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# **OSTRACODE METACOMMUNITY DYNAMICS ON SAN SALVADOR ISLAND, BAHAMAS: DISCERNING PATTERNS OF DIVERSITY AND BIOGEOGRAPHICAL DISTRIBUTIONS**

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## **ABSTRACT**

Percent abundances of species preserved as microfossils in lake sediments are frequently used to infer past environments. This method implicitly assumes not only that there is a direct relationship between organisms and their abiotic environment, but also that the metacommunity dynamics of the species involved is dominated by species sorting. This paper tests these assumptions using ostracodes on San Salvador Island, Bahamas, by examining the variability in the abiotic environment of lakes on San Salvador as well as the rate of dispersal of ostracodes between those lakes. Twenty lakes were sampled for ostracode communities and nineteen physio-chemical variables during June 2008 and March 2009. The lakes sampled demonstrated variability in environmental factors known to influence ostracode community assembly. Additionally, the dissimilarity of ostracode communities is independent of the distance between lakes, indicating a high rate of dispersal between lakes. Taken together, it appears that metacommunity dynamics is dominated by species sorting, although mass effects cannot be ruled out. Detrended correspondence and canonical correspondence analyses indicate that conductivity, lake area, lake depth, and spatial position of lakes (latitude, longitude) are the

principle environmental factors controlling ostracode community assembly. Future work will focus on using ostracodes as proxies for past environments in order to understand late Holocene environmental change on San Salvador Island.

## **INTRODUCTION**

There is a need to produce quantitative records of past terrestrial environments both to test hypotheses regarding past climates and to understand how climate has changed in the past. High resolution, quantitative records of past salinity, water depth or temperature from lake sediments can be used to understand how global climate events affect local environments (Edlund and Storermer, 2000), how local biological communities are affected by changing climates (Walker et al., 1991), and even how human societies may affect the local environment and climate (Bush et al., 2007).

Microfossils, such as ostracodes, that get preserved in lake sediments, have the potential to provide quantitative reconstruction of past terrestrial environments (Cronin, 1999). This method, however, assumes a direct relationship between the environment (and often only one aspect of the environment) and the organisms under study. Equating assemblages of organisms representing paleocommunities with the environment ignores

variables other than those from the abiotic environment that might be influencing community assembly. These variables might include historical effects (Chase, 2003), neutral dynamics (Hubbel, 2001), biological interactions (Wellborn et al., 1996), and complex or non-equilibrium dynamics between organisms and their abiotic environment (Belyea, 2007). They also assume that the species involved conform to a species sorting metacommunity model (Holyak et al., 2005). This paper examines the metacommunity dynamics of ostracodes on San Salvador Island to determine if this taxa would be effective in reconstructing past environments; and if so, what aspect(s) of the environment do ostracodes respond most strongly to.

By assuming that percent abundances of species can be expressed as an environmental variable, paleoenvironmental methods make substantial assumptions, mainly that 1) ostracode metacommunity dynamics are dominated by species sorting (*sensu* Holyoak et al., 2005) such that the abiotic environment alone controls which species are found in which lakes and at what percent abundance, and 2) metacommunity dynamics are driven by one abiotic factor alone. This project will test these two key assumptions.

### Study Organism

Ostracodes are a class of bivalved microcrustaceans (Phylum Arthropoda) that live in all manner of aquatic habitats, from the deep ocean to ephemeral ponds (Horne et al., 2002). Most ostracode species live as benthic organisms and are sensitive to changes in the abiotic environment such as salinity, water depth, temperature or dissolved oxygen concentration (Frenzel and Boomer, 2005). Their low-Mg calcite shells range from 0.5-2mm in size and are often preserved as fossils, making them useful as biological proxies for past environments, including lakes (Frenzel and Boomer, 2005; Mischke et al., 2007; Mezquita et al., 2005; Mourguiart et al., 1996; Mourguiart and Carbonel 1994; Alin and Cohen, 2003; Viehberg, 2006). Each individual ostracode secretes 8-9 molted shells over its lifetime with the adult stage containing definitive characteristics that allow for species-level identification

(Holmes, 2008). Further, their shells can be used for trace elements (Mg and Sr) as well as isotopic information related to lake chemistry and climate (Holmes, 2008).

### Study Area

San Salvador Island is a small (163 km<sup>2</sup>) carbonate island within the Bahamian archipelago that lies approximately 380 miles southeast of Miami, Florida (24°30'N/74°30'W), on an isolated platform surrounded by deep ocean. During times of elevated sea level throughout the late Pleistocene and early Holocene, dune sediments were deposited across the San Salvador platform. Many lakes occur on the island today between these ancient dunes or may occur as karst dissolution features in the carbonate bedrock (Bain, 1991; Teeter, 1995; Park and Trubee, 2008). Lake sediments on the island are capable of preserving paleocommunities of ostracodes in sufficient abundance to be used in paleoenvironmental reconstruction (Teeter, 1995; Park et al., 2009). These quantitative paleoenvironmental records can help us to understand causes of environmental fluctuations over time (Teeter, 1995) as well as to interpret archaeological records on the island (Blick, 2007).

### Metacommunity dynamics

Metacommunities are groups of communities connected by dispersal. Holyoak et al., (2005) describes four models of metacommunity dynamics: patch dynamics, species sorting, mass effects, and neutral. The patch dynamic model is characterized by low rates of dispersal between similar habitats such that individual species are dispersal-limited and individual community assembly is influenced by stochastic dispersal. The species sorting model involves high rates of dispersal between heterogeneous environments such that all species can reach all communities, implying that community assembly is driven principally by the abiotic environment. The mass effects model is similar to the species sorting model, except that some species have such high rates of dispersal that they may be maintained regionally

in source-sink dynamics (Holyoak et al., 2005). Finally, the neutral metacommunity dynamics model (*sensu* Hubbell, 2001) assumes that species have evolved to be ecologically equivalent and can be modeled as having equivalent *per capita* birth and death rates and are dispersal limited. In this case, community assembly in individual environments is independent of the abiotic environment and is driven by the stochastic process of dispersal and ecological drift.

Thus, variability of environmental parameters and the rate of ostracode dispersal between lakes were used to distinguish between the four metacommunity models. Community patterns consistent with low and high rate of movement between lakes were determined by examining how dissimilarity of communities relate to the distances between those communities (Thompson and Townsen, 2006). A low rate of movement between communities would be inferred if communities closer together are more similar than communities further apart. This distance decay pattern would be caused by dispersal limitations of individual species (Volkov et al., 2003). Conversely, if community dissimilarity is independent of distance between communities, then a high rate of dispersal can be inferred.

## METHODS

A dataset consisting of ostracode communities and nineteen-physiochemical variables, including latitude, longitude, lake area, depth, dissolved oxygen, conductivity, water temperature, pH, total dissolved solids, alkalinity, and iron, manganese, sodium, potassium, calcium, magnesium, strontium, chloride, sulfate concentrations, from twenty lakes was created based on two trips to the island in June, 2008 and then in March, 2009. Further studies will later expand the number of lakes to at least thirty-six. Lakes to be included in this dataset are indicated in Figure 1.

### Field and Laboratory Methods

In June, 2008 and March, 2009, surface sediments and water samples were collected from 20 lakes on San Salvador Island. Surface sedi-

ments were collected by sweeping a net with attached jar across the sediment-water interface, recovering the upper 1-2 cm of sediment. All samples were collected ~10 m from the shore. Based on previous work (Dalman, 2009), this upper sediment represents about ~40 years worth of sediment accumulation. The ostracodes in these samples are “modern” assemblages. Sediment samples were kept in 125mL plastic jars for analysis at the University of Akron. Water samples were collected in the same 125mL jars at the sediment-water interface.

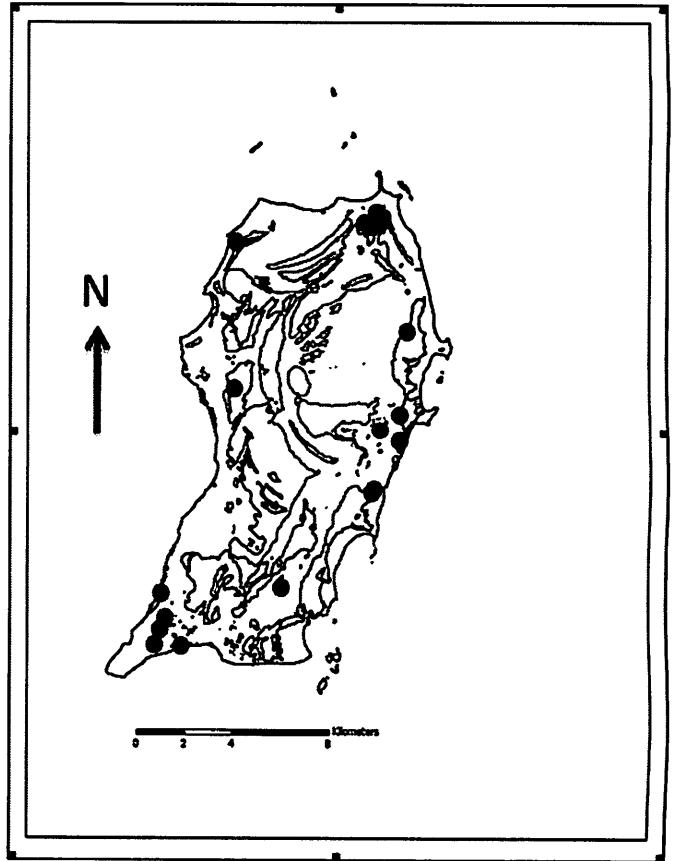


Figure 1. Map of San Salvador Island showing 20 lakes sampled for ostracode communities and 19 physio-chemical variables. Modified from Robinson and David (1999).

Conductivity, salinity, total dissolved solids, pH, dissolved oxygen, and water temperature were determined in the field with a YSI model field meter. Alkalinity was determined in the field using a Hach titration kit. Water depth was determined at the site of collection within +/- 1 cm. Latitude and longitude at the site of collec-

tion as well as lake area were determined using the San Salvador GIS database (Robinson and Davis, 1999).

Sediments sampled were sieved using 125  $\mu\text{m}$  ( $\phi$ -size 3) and 63  $\mu\text{m}$  ( $\phi$ -size 4) sieves with deionized water at the University of Akron. Upon drying, ostracodes were picked using a dissecting microscope. They were identified using reference material from the ostracode collection at the University of Akron (Trubee, 2002). In all cases, at least 400 ostracodes were picked from each sample and all adults were identified to species level (with the exception of *Propontocypris* sp. which could only be identified to genus). All samples included in this analysis contained more juveniles than adults indicating that the assemblage accumulated where the ostracodes lived and were not transported from another location (Mischke et al., 2007). Additionally, all samples to be included in this analysis reached asymptotes when a rarefaction analysis was done (Raup, 1975) indicating that all species were identified from each sediment sample.

Water samples were analyzed for the concentration of major cations using a Perkin Elmer Analysis 700 atomic absorption (AA) analyzer at the University of Akron using the flame AA technique. Water samples were analyzed for chloride and sulfate anions using a Dionex DX-120 ion chromatograph.

#### Statistical Methods

The statistical significance of individual environmental variables in controlling ostracode community was determined by Monte Carlo permutations tests (9999 unrestricted permutations). The dissimilarity of communities was compared using the Bray-Curtis dissimilarity index (Bray and Curtis, 1957). Detrended correspondence analysis (DCA, Hill and Gauch, 1980) with detrending by segments, square-root transformation of species abundances and non-linear rescaling using the program CANOCO (ter Braak, 1990) was run to determine the amount of community change ( $\beta$ -diversity or gradient length) represented in the dataset. Canonical ordination was run with forward selection of environmental vari-

ables and square-root transformation of species abundances in order to identify a minimum of environmental variables that could account for the majority of variation in the ostracode dataset (Legendre and Legendre, 1998; Mischke et al., 2007).

## RESULTS

The physical environments of the lakes sampled displayed a high degree of variability as measured by relatively high standard deviations compared to their means in parameters known to influence ostracode community distribution (Table 1). Lake area was the most variable of these parameters, ranging from 133m<sup>2</sup> to 5,864,078m<sup>2</sup> (coefficient of variation= 2.58), while pH was the least variable of these parameters, ranging from 7.2 to 8.7 (coefficient of variation= 0.0464). Conductivity varied between 13.87 to 152.2 $\mu\text{S/cm}$  with the mean being 66.7 $\mu\text{S/cm}$ . Depth varied from 2 to 210 cm and dissolved oxygen ranged from 2.45 to 12.8mg/L.

| Variable                          | Min    | Max     | Mean   | SD      |
|-----------------------------------|--------|---------|--------|---------|
| lake area (m <sup>2</sup> )       | 133.05 | 5864078 | 515984 | 1328960 |
| depth (cm)                        | 2      | 210     | 63.78  | 53.68   |
| conductivity ( $\mu\text{S/cm}$ ) | 13.87  | 152.2   | 66.77  | 32.54   |
| DO (mg/L)                         | 2.45   | 12.8    | 7.65   | 2.74    |
| pH                                | 7.2    | 8.7     | 7.89   | 0.366   |
| Ca (mg/L)                         | 188.8  | 2184    | 592.39 | 503.33  |
| Fe (mg/L)                         | 0.006  | 0.644   | 0.170  | 0.155   |

Table 1. Variability and ranges of selected physio-chemical parameters measured from the 20 lakes from this study. Variables are chosen based on those known to influence ostracode community assembly from previous studies in lakes from both temperate and tropical areas (e.g. Mezquita et al., 2005; Mischke et al., 2007; Viehberg, 2006).

In total, 14 ostracode species from 13 genera and 9 families were found in the 20 lakes from this study. These species are members of the Caribbean non-marine fauna of Park and Beltz (1998) and included: *Actinocythereis bahamensis*, *Aurila*

*floridana*, *Cyprideis americana*, *Cytherella arostrata*, *Dolerocypria inopinata*, *Hemicyprides setipunctata*, *Loxonconcha dorsotuberculata*, *Loxonconcha pursubrhomboidea*, *Paramesidea harpago*, *Perissocytheridea bicelliforma*, *Propontocypris sp.*, *Quadracythere producta*, *Reticulocythereis multicarinata*, and *Xestoleberis curassavica* (Table 2).

Podocopida

Podocopina

Bairdiidae

*Paranesidea harpago*

Candonidae

*Dolerocypria inopinata*

Cytherellidae

*Cytherella arostrata*

Cytherideidae

*Cyprideis americana*

*Hemicyprides setipunctata*

*Perissocytheridea bicelliforma*

Hemicytheridae

*Aurila floridana*

*Quadracythere producta*

Loxoconchida

*Loxoconcha dorsotuberculat*

Pontocyprididae

*Propontocypris sp.*

Trachyleberididae

*Actinocythereis bahamensis*

*Reticulocythereis multicarinata*

Xestoleberideidae

*Xestoleberis curassavica*

Table 2- Species list of the ostracodes from this study.

The relationship between spatial distance and community dissimilarity of the 20 ostracode communities from the 20 lakes of this study was determined by Monte Carlo permutations tests (9999 unrestricted permutations) and the dissimilarity of communities was compared using the Bray-Curtis dissimilarity index. The 190 pairwise comparisons show no spatial autocorrelation of ostracode communities (Figure 2).

Detrended correspondence analysis (DCA) was run to determine the amount of community change ( $\beta$ -diversity or gradient length) represented in the dataset. The first two axes of the DCA represent 3.5 and 1.7 SD units respectively (Figure 3), indicating that  $\beta$ -diversity is high enough for unimodal methods of direct gradient analysis to be used (Hill and Gauch, 1980; ter Braak and Prentice, 1988; Jongman et al., 1995). Longitude, conductivity, lake area, and depth were the environmental variables with the highest loadings on the first two environmental axes.

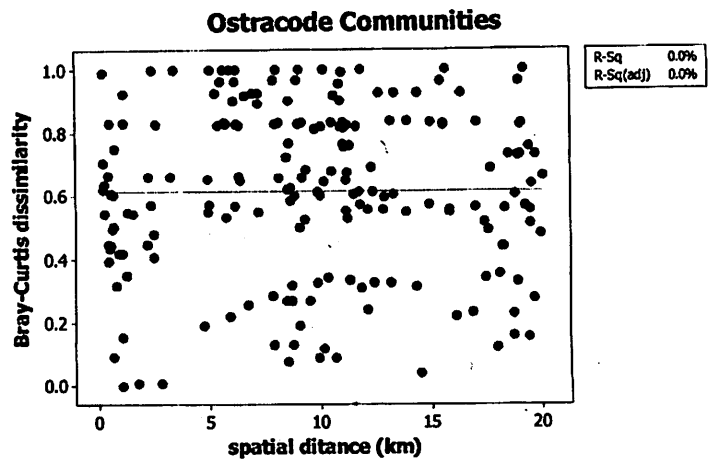


Figure 2. Relationship between spatial distance and community dissimilarity of 20 ostracode communities from the 20 lakes of this study. Each dot represents a pairwise comparison between two communities, resulting in 190 pairwise comparisons. The y-axis is the Bray-Curtis index of dissimilarity and the x-axis is spatial distance between each paired comparison. This shows the lack of spatial autocorrelation of ostracode communities.

Since the gradient of ostracode community change was large, canonical correspondence analysis (CCA) was used to identify the minimum of environmental variables that could account for the majority of variation in the ostracode dataset. The CCA chose conductivity, lake area, and latitude as the variables that significantly control ostracode community distribution, with communities having similar conductivity, lake area, and latitude having similar communities (Figure 4).

DISCUSSION

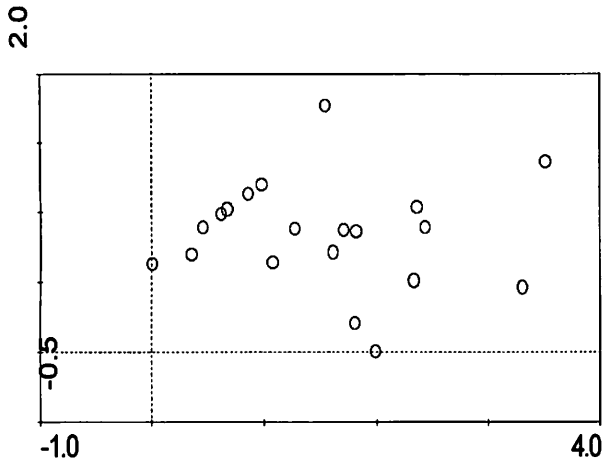


Figure 3. Detrended Correspondence Analysis (DCA) of 20 the ostracode communities from the lakes in this study. The first environmental axis (3.5 SD units) separates the communities based in lake area, conductivity, and depth, while the second environmental axis (1.7 SD units) separates the communities based on lake area and longitude.

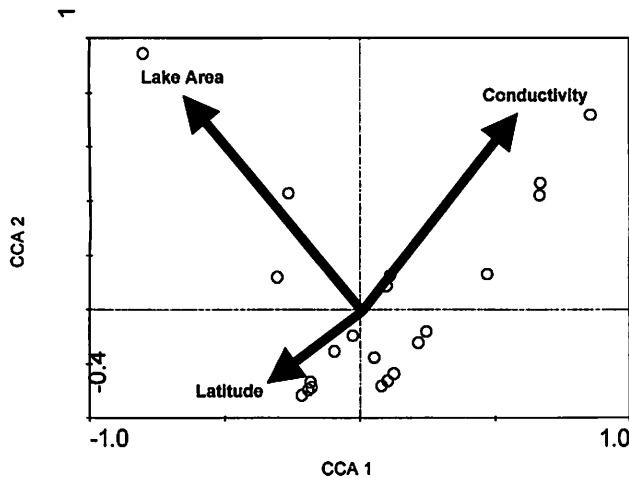


Figure 4. Canonical Correspondence Analysis (CCA) of the 20 ostracode communities in this study, with forward selection of environmental variables showing only those variables that significantly control ostracode community assembly (based on 9999 permutations,  $\alpha = .05$ ).

Taken together, Table 1 and Figure 2 support a metacommunity dominated by species sorting (*sensu* Holyoak et al., 2005). Table 1 shows that the lakes sampled are indeed different in key abiotic variables that may influence ostracode community assembly. The pattern of Figure 2 indicates that communities are not dispersal-assembled (*sensu* Hubbell, 2001) because distance cannot explain why communities of ostracodes on San Salvador are different at all ( $R^2=0$ , Figure 2). The lack of relationship between distance and community dissimilarity means that communities are not spatially autocorrelated, both very dissimilar and very similar communities may be close together or far apart. Distance between communities gives no information about how similar they are. If species were dispersal-limited, then we would expect to see more similar communities closer together and a positive relationship between distance and community dissimilarity. Instead, no relationship is observed between distance and community similarity. This indicates that on the spatial scale of this study, species are not dispersal limited. Thus, it appears that the abiotic environmental within individual lakes controls which species live in those lakes.

However, while the species sorting metacommunity model is suggested by these data, a mass effects model cannot be ruled out. While Figure 2 suggests a high rate of dispersal across the island, the direction of dispersal cannot be inferred from these data. It is possible that some lakes with a high relative abundance of species may be acting as source populations for sink populations in other lakes. But, the lack of spatial autocorrelation of communities and variance in abiotic environment does suggest a very strong role for the abiotic lake environment in determining community assembly of ostracodes on San Salvador. The next question then, is what are the main abiotic drivers of ostracode community assembly?

Figures 3 and 4 show that conductivity, lake area, lake depth, and spatial position (longi-



tude, latitude) determine ostracode community assembly.

Ostracodes have been shown to respond to conductivity in past studies (Mischke et al., 2007; Park and Trubee, 2008) as osmoregulatory systems have evolved differently in different species. Ostracode communities may respond to lake area by having higher diversity in larger lakes owing to the increased probability of having more diverse habitats in larger lakes. This relationship between diversity and lake area within San Salvador ostracodes may be complex or non-linear since there is no relationship between lake area and ostracode species richness in this dataset (not shown).

Why ostracode communities would respond to spatial position on San Salvador is more difficult to explain; it is most likely that communities are responding to an unmeasured abiotic gradient that is closely related to latitude and/or longitude, like precipitation patterns (see Gamble and Jordan, 2006) rather than latitude or longitude *per se*. Additionally, the physical environment of lakes on San Salvador can be quite variable with differences in conductivity as high as 13  $\mu\text{S}/\text{cm}$  between wet and dry seasons (Dalman, 2009). Therefore, the variability in conductivity, water depth, and other parameters should be measured and incorporated into further work to see if variability in physical parameters could control ostracode community distribution.

## CONCLUSIONS

- Ostracode metacommunity dynamics on San Salvador are dominated by species sorting, although mass effects dynamics cannot be ruled out.
- It should be possible to use preserved ostracode communities on San Salvador Island to reconstruct past environments, most promisingly conductivity since it has the most direct relation to climate.

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