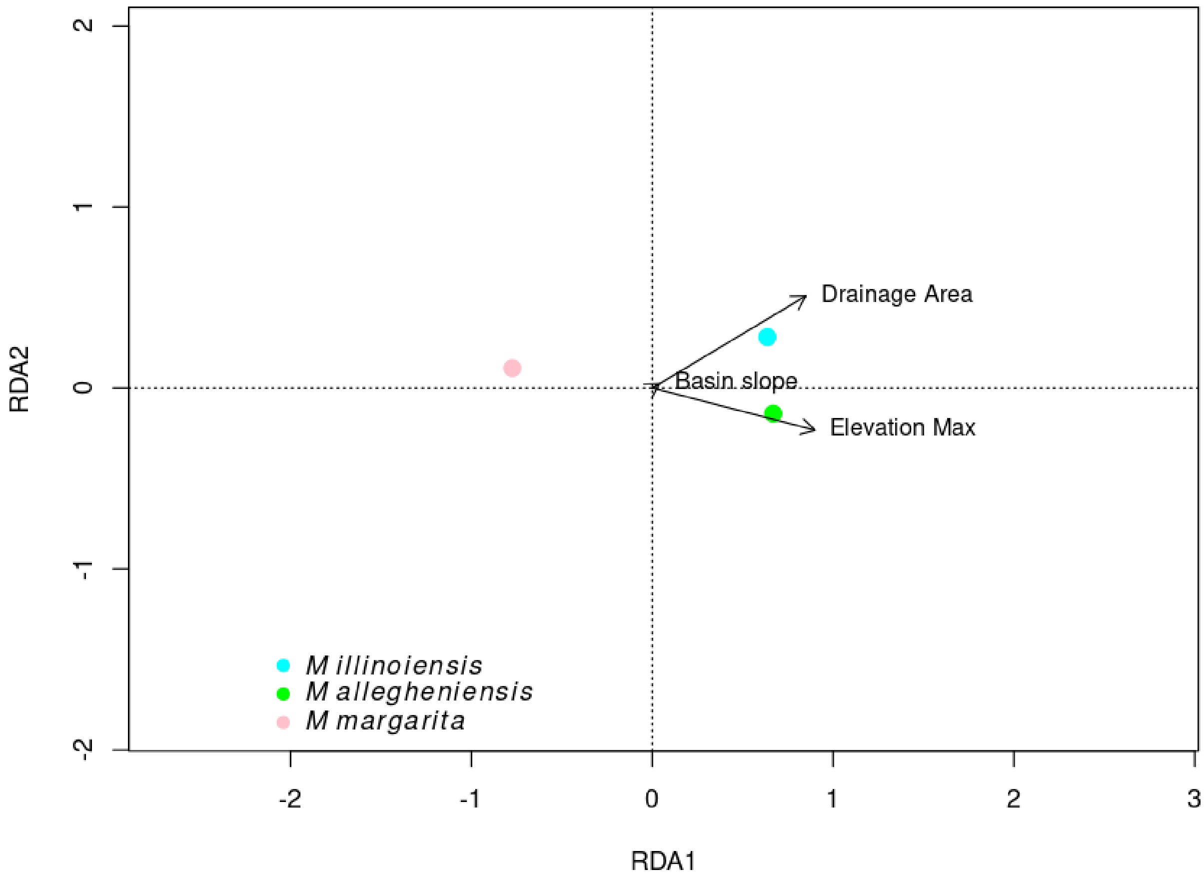

**Figure 7**. Redundancy analysis biplot showing relationship between *Macromia* species and environment gradients. Arrows represent environmental gradients where vector length indicates the strength of the correlation with ordination axis and direction indicating the gradient of increasing values.

Table 4. Standard deviations and proportion of variance in land coverage variables explained by 9 principal components

| | PC1 | PC2 | PC3 | PC4 | PC5 | PC6 | PC7 | PC8 | PC9 |
|---|---|---|---|---|---|---|---|---|---|
| Standard deviation | 1.914 | 1.6660 | 1.3176 | 0.67234 | 0.52439 | 0.27086 | 0.14041 | 0.07155 | 0.0033958 |
| Proportion of Variance | 0.407 | 0.3084 | 0.1929 | 0.05023 | 0.03055 | 0.00816 | 0.00219 | 0.00057 | 0.000 |
| Cumulative Proportion of Variance | 0.407 | 0.7154 | 0.9083 | 0.95853 | .98908 | 0.99724 | .999431 | 1.000 | 1.000 |

Table 5. Loadings of each of the 9 land coverage variables on the principal components.

| | PC1 | PC2 | PC3 | PC4 | PC5 | PC6 | PC7 | PC8 | PC9 |
|---|---|---|---|---|---|---|---|---|---|
| Barren | -.2924 | .4608 | -.1821 | .1230 | .0674 | -.6081 | -.4644 | -.2525 | -.0027 |
| Hay | -.2970 | -.4168 | .0083 | -.6448 | -.0732 | -.2110 | -.2744 | .2525 | .3651 |
| Developed | -.4275 | .3214 | .1217 | -.0755 | -.0453 | .4224 | .1861 | -.4206 | .5488 |
| Forest | .5028 | .0180 | -.1189 | .3128 | .0649 | -.1984 | -.0164 | .1843 | .7486 |
| Grass | -.3475 | -.4120 | .1055 | .2975 | .1070 | -.4842 | .5806 | -.1541 | .055 |
| Impervious | -.4183 | .3364 | .1014 | .2224 | .0562 | .0636 | .1085 | .7955 | .0138 |
| Shrub | -.2531 | -.4629 | .1039 | .5539 | .0233 | .3013 | -.5547 | -.0562 | .0421 |
| Water | .1162 | .0898 | .6758 | .0695 | -.6879 | -.1977 | -.0666 | -.0092 | .0085 |
| Wetland | .1313 | .0704 | .6699 | -.1259 | -.1259 | -.0536 | -.1142 | -.0408 | .0021 |

## Abundance Data

Species-specific abundance-environment relationships were quantified using generalized linear models with Poisson error distribution and log link function. For each *Macromia* species, abundance was modeled as a function of individual environmental predictors (drainage area, maximum elevation, and slope) in separate univariate models. Analysis was restricted to sites with non-zero abundance for the focal species to determine variation in abundance rather than occurrence and avoid zero inflation. Model predictions were generated over the observed range of each predictor while holding all other variables constant. Species abundance was not significantly influenced by drainage area (*M. margarita p=.98, M. alleghaniensis* p=.424. *M. illinoiensis* p=.0918). Species abundance was not significantly influenced by max elevation. (*M. margarita* p = 0.719, *M. alleghaniensis* p=.884, *M. illinoiensis* p=.226). Species abundance was not significantly influenced by slope (M. *margarita p=.107, M. alleghaniensis* p=.363, *M. illinoiensis* p=.289).

## Discussion

*M. margarita* and *M. illinoiensis* exhibit a clear pattern of spatial segregation, as they were never observed at the same site. This included sites that were within the observed drainage area range of *M. margarita*. The consistent absence of *M. margarita* in sites where *M. illinoiensis* was present suggests a strong spatial partitioning mechanism that prevents co-existence between these species. This nonrandom segregation likely reflects ecological interactions, such as competitive exclusion or behavioral avoidance, which are both factors that can contribute to distinct distributions despite potential habitat similarities. One plausible explanation for this segregation is asymmetric intraguild predation, where one species outcompetes or preys upon the other one, influencing their spatial distribution

(Holt 1996; Polis 1989). Other studies have documented asymmetric intraguild predation between similar sized Odonate nymphs (Suutari 2004). This dynamic highlights the importance of interspecific interactions in influencing community structure and species distribution within aquatic ecosystems.

*M. alleghaniensis* did not display the same strict spatial distribution as the other Macromia in this study. *M. alleghaniensis* was found at sites with *M. margarita* as well as sites with *M. illinoiensis*. *M. alleghaniensis* was found at all ranges of drainage area, with seemingly no preference or exclusion patterns. It is likely that *M. alleghaniensis* is not subject to the same competitive or intraguild predation dynamics that is possibly occurring between *M. margarita* and *M. illinoiensis*. Its ability to exist across a wide range of environmental conditions suggests a different role within the community structure than the other Macromia or niche flexibility, which allows it to avoid competition with the other species.

Future research should aim to clarify the mechanisms for the resource partitioning displayed by Macromia species. Detailed behavior studies focusing on foraging strategies and habitat use would help show how the species avoid competition and coexist, or in the case of *M. illinoiensis* and *M. margarita* reveal where they encounter competition. Diet analysis could be performed on gut content or stable isotope analysis (Do et al. 2019) could be used to reveal the extent of dietary overlap or specialization. Experimental approaches would be valuable in testing the hypothesis of the intraguild predation between *M. margarita* and *M. illinoiensis* and would provide direct evidence of interspecific interactions between those species. In other prior research of resource partitioning among Odonata in a lotic environment, few cases of mutual predation and no cases of cannibalism were observed (Dudgeon 1989). Predatory interactions are typically more important in structuring lentic Odonata communities (Benke 1975) rather than the lotic environments Macromia are found in.

Understanding the habitat preferences of these Macromia species has important implications for their conservation and management in the future. *M. alleghaniensis* was shown to have a much broader habitat tolerance meaning they are more likely to be resilient to environmental changes. *M. margarita* being restricted to low drainage area sites as well as conflicting with *M. illinoiensis* means that it might be more vulnerable to habitat alteration and hydrological changes than previously known. The population of *M. margarita* is unknown, and its possible habitats could be more restricted than previously believed. Future conservation strategies for *M. margarita* should prioritize protecting the lower drainage systems where they are more likely to be present. For *M. illinoiensis* and *M. alleghaniensis*, maintaining water quality across their broader habitat ranges will support population stability.

# Acknowledgments

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