Hierarchical Spatial Patterns in Paleocommunities of the Late Pennsylvanian Ames
Limestone

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This thesis titled
Hierarchical Spatial Patterns in Paleocommunities of the Late Pennsylvanian Ames
Limestone

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ABSTRACT

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Hierarchical Spatial Patterns in Paleocommunities of the Late Pennsylvanian Ames Limestone

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Late Pennsylvanian Ames Limestone was analyzed along its depositional strike to understand the spatial heterogeneity of Ames paleocommunities. Paleocommunity structure and its variability at multiple spatial scales were assessed from field data collected at seven outcrops of the Ames Limestone in the southeastern Ohio, along the northwestern outcrop belt of the Conemaugh Group. Invertebrate fossils were identified in the field and abundance counts were recorded for discrete taxa. Multivariate analyses, cluster confidence intervals and guild analysis were used to delineate geographic partitioning of paleocommunity structure at various spatial scales (local through regional).

A clear partitioning of paleocommunities in geographic space between northeastern and southwestern study sites was observed. The likely environmental control for this regional scale faunal distribution was differences in water turbidity and substrate composition along the depositional strike. At locality scale, the large-scale regional structure was dampened by variations within local paleocommunities.

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CHAPTER 1: INTRODUCTION

Modern shallow marine communities exhibit variability on a variety of hierarchical levels, both spatially and temporally (Valentine, 1973; Wu and Loucks, 1995; Underwood and Chapman, 2008). Communities and their environments form open natural systems or ecosystems. Environmental changes affect the limits of ecosystems and different ecosystem structures are recognized consisting of characteristic communities as an adaption to environmental influences (Valentine, 1973). Hierarchical spatial studies in ecology are important for understanding effects of scale in operating environmental processes and detection of patterns (Noda, 2004). Thus, understanding how communities are structured in both time and space is important for identifying potential impacts of the current changes in the ocean system (Brett et al., 2007; Moffitt et al., 2015).

Studies of ancient marine communities preserved in the fossil record provide a framework to test the impacts of environmental perturbations in both temporal and spatial dimensions (Lafferty and Miller, 1994; Brett et al., 2007; Holland and Patzkowsky, 2007; Daley, 2002). Processes like onshore-offshore transitions that take place over long time intervals (Holland and Patzkowsky, 2007), presence of bioturbation in the depositional setting resulting in different community structures (Daley, 2002) and how water temperature, nutrients, turbidity and oxygen content could influence ecosystem structure and stability at the depositional settings (Holland and Patzkowsky, 2007; Lebold and Kammer, 2006) are a few of the many such environmental perturbations addressed in paleocommunity analyses. In addition to studying differences in paleocommunities

resulting from environmental perturbations, one can also address instances where recurrent associations of taxa present in different sedimentary cycles separated by millions of years have similar species compositions and trophic structures (Brett et al., 2007). These groups of species are formed as they all respond to a common environmental signal and follow a preferred habitat, a phenomenon described as habitat tracking (Brett et al., 2007).

In this study, paleocommunity structure and variability are examined within paleocommunities preserved in a widespread shallow marine unit deposited during an interglacial interval of the Late Paleozoic Ice Age. Specifically, this study examines paleocommunity structure within the Pennsylvanian (Virgillian) limestone of the Ames Member of the Conemaugh Group (=Ames Limestone) (Heckel, 2008) in southeastern Ohio. Because the Ames Limestone represents a short-lived interval of maximum global warmth, this interval could also be a potential analog for circumscribing spatial heterogeneity in modern marine systems related to modern climate change. Hypotheses about paleocommunity heterogeneity of Ames Limestone at different spatial scales parallel to depositional strike within the Appalachian basin are addressed using multivariate analyses, guild analysis and cluster confidence intervals on taxon occurrence and abundance data collected from the Ames Limestone. The depositional strike of the Ames Limestone within the Appalachian Basin is parallel to the shoreline of the Ames Sea, which is located approximately through central West Virginia (Merrill, 1993).

Paleocommunity structure was assessed among outcrops and at regional (basin) level to examine the following research questions: 1) How do local paleocommunities of

Ames Limestone vary among outcrops? 2) Does the paleocommunity structure of the Ames Limestone vary across the basin along depositional strike? and 3) Does variation in Ames community structure exhibit hierarchical structure within a spatial dimension? This framework allows the differentiation of local paleocommunities vs. the regional paleocommunity assemblage.

Communities, Paleocommunities and Spatial Scale

A paleocommunity can be broadly defined as the recurrence of species among fossil assemblages with a characteristic pattern of relative abundances (Bennington and Bambach, 1996). This differs somewhat from the definition of community in neo-ecology, wherein a community is defined as an assemblage of interacting species (Puttman and Wratten, 1984; Holt, 2009). This difference in these definitions is a reflection of the sources of data available for studies of modern and ancient communities (Miller, 2001). In modern communities, time scales of observation are often restricted to a few months to several years (Redman et al 2007). It may be possible to directly observe organism interactions either visually or via experimental techniques. However, the limited timescale of observation means that patterns such as seasonal changes can swamp the ability to identify fluctuations in relative abundance over time (Schopf and Ivany, 2013). Therefore, macroecological patterns are often poorly constrained (Cobabe and Allmon, 1994; Schopf and Ivany, 2013). Fossil assemblages, on the other hand, have been subjected to taphonomic filters and time-averaging that typically limit the potential to infer direct interactions between members present in the ancient community. However, the same processes produce a record that preserves a clear signature of the long-term

variation in community structure. Thus paleoecological analysis of community structure differs from analysis of ecological communities (Bennington and Bambach, 1996); paleocommunity analyses provide information about ecological mechanisms that are different from neoecological views, notably processes that operate over longer temporal intervals.

This study employs the classification system of paleoecologic units proposed by Bambach and Bennington (1996) where, a fossil assemblage collected from a single bed at one outcrop is defined as a *local paleocommunity*. It is critical that the fossil deposit reflect a peri-autochthonous assemblage, which must be confirmed from sedimentologic and taphonomic evidence. A *paleocommunity* is comprised of local paleocommunities that are not statistically significantly different from each other. Accordingly, one can predict that the fossil assemblage of Ames Limestone is likely to represent one or more paleocommunities; whereas fossil assemblages at different outcrops that can be compared across hierarchical spatial scales can be categorized as local paleocommunities. Assessing the degree to which this expectation holds is a core goal of this study.

The spatial scale on which measurements are collected controls the ability to detect spatial ecological patterns in nature (Bennington, 2003; Brett et al., 2007). Thus, it is important to study the system at an appropriate scale that overlaps with how organisms experience the environment to understand their range of patterns (Wiens, 1989). In this study, the fauna of Ames Limestone is considered as a system consisting of a suite of species that utilized the environment in a variety of ways that can be addressed at the spatial scales used in this study. Changes in sea level, climate and sediment content also

drive the spatial distribution of organisms that can be observed at a variety of scales (Brett et al., 2007). Many epicontinental ramp settings similar to Ames depositional setting display elongate, laterally extensive belts of species associations aligned roughly parallel to the depositional axis or the shoreline of gently sloping ramps (Ziegler et al., 1968; Brett et al., 2007). Such facies belts have, in fact, been reported by Lebold and Kammer (2006) for the Ames Limestone. This suggests that outcrop belts parallel to the depositional axis should be associated with limited lateral changes in the biofacies along time planes (Brett 2007), an expectation that this study will directly test.

Geologic Setting

The Ames Limestone was deposited within an epicontinental sea in Laurentia at the boundary of the Kasimovian and Gzhelian Stages of the Late Pennsylvanian Period (Stevens and Stone 2007; Heckel, 2008; Heckel et al., 2011; Richards 2013). During the Late Pennsylvanian, Laurentia was equatorially situated and rotated approximately 90 degrees clockwise from its present orientation (Fig. 1). The assembly of Pangea was ongoing, and the Alleghenian orogeny resulting from the collision of northwest Africa with eastern North America was active at this time (Klein and Willard, 1989; Heckel, 2008) (Fig. 2). The Alleghenian orogenic process deformed the Laurentian craton north of the rising Appalachian mountains and formed the elongated Appalachian foreland basin (Martino, 2004). Southeastern Ohio was located at the distal edge of the Appalachian foreland basin and experienced tropical climatic conditions due to its paleoequatorial position (Heckel, 2008) (Fig. 2). Intermittent flooding of the Appalachian foreland basin by shallow seas due to glacial-eustatic sea level fluctuations, tectonic

subsidence, and delta progradation resulted in cyclic sedimentation sequences of transgressive-regressive marine units and nonmarine deposits (Klein and Willard, 1989; Heckel, 1995; Nadon and Kelley, 2004). The marine zones of correlative Pennsylvanian cyclothems of North America are also exposed in the Midcontinent and Illinois basins (Heckel, 2008).

Figure 1. Late Pennsylvanian paleogeographic reconstruction. Red star indicates the location of the Appalachian basin. Map modified from <http://cpgeosystems.com>.

Figure 2. Late Pennsylvanian reconstruction of Laurentia indicating the extent of marine deposition during Ames time. The red ellipse northwest of Alleghenian orogeny approximates the extent of Ames Limestone deposition within Conemaugh Group. Map modified from <http://cpgeosystems.com>.

The Ames marine zone is the final of the four major marine units found in the Glenshaw Formation of the Conemaugh Group (Fig. 3). This unit is sometimes referred to as the Ames Member of the Glenshaw Formation. This usage incorporates the shale units above and below the limestone unit within the Ames marine zone. In this study, we

focus exclusively on the limestone lithology, which we refer to as the Ames Limestone herein. It represents the uppermost unit of the Glenshaw Formation and records a maximum flooding interval that occurred during the interglacial interval of a glacioeustatically influenced fifth order sea level cycle (Martino, 2004). The Ames Limestone (marine zone) has been correlated with the Oread Cyclothem (Heebner marine zone) in the Midcontinent basin and the Shumway marine zone in the Illinois basin

GLOBAL SERIES	GLOBAL STAGE	NORTH AMERICAN REGIONAL STAGE			
UPPER PENNSYLVANIAN	298.9 Ma		Conemaugh Group	Casselman Formation	Pittsburgh Coal
	Gzhelian	Virgilian			
	303.7 Ma			Glenshaw Formation	Ames marine zone
	Kasimovian	Missourian			Cambridge marine zone
					Upper Bush Creek
					Lower Bush Creek
	307.0 Ma				Upper Freeport Coal

Figure 3. Simplified stratigraphic section of Conemaugh Group denoting the position of the Ames Limestone and other major marine units in the Glenshaw Formation (after Richards (2013); Lebold and Kammer (2006)).

based on similar conodont faunas of lower Virgilian Stage in North American nomenclature (approximately the boundary between global Kasimovian and Gzhelian Stages) (Heckel, 2008; Heckel et al., 2011; Stevens and Stone 2007; Richards 2013).

The Ames Member is the most extensive and uniform marine unit in the Appalachian basin and records the last significant marine transgression across much of the northern to central Appalachian basin (Donahue and Rollins, 1974; Cassel, 2005). Similar to rest of the stratigraphic section of southeastern Ohio, the Ames Member represents deposition within a ramp setting in the distal Appalachian foreland basin (Saltsman, 1986; Nadon and Kelly, 2004) deposited in less than 400 k.y (Lebold and Kammer, 2006). The Ames Limestone has been interpreted as a transgressive unit deposited within an offshore marine environment (Saltsman, 1986; Nadon and Kelly, 2004). Most outcrops exhibit fossiliferous wackstone to packstone lithologies.

Previous paleoecological analyses of the Ames Member fossil assemblage have identified discrete lithofacies and biofacies associated with different depositional environments within the Ames Member (Donahue and Rollins, 1974; Saltsman, 1986; Lebold and Kammer, 2006). Fossils of the Ames Member comprise a diverse normal marine fauna that includes macrofossils (e.g., crinoids, bivalves, gastropods, brachiopods, bryozoans, rugose corals, trilobites and cephalopods), microfossils (e.g., foraminifera, conodonts and ostracods), and ichnofossils (Windle, 1970; Webb, 1972; Hoare et al., 1997; Cassel, 2005; Lebold and Kammer, 2006; Smilek, 2009). The fauna was taxonomically described and the stratigraphic and geographic distributions of the species were recorded in a series of publications during the 20th century (i.e., Sturgeon, 1964;

Murphy, 1970; Windle, 1970; Webb, 1972; Hoare et al., 1997). This set of publications remains the most comprehensive systematic work on the Ames fauna.

The majority of previous paleoecological analyses have focused on Ames Member outcrops in northeastern and eastern portions of the Conemaugh outcrop belt in present day Pennsylvania and West Virginia (Fig. 4). Most recently, Lebold and Kammer (2006) reconstructed and compared biofacies distribution of the Ames Member perpendicular to the strike of the depositional basin from West Virginia to southeastern Ohio. Their analyses examined the relative abundance of guilds within fossil assemblages, and they observed that Ames Member outcrops in eastern Ohio included abundant crinoids, rhynchonelliform brachiopods and bryozoans deposited under well-oxygenated normal marine conditions. The biofacies they observed in Ohio were clearly different from most of the West Virginia biofacies in terms of paleocommunity composition, and there was a lateral lithological change associated with this that corresponded to shift from clastic-dominated West Virginian outcrops to carbonate-dominated Ohio outcrops. Four distinct biofacies were identified by Lebold and Kammer (2006): Biofacies 1 and 2 were dominated by eurytopic molluscs, Biofacies 3 was dominated by the opportunistic brachiopod *Neochonetes* and Biofacies 4 included a diverse suite of stenotopic normal marine taxa. Biofacies distribution was primarily controlled by salinity, turbidity and oxygen levels that were associated with the Ames depositional basin and relative sea level change (Lebold and Kammer, 2006). Abundant ichnofossils within the Ames Limestone also support the interpretation of normal marine

conditions and sufficient oxygen and nutrients during the deposition (Smilek, 2009).

Smilek (2009) further noted that the lack of ichnodiversity and simple nature of biogenic

Figure 4. Geographic distribution of the Conemaugh Group (shaded) within the Appalachian basin (modified from Cassel, 2005). The Ames Limestone crops out throughout much of the shaded region.

structures within the Ames Limestone were indications of the highly fossiliferous matrix limiting the number of different organisms that can burrow, resulting in the reduced number of burrowing styles observed (Smilek, 2009). Above the Ames Limestone, beds show increased clastic influence but still within normal marine conditions as indicated by high ichnofossil abundance and occasional body fossils. In contrast, the beds underlying the Ames Limestone were considered by Smilek (2009) to have formed under stressed conditions due to the lack of body fossils and rare occurrence of ichnofossils.

Bjurstrom (1960) considered the bulk of the Ames Limestone in southeastern Ohio (Athens and Morgan Counties) to be autochthonous in origin with portions having an allochthonous origin as well. The matrix of the Ames Limestone in his study sites included both fine-grained material and crystalline calcite with evidence for recrystallization and replacement. Bjurstrom (1960) further noted that variation in abundance of glauconite, sand grains, oolites and foraminifera indicate that localized conditions were of significance relative to the environment of deposition. Local controls were more significant in the northern portion of the study area in Morgan County than in the southern region around Athens County where the limestone was noted to be chemically purer. In a petrologic analysis of Ames Limestone outcrops in Meigs, Gallia and Lawrence Counties, Haines (1965) identified purer crystalline limestone areas in northern Meigs County that grades into the Ames Limestone in Athens County. These limestones consisted of brachiopods like *Neochonetes* and *Linoproductus* in general with fusulinids often present in northern Meigs County. The southern Meigs County Ames Limestone grades into an unfossiliferous calcareous sandstone towards the Lawrence County. Using microfacies analysis, Chamberlain (1981) identified fifteen different microfacies fabrics in Ames Limestone in east-central Ohio indicating depositional environments that ranged from shallow offshore to low supratidal in a west to east facies belt within the study area. Offshore conditions identified in western portion of Ames Limestone samples from Noble, Guernsey, Muskingum and Carroll Counties were interpreted as well oxygenated, normal marine depositional environments (Chamberlain, 1981).

CHAPTER 2: METHODS AND DATA

Sampling

Seven Ames Limestone exposures in the southeast Ohio were selected for paleoecological sampling (Fig. 5). These localities form a northeast to southwest transect

Figure 5. Map of Ames Limestone outcrops where ecological data were collected. Ohio outcrop map modified from Webb (1972). Abbreviations: WH=Witches Hill, 682=Highway OH-682, MD=McDougal, AM=Amesville, CD=Caldwell, BV=Belle Valley, I70=Interstate 70).

across the Conemaugh Group outcrop belt roughly parallel to the depositional axis of the Appalachian basin (Fig. 5). The seven target localities were identified for analysis after revisiting numerous sites previously identified as Ames Limestone outcrops within theses and literature sources (e.g. Sturgeon, 1958; Bjurstrom, 1960; Windle, 1970; Webb, 1972; Nadon and Kelly, 2004; Smilek, 2009). Because the primary data collected for this study are abundance counts taken on exposed bedding planes, it was important to select outcrops with extensively exposed lateral surfaces and similar taphonomic properties (Fig.6). Thus, localities were considered for inclusion in the study only if their exposures were sufficient for the research protocol outlined in the next paragraph. Latitude and longitude coordinates, thickness, elevation and basic lithologic features of each locality are given in Table 1.

At each locality, the lateral distribution of exposed fossiliferous surface areas of the suitable Ames Limestone outcrops were measured and recorded. Limestone thickness and lithological characters were recorded. Then loose debris was removed and bedding plane surfaces were scrubbed clean using water and a soft brush. Surfaces were allowed to dry before continuing with data collection. In-situ abundance data were collected for multiple sample positions per locality that ranged between 4-10 exposed surfaces of various sizes depending on the outcrop distribution. Sub-sites from each locality/outcrop were included in the final data set. At each sample position, the fossiliferous surface was subdivided using a 12x12 cm grid. Abundance counts were conducted for each grid

Figure 6. Field sites; A= one of the bedding surfaces sampled in Witches Hill, B= 12x12 cm grid on a bedding surface; C= portion of Amesville outcrop; D= portion of the McDougal outcrop, E= Amesville outcrop from distance; F= Outcrop sampled at Belle Valley; G= portion of the outcrop sampled at Caldwell.

square. The smaller areas of the bedding surface one at a time to identify and count fossils. When necessary for identification purposes, bulk samples were also collected.

Table 1

Descriptions of sampling localities

	Outcrop	Geographic coordinates	Elevation (ft)	Lithologic descriptions	Avg. limestone thickness (cm)	Most abundant taxa, in descending order
Southern sites	Witches Hill (WH), Athens County	N39.3235° W082.0879°	730	Greenish gray wackstone, orange-yellow staining in certain parts	32.5	<i>Neochonetes</i> , <i>Crurithyris</i> , Crinoids, Fusulinids, Encrusting bryozoa, <i>Neospirifer</i> , <i>Derbyia</i>
	Highway OH-682 (OH - 682), Athens County	N39.3169° W082.1005°	761	Greenish gray wackstone, orange-yellow staining in certain parts	37	<i>Crurithyris</i> , <i>Neochonetes</i> , <i>Crinoids</i> , Encrusting bryozoa, Branched byozoa, Fusulinids, <i>Derbyia</i>

Table 1: continued

	Outcrop	Geographic coordinates	Elevation (ft)	Lithologic descriptions	Avg. limestone thickness (cm)	Most abundant taxa, in descending order
	McDougal (MD), Athens County	N39.4036° W082.0383°	756	Greenish gray wackstone	43.5	<i>Neochonetes</i> , <i>Crurithyris</i> , Crinoids, Fusulinids, <i>Neospirifer</i> , Branched byozoa
	Amesville (AM), Athens County	N39.4377° W081.9757°	678	Greenish gray wackstone, orange-yellow staining in certain parts	38.5	<i>Crurithyris</i> , <i>Neochonetes</i> , Crinoids, <i>Stereostylus</i> , <i>Neospirifer</i>
Northern sites	Caldwell (CD), Noble County	N39.7070° W081.5051°	690	Dark gray to reddish brown wackstone, orange-yellow staining in certain parts, Slicken sides	26	<i>Neochonetes</i> , Crinoids, Branched bryozoa, <i>Juresania</i> , <i>Neospirifer</i>

Table 1: continued

	Outcrop	Geographic coordinates	Eleva- tion (ft)	Lithologic descriptions	Avg. limestone thickness (cm)	Most abundant taxa, in descending order
	Belle Valley (BV), Noble County	N39.7823° W081.5549°	817	Dark gray to reddish brown wackstone, orange- yellow staining in certain parts, Slicken sides	37	<i>Neochonetes</i> , Crinoids, Branched bryozoa, <i>Juresania</i> , <i>Neospirifer</i>
	Interstate 70 (I-70), Muskingu m County	N39.9758° W081.7869°	907	Dark gray to reddish brown wackstone, orange- yellow staining in certain parts	37.5	<i>Neochonetes</i> , Crinoids, Branched bryozoa, <i>Neospirifer</i>

Fossils were identified to the genus level where possible in the field based on published literature for Pennsylvanian fossils of Ohio and museum collections of Conemaugh Group fossils at the Ohio State University Orton Museum.

A total of 8112 specimens representing 24 different taxa (Fig. 7) were identified over a total area of approximately 63554 cm² (Appendix 1). These taxa included: rhynchonelliform brachiopods, bivalves, gastropods, bryozoa, rugose corals, crinoids, regular echinoids, trilobites, chondrichthyes, sponges and foraminifera (Fig.7). Skeletal elements, such as shells, that were fragmented or oriented in such a way that entire element was not visible but was nevertheless still identifiable were also counted. Minimum number of individuals (MNI) (Gilinsky and Bennington, 1994) was considered for bivalved taxa (brachiopods and bivalves) by dividing the total number of shells counted by two. For bryozoa and sponges, which are colonial organisms, a measured length of 0.5 cm was counted as a single organism as these were less common. Crinoids were mostly preserved as aggregations of separated columnals or segments of columnals that grouped mainly into four diameter classes (1 mm, 2 mm, 3 mm & >4 mm). Because columnals were not abundantly distributed across all of the bedding surfaces, the presence of one or more columnals belonging to each of the diameter classes were given a count of one. In addition, when crinoid brachial plates were present one plate was given a count of one since these occur infrequently. If only fragments or articulated portions of columns or fragments of brachial plates were observed their total length was measured and a count of one was given to each 1 cm length measured. Individual horn corals, fusulinids and trilobite cranidia or pygidia were each given a count of one. Individual shark teeth and each echinoid spine were also given a count of one as these were rare.

Figure 7. Some of the common taxa identified during this study. A=*Crurithyris*, B=*Neospirifer*, C= Chondrichthyes tooth, D=*Jurasenia*, E=*Stereostylus*, F=*Neochonetes*, G=*Palaeolima*; H=Fenestrate byrozoa; I=*Linoproductus*; J=Trilobite pygidium, K=Branched bryozoa, L= Encrusting bryozoa, M=Fusulinid.

Data Analysis

In order to assess sample-area affects, total counts from each of the seven sites were plotted against the total surface area studied in each site. Results of the linear correlation analysis (Fig. 8) returned a R^2 value of 0.0562, which confirms that abundance counts were not correlated with sampled area indicating that localities were sufficiently sampled to overcome collecting bias. Log-log correlation is similarly not significant ($R^2=0.1886$).

Paleocommunity structure was analyzed quantitatively using cluster and ordination analyses (Davis, 2002) and qualitatively using guild analysis (cf. Bambach, 1993). Data analyses were conducted in order to delineate paleocommunity structure at different hierarchical spatial scales outlined in the introductory research questions. The combination of scales can provide a context to analyze how community variation is partitioned in geographic space. In addition, joint and separate occurrences of taxa can indicate differences in taxon preferences of particular environmental conditions.

For all analyses, initial abundance data was subjected to within sample percent transformation and within taxon percent transformation to reflect relative proportions of taxa. Cluster analysis was conducted to investigate whether taxa or localities are grouped within a hierarchical structure. Cluster analysis allows delineation of the associations of fossil taxa considering their variations among and within samples through Q-mode (taxon-based) analysis and R-mode (locality-based) analysis (Hammer and Harper, 2006). Cluster analyses were conducted using the vegan package (Oksanen et al., 2016) within the R programming language (R Core Team, 2015); distances were calculated

using Bray-Curtis similarity matrix and clustering was accomplished via the Wards agglomeration method. Analysis of group similarities (ANOSIM) was also performed to test if groups obtained from the cluster analysis are significantly different from each other.

Figure 8. Plot of linear regression of total abundance counts vs. total surface area from seven localities. Abbreviations as in Figure 5.

In order to delineate gradational transitions in the compositions of samples in corresponding communities, Detrended Correspondence Analysis (DCA) was performed on abundance data. Ordination analyses like DCA are commonly used in paleoecology because greater emphasis is placed on finding variation among samples based on associations of taxa rather than a single taxon (Foote and Miller, 2007). Data treatment prior to DCA followed by the same data transformations noted above, but additional

down weighting of rare taxa was also performed. Ordination analyses were implemented within the R programming language (R core team, 2015) using the vegan package (Oksanen et al., 2016).

Guild analysis was implemented in order to examine ecospace partitioning among taxa within the Ames Limestone. Root (1967) originally defined a guild as “a group of species that exploit the same class of environmental resources in a similar way. This term groups together species, without regard to taxonomic position, that overlaps significantly in their niche requirements”. Bambach (1983) later extended the concept for paleontological use. Within the Bambach (1983) definition, guilds can be formed by grouping species within a community based on their food resource, space utilization and/or body plan. The guild concept has been used effectively for analyzing paleocommunity structure and ecospace utilization in both spatial and temporal scales in paleoecological studies (Bambach, 1983; Aberhan, 1994; Daley, 2002; Lebold and Kammer, 2006). Guild membership was assigned to genera of the Ames fauna based on information on habitat, food source and morphology of Pennsylvanian marine invertebrates in literature (e.g., Walker and Bambach, 1974; Aberhan, 1994; Lebold and Kammer, 2006) and their modern relatives. The relative abundance of each guild was calculated for each of the seven study sites and the sub-sites within each locality. Guild distributions were compared using pie charts.

To further examine spatial hierarchical structure within the community data, cluster confidence intervals were calculated for the five most abundant taxa (*Neochonetes*, *Crurithyris*, crinoids, branched bryozoa and fusulinids) using the formula

described in Buzas (1990) and Bennington and Rutherford (1999). Cluster confidence intervals allow determination of the statistical significance of differences between mean relative taxon abundances (Bennington, 2003). 95% confidence intervals generated in this way were used to compare of taxon abundances between outcrops and across the basin based on multiple samples collected from each locality. Calculations were performed in Microsoft Excel 2007 software application (Microsoft Corporation).

CHAPTER 3: RESULTS

Multivariate Analyses

Separate Q-mode cluster analyses of the seven sites and 28 sub-sites both recovered two primary groups (Fig. 9). Analysis of group similarities (ANOSIM) result indicates that the two primary groups of samples obtained in above analyses are statistically significantly different with the ANOSIM statistic of $R = 0.6018$ at a significance of $p = 0.001$ after 999 permutations.

Figure 9. Dendrograms produced from q-mode cluster analyses of study sites and sub-sites. Sites are abbreviated: WH=Witches Hill, X682/OH-682= Highway OH-682, MD=McDougal, AM=Amesville, CD= Caldwell, BV=Belle Valley, I-70=Interstate 70. Sub-sites are indicated by numbers 1 to 4 following the site abbreviation (e.g., WH1 = Witches Hill sub-site 1).

In the analysis (Fig. 9) aggregating the full data for each of the seven sites, geographic proximity exerts a primary control over dendrogram topography. One cluster contains the Caldwell, Belle Valley, and I-70 sites, all of which are located in Muskingum or Noble Counties in the northern portion of the depositional basin. Within this cluster, Caldwell and Belle Valley are more similar to each other than to the I-70 section. The second cluster contains all the localities from Athens County in the southern portion of the depositional basin, namely the Witches Hill, OH-682, Amesville, and McDougal sites. Among these sites, Witches Hill and OH-682 are the most similar followed by McDougal and then Amesville. The primary separation into the two main clusters matches the geographic separation between northern and southern localities. Furthermore, within each cluster, sites tend to cluster with geographic proximity, with the exception that McDougal clusters with the two Athens city sites (Witches Hill and OH-682) instead of with the geographically closer Amesville site.

In the Q mode analysis of sub-sites, the same basic clustering pattern is observed within southern sites where Amesville sub-sites branch off early from the rest of the localities. Then the sub-sites of other localities form two clusters; one containing Witches Hill sub-sites 1 and 2 plus all of the McDougal sub-sites and the other cluster containing Witches Hill sub-sites 3 and 4 and all of the OH-682 sub-sites. In the northern cluster, the Caldwell and Belle Valley sub-sites are dispersed among smaller clusters within the major cluster, whereas the I-70 sub-sites cluster at the base of this group, although not as a coherent cluster. Like the larger scale pattern, geographic proximity exerts a control on

the clusters, but the shuffling of sub-sites among clusters indicates that additional local controls are also present.

The same geographic separation was observed in the DCA results as a clear separation of northern and southern sub-sites along axis 1 (Fig. 10). When axis 2 is considered sub-sites from northern region show a greater spread across this axis whereas

Figure 10. DCA plot of sub-sites showing how two primary groups obtained from cluster analysis grades into each other. Sites are abbreviated: WH=Witches Hill, X682/OH-682= Highway OH-682, MD=McDougal, AM=Amesville, CD= Caldwell, BV=Belle Valley, I-70=Interstate 70. Sub-sites are indicated by numbers 1 to 4 following the site abbreviation (e.g., WH1 = Witches Hill sub-site 1).

sub-sites from southern region lie near the zero value. Within the southern group, the Amesville sub-sites occupy the most distinct region of the plot; whereas the Witches Hill, OH-682, and McDougal sub-sites overlap along axis 1 and 2. In the northern cluster, the I-70 sub-sites are the least similar and plot peripherally to the other sites, whereas the Belle Valley and Caldwell sub-sites tend to plot near each other.

R-mode cluster analysis recovered two primary groups, which were named after the most abundant taxon present the group; a *Crurithyris* dominated community and a *Neochonetes* dominated community (Fig. 11). The *Crurithyris* community includes taxa such as the rugose coral *Stereostylus*, fusulinids and echinoids. The *Neochonetes* community includes taxa such as the spirifid brachiopod *Neospirifer*, fenestrate bryozoans, and productid brachiopods *Derbyia* and *Juresania*.

Further, similar group separation was observed in the DCA analysis, primarily along axis 1 (Fig.12) (Taxon abbreviations used in the DCA plot in Fig. 12 are explained in Table 2). Taxa within the *Crurithyris* community primarily plot to the right of axis 1 and plot close to the zero value on axis 2. The *Neochonetes* community occupies a wider range of values on both axes, including a much wider spread along axis 2. However, the DCA result is significant because patterns appear that are not present in the cluster analysis like the gradational transition of taxa between the two major communities identified in the cluster analysis. For instance some of the taxa (i.e., *Derbyia*, *Neospirifer*) that clustered within the *Neochonetes* community in the cluster analysis, lie in the center of the DCA plot. Taxa like trilobites and sponges are found in the *Neochonetes* community according to the cluster analysis but in the DCA they lie close together with

Crurithyris community taxa. Spread of taxa in the DCA axes is a better manifestation of arrangement of taxa according to an environmental control.

Table 2

Taxon name abbreviations used in the DCA analysis

Taxon name	Abbreviation
<i>Neochonetes</i>	Neoch
<i>Crurithyris</i>	Crur
<i>Neospirifer</i>	Neosp
<i>Derbyia</i>	Derb
<i>Punctospirifer</i>	Punct
<i>Juresania</i>	Juresania
<i>Antiquatonia</i>	Antiq
<i>Linoproductus</i>	Lino
<i>Echinaria</i>	Echina
<i>Reticulatia</i>	Reticu
<i>Palaeolima</i>	Palaeoli
<i>Astartella</i>	Astart
<i>Aviculopecten</i>	Avi

Table 2: Continued

Taxon name	Abbreviation
<i>Straporollus</i>	Strap
Trilobites	Trilo
Branched bryozoa	Bry branch
Encrusting bryozoa	Bry encrust
Fenestrate bryozoa	Bry fenest
Echinoids	Echin S
Stereostylus	Stereosty
Crinoids	Cri total
Fusulinids	Fusuli
Sharks	sharkT
Sponges	sponge

Figure 11. Dendrogram produced from r-mode cluster analysis showing separation of taxa into *Crurithyris* and *Neochonetes* communities.

Figure 12. DCA plot of taxa showing how *Neochonetes* and *Crurithyris* communities grades into each other. Colored labels indicate the two groups obtained from cluster analysis.

The two-way cluster analysis (Fig. 13) indicates that the northern sites are dominated by the *Neochonetes* community and the southern sites are dominated by the *Crurithyris* community. Certain taxa, such as branching bryozoans, *Neochonetes*, and crinoids occur in all sites, but there is a clear absence of key *Crurithyris* community taxa in the northern sites. Because the two way cluster analysis also illustrates the abundances of taxa in the form of color variations, this output illustrates how major clusters are represented by actual taxon abundances. As mentioned above, although some of the taxa are clustered in either of the two major clusters representing *Neochonetes* or *Crurithyris*

community, their actual abundance is not shown in the clustering (Fig. 13). The differentiation of taxa with diverse ecologies among the geographic clusters indicates that environmental factors, not only geographic proximity, form key controls on community structure within the Ames Limestone.

Figure 13. Two way cluster analysis showing Northern sites dominated by the *Neochonetes* and crinoid rich community while Southern sites dominated by the *Crurithyris*, corals, and fusulinid rich community.

Guild Analysis

Guild analysis resulted in recognition of 16 different guilds as shown in Figure 14. Guilds identified in this study represent a range of life modes, feeding methods and morphologies that exhibit adaptations suited for normal marine conditions. Life modes include pelagic, epifaunal, and infaunal styles with a diverse group of epifaunal taxa. Feeding techniques present in the fauna consist of predation, grazing, detritus feeding, and suspension feeding. Analysis further allowed epifaunal taxa to be characterized as suited for either muddy or firm substrates based on morphological characteristics. For example, brachiopods that lived on firmer substrate had features like pedicular stalks or ventral valve cementation. Brachiopods and bivalves that were common in muddier substrate were free-lying or burrowed into the substrate as evidenced by pallial line deflections. Epifaunal suspension feeders were grouped into two categories: low-level or high-level suspension feeding. Crinoids that elevate their feeding apparatus above the substrate were classified as high level suspension feeders, whereas brachiopods, bryozoa and bivalves with feeding apparatuses within 5 cm of the on the sediment water interface were classified as low level suspension feeders.

The relative abundances of these guilds per locality are illustrated in Figure 15 (Appendix 2). According to this analysis, northern sites were dominated by the low level suspension feeding reclining brachiopods and low level suspension feeding crinoids guilds with a notable presence of low level suspension feeding spiny Reclining brachiopods. In contrast, southern region was differentiated by low level suspension feeding Stalked brachiopods and epifaunal rolling grazer fusulinids. The presence of

epifaunal passive predator guild represented by rugose corals in this region in contrast to the north was also significant. These results indicate the biological and ecological underpinnings that lead to the differentiation of community types between the northern and southern regions of the Ames Limestone outcrop belt.

Taxa	Guilds	Guild abbreviations and colors used in pie charts
<i>Neochonetes, Neospirifer</i>	Low Level Suspension Feeding Reclining brachiopod	LLSFR
<i>Crurithyris, Punctospirifer</i>	Low Level Suspension Feeding Stalked brachiopod	LLSFS
<i>Derbyia</i>	Low Level Suspension Feeding Cemented brachiopod	LLSFC
<i>Juresania, Antiquatonia, Linoproductus, Echinaria, Reticulatia,</i>	Low Level Suspension Feeding Spiny Reclining brachiopod	LLSFSR
<i>Palaeolima, Aviculopecten</i>	Low Level Suspension Feeding Epibyssate bivalve	LLSFE
<i>Astartella</i>	Low Level Suspension Feeding Burrowing bivalve	LLSFB
<i>Straporollus, Echinoids</i>	Epifaunal Grazer	EG
Bryozoa(branched)	Low Level Suspension Feeding Branched Bryozoa	LLSFBB
Bryozoa(encrusting)	Low Level Suspension Feeding Encrusting Bryozoa	LLSFEB
Bryozoa(fenestrate)	Low Level Suspension Feeding Fenestrate Bryozoa	LLSFFB
Sponges	Low Level Suspension Feeding Sponge	LLSFAS
<i>Stereostylus (coral)</i>	Epifaunal Passive Predators(Straight /Partially burrowed)	EPP(S/PP)
Total Crinoids	High Level Suspension Feeding Stalked	HLSFS
Fusulinids	Epifaunal Rolling Grazer	ERG
Shark Teeth	Pelagic Active Predator	PAP
Trilobite	Epifaunal Detritus Feeder	EDF

Figure 14. Guilds identified in the study

Figure 15. Guild relative abundances as presented by different colors in the pies charts. Representative color for each guild is given in Figure 14.

Variation in Abundance at Different Spatial Scales

Cluster confidence intervals (CCI) were calculated at locality (Fig. 16) and regional scales (Fig. 17). Results from these analyses indicate the amount of variability of mean relative abundances of five most abundant taxa (*Neochonetes*, *Crurithyris*, crinoids,

fusulinids and branched bryozoa). At the locality scale, cluster confidence intervals of the most abundant taxa overlap in many site by site comparisons indicating that there is no statistically significant variability in abundance among these outcrops for those taxa. For example, *Neochonetes* cluster confidence intervals for I-70 overlaps with the intervals for OH-682, Witches Hill and McDougal indicating no significant variability among those sites. Certain taxa or sites, however, demonstrate clear differences. For example, fusulinid abundances are similar for Witches Hill, OH-682, and McDougal, but the other four sites lack appreciable fusulinids. Similarly, the four southern sites have statistically greater amounts of *Crurithyris* than the northern sites. Most of the abundance values for southern sites are similar to each other, as are abundances of the northern sites. However, the Amesville site has statistically different amounts of *Neochonetes*, *Crurithyris* and crinoids from all other sites. The I-70 site also differs from Belle Valley and Caldwell in crinoid abundances.

At regional scale, cluster confidence intervals of four (*Neochonetes*, *Crurithyris*, fusulinids and branched bryozoa) of the five most abundant taxa do not overlap (Fig. 17) which indicates statistically significant variability in abundance of these taxa between northern and southern regions of the outcrop belt. However, there are instances where cluster confidence intervals for all four outcrops in southern region (e.g., *Neochonetes*, and *Crurithyris* CCI between southern sites) or all three outcrops of northern region (Crinoids CCI between northern sites) did not overlap at locality scale, which indicates that differences in abundances of taxa present at the local scale are obscured at the regional scale. This result supports the interpretation of a differentiation of processes

Figure 16. Plot of mean relative abundance and 95% cluster confidence intervals by locality for five most abundant taxa in the Ames Limestone. Abbreviations as in Fig.5.

between the local and regional hierarchical scale. Thus, results of this analysis indicate that a pattern is discernible at larger basin-wide regional scale, which is congruent with the local patterns. Regional CCI results support the results of the cluster analysis and DCA in recognizing the major patterns in the data set. Cluster confidence intervals at locality scale can be regarded as a means of comparing local paleocommunities within the Ames Limestone, which is discussed at length in the discussion section. Hence, there is a possibility of describing the variation between localities in terms of local paleocommunity variations.

Figure 17. Plot of mean relative abundance and 95% cluster confidence intervals at regional scale for five most abundant taxa in the Ames Limestone.

CHAPTER 4: DISCUSSION

Ames Limestone Paleocommunity Structure at Various Spatial Scales

The primary goal of this study was to examine the paleocommunity structure of Ames Limestone at different spatial scales, emphasizing the outcrop and regional scales. When combined, multivariate and guild analyses document a clear change in community structure that is parallel to the depositional axis of the Appalachian basin relating to paleocommunity differentiation at the regional scale. Detailed cluster analyses and cluster confidence intervals further allow delineation of variation at the outcrop level that delimits local paleocommunities. Scalar differences are clear among these analyses, which indicate that variation in Ames Limestone paleocommunity exhibited hierarchical structure within a spatial dimension.

Regional Paleocommunity Structure of Ames Limestone

Faunal assemblages present in the northern and southern outcrops of the Ames Limestone are distinct and represent two paleocommunities that are statistically distinct. These two main paleocommunities in the Ames Limestone were both deposited under normal marine shallow water conditions as evidenced by the prominence of crinoids and other stenotopic taxa. The most important environmental factors for establishing the regional paleocommunity structure were turbidity and substrate composition. Evidence supporting this hypothesis is found in the ecospace partitioning patterns observed in the guild analysis and specific morphological features of key taxa within each paleocommunity.

The prevalence of different guilds in the two geographic regions implies underlying differences in ecospace utilization in the northern and southern regions. The distributions of *Neochonetes*, *Crurithyris*, fusulinids and corals are significant for determining and understanding the large-scale paleocommunity structure of Ames Limestone. Although both *Neochonetes* and crinoids are distributed throughout the basin in large numbers, relative abundance of *Neochonetes* was significantly greater in the northern region relative to the south (Fig. 15) indicating that their distribution was controlled by an environmental factor. *Crurithyris*, however, showed limited geographic distribution in this study, which is similar to the pattern exhibited by fusulinids and rugose corals, and is indicative of environmental control.

The *Neochonetes* paleocommunity, which dominates the northern sites, include a set of suspension feeding taxa capable of living in soft substrates and turbid conditions that do not occur outside of this paleocommunity. The productid brachiopods *Juresania* and *Linoproductus* are common within this paleocommunity; they employ the spiny extensions on the ventral valve to stabilize and maintain body support on a soft, muddy substrate (Rudwick, 1970). The most abundant taxon, *Neochonetes*, is a eurytopic taxon found in well-oxygenated environments (Lebold and Kammer, 2006; Olszewski and Patzkowsky, 2001). Morphological adaptations enabled *Neochonetes* to live unattached at the sediment water interface, and they were probably able to reorient themselves if disturbed (Cate and Evans, 1992). It appears that *Neochonetes* is relatively more abundant in turbid and muddy environments where other taxa are challenged by these stresses.

Another line of evidence supporting a turbid and muddy environment in northern sites is the absence of the rugose coral, *Stereostylus*, in these samples. Similar conditions have been recorded from the Middle Pennsylvanian Naco Formation in Central Arizona where absence of corals has been attributed to turbidity due to presence of muddy sediments by Brew and Beus (1976). The Naco Formation represents a marine environment no deeper than 15-20 m that was at least occasionally turbid (Brew and Beus, 1976). Conversely, *Stereostylus* was recorded from all four Ames localities in the southern study sites, which are dominated by the *Crurithyris* paleocommunity, indicating that conditions in this region favored the growth of corals. The southern paleocommunity is also characterized by fusulinids, whose presence is indicative of depositional environments deeper than 13 m (Stevens, 1969). It was assumed that northern paleocommunity was also deposited under similar depth conditions considering the presence of crinoids and similar brachiopod fauna and recorded between Ames Limestone and Naco Formation which was 15-20 m deep (Brew and Beus, 1976).

Crurithyris, the most abundant taxon in the *Crurithyris* paleocommunity is a stalked suspension feeder (Cate and Evans, 1992), which indicates the presence of predominantly firm substrates in the southern region where this community was distributed. *Crurithyris* was regarded as eurytopic taxon by Hickey and Younker (1981) and Lebold and Kammer (2006), but the co-occurrence of the stenohaline corals and echinoids indicates normal marine conditions for the *Crurithyris* palaeocommunity.. *Crurithyris* is rare in all the northern localities investigated in this study, which is consistent with a muddy environment interpretation for the northern region. Lebold and

Kammer (2006) also noted a lack of *Crurithyris* in their southeastern Ohio outcrops, but they noted that *Crurithyris* was present in Belle Valley and certain West Virginia samples where there was an increased terrigenous influence due to close proximity to detrital source areas (Heckel, 2008; Nadon and Kelly, 2004). These observations suggest that *Crurithyris* was eurytopic with regard to turbidity and clastic sediments but preferred environments with firm substratum where it could attach with the thick pedicle.

Although the study sites are situated in similar positions with respect to the depositional axis of the Appalachian basin, there is clear differentiation among northern and southern paleocommunities. These differences in ecospace utilization of organisms in the two regions indicate that they must have subjected to different environmental conditions. Thus, northern sites consisted of taxa that are more or less tolerant of turbid waters and muddier substrates such as reclining brachiopods and crinoids. In contrast guilds of southern sites indicate clear water conditions with firmer substrates particularly with high abundances of *Crurithyris* (stalked brachiopods) and presence of corals in these sites.

Thus, Ames Limestone paleocommunity in the distal Appalachian basin displays lateral variation in paleocommunity composition among outcrops parallel to depositional strike. This contrasts with the general observation that one should expect limited lateral changes in biofacies distribution parallel to the depositional axis (Ziegler et al., 1968). Because the sites examined in this study occurred within a similar depositional context, these study sites were expected to display less variation in paleocommunity structure than reported by Lebold and Kammer (2006), who examined biofacies distribution

perpendicular to the depositional axis. Lebold and Kammer (2006) reported substantial differences in biofacies of Ames Member localities in southeastern Ohio and West Virginia in terms of paleocommunity composition, which can be interpreted as laterally extensive belts of species associations aligned roughly parallel to the depositional strike similar to species associations explained by Ziegler et al. (1968).

Previous analyses of Ames Limestone petrography provide additional support for the interpretation of increased turbidity in the northern region versus a firmer substrate and clearer water in the southern region. According to previous work on the petrology of Ames Limestone (Haines, 1965; Bjurstrom, 1960), a purer crystalline limestone unit was present in Athens area and northern Meigs County, which graded into a more argillaceous limestone toward Morgan County in north and southern Meigs County in south. Thus, there is lithologic evidence to support that clearer waters in Athens County starts to become turbid with increased detrital influence towards Noble County and Muskingum County where all the northern localities are found in the present study. Furthermore, studies by Bjurstrom (1960) and Haines (1965) provide evidence for greater paleoecological variability within the Ames Limestone paleocommunities due to terrigenous influence when study area is expanded from Athens County to include more Ames Limestone outcrops in southeastern Ohio. Notably, Burstrom (1960) describes Ames Limestone to be chemically purer to the south in Athens County and the deposition in northern area in Morgan County to be in closer proximity to the land area. Overall, Ames Limestone outcrops in southeastern Ohio appears to consist of purer limestone areas in northern Meigs County and Athens County bracketed by more argillaceous

limestone outcrops in Morgan, Noble and Muskingum Counties towards north and in southern Meigs County towards further south (Bjurstrom, 1960; Haines, 1965).

Another explanation for this observation can be found in a modern analogue for the Appalachian mountain system in Papua New Guinea (Baldwin and Butler, 1982). Coral reefs were established in the continental shelf of Papua New Guinea in an environment of high terrigenous mud brought in by the Fly River because the Coral Sea Coastal Current allowed coral reefs to develop by maintaining a supply of clear water (Harris et al., 1996). Similar coastal currents may have existed in the Ames Sea during the deposition of the Ames Limestone that created less turbid depositional settings near Athens and Morgan Counties otherwise surrounded by environments of increased terrigenous input. Located at the distal end of major glacial-eustatic inundation in Midcontinent, Ames Limestone outcrops in southeastern Ohio are much closer to the detrital source areas of the Appalachian highlands (Heckel, 1995). As such there is a greater chance for Ames Limestone outcrops in southeastern Ohio to experience increased detrital input within the depositional basin brought in as fluvial sediments. Existence of coastal currents in the shallow epeiric Midcontinent sea closer to the Appalachian basin could explain the existence of clear water currents that allowed the growth of corals and maintained firm substrates devoid of mud.

Localized Paleoecological Patterns of the Ames Limestone

In addition to the regional scale paleocommunity differentiation prevalent in the Ames Limestone outcrops in the southeastern Ohio, community structure varies among geographically close outcrops reflecting the variability at the level of local

paleocommunities. Following the definition of Bennington and Bambach (1996), each of the seven localities used in this study is regarded as a local paleocommunity because each is an assemblage of fossils collected from a single bed at one outcrop. Even among geographically proximate outcrops, there is variation in relative abundance and presence/absence of taxa (Fig. 13). For instance, abundance counts for common taxa, like *Neospirifer* or productid brachiopods vary between Witches Hill and OH-682, which are only 1.43 km apart. When sub-sites within a locality were considered, taxon abundances could still vary (e.g. fusulinids between Witches Hill sub-sites 2 and 4, which are only 10.25 m apart in Fig.13). Differentiation of local paleocommunities is also apparent in the cluster confidence intervals (CCI) values calculated for localities (Fig.16). CCI analyses indicate that certain localities exhibited larger confidence intervals—indicative of local habitat patchiness—due to an elevated number of individuals in a single sub-site sample (e.g. *Neochonetes* at I-70). The impact of such local patchiness, however, was only expressed in at the fine-spatial scale. At the broader scale, sampling of multiple sub-sites per outcrop reduced the signal of this patchiness within local paleocommunities.

At the locality level, cluster confidence intervals were used to quantify the variation between different local paleocommunities based on the mean relative abundance of five most abundant taxa found in this study. Notably, local paleocommunities that are closer together in geographic space exhibit the highest degree of similarity. For example, Witches Hill and OH-682 represent similar local paleocommunities as CCI for all five taxa overlap (Fig.16), whereas all five taxa do not consistently overlap among all four of the localities (Amesville, McDougal, Witches Hill,

and OH-682) within the southern paleocommunity. Similarly, the Caldwell and Belle Valley local paleocommunities are more similar to each other than either is to I-70, the other northern paleocommunity locality (Fig. 16). This differentiation of local paleocommunities with geographic distance reflects the hierarchical structure in spatial distribution of community assembly. Notably, this geographically controlled local differentiation within the two (regional) paleocommunities indicates a strong hierarchical structure to spatial distribution within Ames communities.

Local paleocommunity differentiation within the northern and the southern paleocommunities indicates that environmental conditions were not homogenous within each geographic region. Guild analysis results also indicate differences in guild relative abundance between different local paleocommunities within the two main paleocommunities. For instance the guild relative abundances of low level suspension feeding reclining brachiopod, low level suspension feeding stalked brachiopod, high level suspension feeding stalked and epifaunal rolling are generally similar between Witches Hill, OH-682 and McDougal compared to Amesville as shown in the pie charts (Fig. 15). Environmental differences at this scale likely reflect habitat heterogeneity related to local topography, habitat patchiness due to aggregate biotic effects, and/or biotic processes such as competitive exclusion, bioconstruction feedbacks, or commensalism. These localized controls at smaller spatial scale were responsible for shuffling of sub-sites between sites in the cluster analysis (Fig. 9). Influence of local controls can be assessed in detail by increasing the sampling effort at localities. Thus, local scale analyses are

informative about aspects of habitat heterogeneity; however, the larger spatial scale is better for identifying the dominant paleocommunity structure at regional scale.

Processes Operating at Different Scales

This study investigated additional Ames Limestone outcrops from southeastern Ohio that were distributed further south of depositional basin compared to the study of Lebold and Kammer (2006). As a result, this study facilitated the differentiation of the Ames Limestone fossil assemblage in southeastern Ohio into two paleocommunities. As opposed to the study conducted by Lebold and Kammer (2006) who examined the biofacies of the Ames Member, the focus of this study was solely the fossil assemblage contained in the Ames Limestone. This faunal differentiation occurs although all outcrops in southeastern Ohio represent roughly similar packstone to wackestone lithologies. Notably, the limestone surfaces sampled in this study do not vary substantially in taphonomic characteristics. Ecological tolerances of different taxa identified in this study were useful for generating paleoenvironmental interpretations at different spatial scales. Since some aspects of the regional scale paleocommunity structure is still preserved at the locality scale CCI comparisons, it is possible that the same environmental controls were largely responsible for structuring both local paleocommunities and (regional) paleocommunities. Although regional and locality scales represent different spatial scales, the primary controls on paleocommunity assembly are turbidity and substrate composition. The finer scale variation exhibited by the local paleocommunities likely derives from habitat patchiness related to biotic processes such as competition, bioconstruction processes, or local topographic expression. Less robust faunal patterns at

finer spatial scales is also encountered when comparing paleocommunities in a single bed or few beds (less than one meter thick stratigraphic scales) contained within closely located vertical successions in the Kope Formation (Webber, 2005). Conversely, the finer stratigraphic scale of single bedding surface used in the present study was effective in delineating faunal patterns at increasingly larger spatial scales (at regional scale) when sufficient sampling localities across the basin were incorporated.

The recovery of both regional and local signals indicates that hierarchical processes of community assembly were significant contributors to the community structure observed in the Ames Limestone. Similar basin scale faunal transitions in the Middle Devonian Hamilton Group of western and central New York State was identified by Lafferty et al. (1994) which were associated with an onshore offshore transect. Lafferty et al. (1994) also noted that at most localities, faunal compositions did not indicate any spatially systematic patterns as in the basin scale pattern. Bennington, (2003) and Zambito IV et al. (2008) also observed spatial heterogeneity in faunal assemblages which indicate the significance of spatial scale in delineating faunal patterns and detecting patchiness in paleocommunity analyses. Although operating at a different temporal scale, similar large scale regional spatial patterns were also noted by Williams et al. (2015) in modern Caribbean reef benthic assemblages. In another modern community study spatial variation in the geographic distribution of reef fish communities in Yucatan Peninsula was observed by Núñez-Lara et al. (2005) using a hierarchical multi-scale surveying design. Both modern and ancient community studies employ hierarchical scales to delineate spatial heterogeneity, although the temporal scales in the

two types of studies are different. In depth understanding of how spatial scale operates in different temporal scales could substantially improve the level of resolution in community studies.

Implications

The Ames Limestone was formed under different regional controls that resulted in differences in paleocommunity structure at different spatial scales along the depositional strike. As a result Ames Limestone shows two geographically separate normal marine paleocommunities in the northern and the southern portions in the depositional basin in southeastern Ohio. Certain taxa identified in this study such as the brachiopods *Neochonetes* and *Crurithyris* and the rugose coral *Stereostylus* were particularly important in understanding the regional paleocommunity structure as their abundances and geographic distributions provided insight on paleoecological drivers of these changes. Quantitative paleoecological analyses implemented in this study were also useful in delineating different aspects of spatial arrangement of paleocommunities. Results of this study indicate that cluster analysis is a useful method to visualize spatially inclusive regional paleocommunity structure. However, DCA and comparison of CCI distributions are better at showing gradational changes of paleocommunities and assessing differences pertaining to locality scale. Paleoecological interpretations of these patterns based on guild analysis enabled the reconstruction of paleoenvironmental conditions that persisted during the deposition of the Ames Limestone in the area. If only one or two analyses were used, this could have resulted in incomplete understanding of the paleocommunity structure at different spatial scales.

The Ames fauna is an example of how contemporary communities growing under different sedimentological and substrate conditions within the normal marine realm could result in two geographically separate paleocommunities. Although the Ames Limestone represents an accumulation over tens of thousands of years, a longer temporal lens than in most analogous modern-day marine communities, evidence for the primary environmental controls is found within the paleocommunity structure. However, when community structure is examined at increasingly finer spatial scales, the large-scale regional paleocommunity structure becomes less clear among local paleocommunities; which indicates a strong hierarchical spatial control on community structure (Lafferty et al., 1994; Zambito IV et al., 2008; Bennington, 2003). The approach used in this study can contribute to ideas in modern community by providing insights to how spatial scales used in paleocommunity analyses detect processes operated in past that are similar to modern depositional settings. This study indicates 1) how the detected paleocommunity patterns can be affected by the spatial scale used in sampling and 2) how can we develop methods to analyze abundance data within a hierarchical spatial approach to detect paleocommunity structures. Notably, Late Pennsylvanian Ames Limestone paleocommunities are formed during an interglacial interval in an analogous setting to modern interglacial interval. Due to its close proximity to detrital source areas in the Appalachian, Ames Limestone paleocommunities in southeastern Ohio are geographically structured. Turbid, muddy environment of the northern region paleocommunity grades into the clearer water, firm substrate conditions in the southern paleocommunity.

CHAPTER 5: CONCLUSIONS

This study focused on determining the spatial patterns evident in the distribution of marine invertebrate fauna in the Ames Limestone based on taxon occurrences, abundances and guild structure. The use of a hierarchical spatial approach in this study was to facilitate the understanding of the processes that lead to geographic variability of fossil assemblages across the Ames Limestone. Cluster analysis and DCA results enabled the visualization of the primary structure that can be observed at larger basin scale, which constituted of two primary groups that corresponded to northern and southern study sites. This regional geographic separation is the outcome of turbid conditions and differences substrate composition within the depositional basin. Variation in these variables resulted in fundamental differences observed in the paleoecological characteristics of *Neochonetes* and *Crurithyris* paleocommunities in northern and southern regions, respectively.

Although it was generally regarded as a more or less similar shallow normal marine limestone unit, Ames Limestone outcrops in southeastern Ohio display quantifiable differences in paleocommunity structure. This study identified the presence of two statically significantly different paleocommunities within the Ames Limestone outcrops in this region. Ames Limestone fauna identified in this study consisted of group of normal marine taxa such as rhynchonelliform brachiopods, bryozoa, rugose corals, crinoids, regular echinoids, trilobites, chondrichthyes, sponges and foraminifera in addition to few eurytopic taxa within a wackstone matrix. These fauna within the Ames

Limestone outcrops exhibited variation in composition and abundance across depositional basin that helped delineating the regional paleocommunity structure.

Small-scale variations considered at the locality level are noted via comparison of local paleocommunities among the seven localities/outcrops. Such variations exhibited by the local paleocommunities likely originated as communities responded to biotic processes and/or local topographic expressions. Local paleocommunity variations are indicators of small-scale variations at a smaller spatial hierarchical level than those contained within the two regional paleocommunities. Furthermore, detailed understanding of small scale variability at locality level could be carried out by increasing the sampling effort at locality scale by producing replicate samples for the each of the four samples collected at the seven study sites.

Paleocommunities of Ames Limestone outcrops in southeastern Ohio contribute to our understanding of use of spatial scales in paleocommunity analyses to detect large scale environmental processes operated in the past that are similar modern depositional settings. Late Pennsylvanian time during the deposition of Ames Limestone bear similarities to modern conditions since both are interglacial intervals.

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APPENDIX A: TOTAL ABUNDANCE COUNTS OF ALL SUB-SITES

Taxa	Witches Hill				OH 682				McDougal			
	WH1	WH2	WH3	WH4	OH 682-1	OH 682-2	OH 682-3	OH 682-4	MD1	MD2	MD3	MD4
<i>Neochonetes</i>	74	61	136	75	129	47	71	140	44	101	41	80
<i>Crurithyris</i>	42	38	88	65	241	39	63	84	14	44	16	48
<i>Neospirifer</i>	4	6	9	3	4	2	1	4	4	5	3	5
<i>Derbyia</i>	2	3	6	4	10	1	2	2	2	0	0	0
<i>Punctospirifer</i>	0	1	0	0	0	1	0	0	1	1	0	0
<i>Juresania</i>	2	2	1	4	2	1	1	2	1	2	0	0
<i>Antiquatonia</i>	0	0	0	0	0	0	0	0	0	0	0	0
<i>Linoproductus</i>	0	0	0	0	0	0	0	0	0	1	1	0
<i>Echinaria</i>	0	0	1	0	0	0	0	0	0	0	0	0
<i>Reticulatia</i>	0	0	1	0	0	0	0	0	0	0	0	0
<i>Palaeolima</i>	0	0	0	0	0	0	0	0	0	0	0	0
<i>Astartella</i>	0	0	0	0	0	0	0	0	0	0	0	0
<i>Aviculopecten</i>	0	0	0	0	0	0	0	0	0	0	0	0
<i>Straporollus</i>	1	1	1	1	1	0	0	0	0	0	1	0
<i>Trilobites</i>	0	3	0	1	4	2	1	1	0	0	0	0
Branched bryozoa	1	2	4	0	8	3	1	11	1	6	1	1
Encrusting bryozoa	2	0	6	14	16	3	1	5	0	5	0	0
Fenestrate bryozoa	0	0	0	0	0	0	0	0	0	1	0	0
Echinoids	4	2	1	1	6	1	0	1	2	2	1	2
Stereostylus	1	1	0	1	1	0	0	3	2	1	0	0
Crinoids	21	17	23	11	24	10	11	15	24	40	8	47
Fusulinids	16	16	11	6	0	0	1	17	0	29	4	37
Sharks	0	0	0	0	0	0	0	0	0	0	0	0
Sponges	0	0	0	0	0	0	0	4	0	0	0	0

Taxa	I-70			
	I70-1	I70-2	I70-3	I70-4
<i>Neochonetes</i>	0	20	69	91
<i>Crurithyris</i>	1	2	0	0
<i>Neospirifer</i>	1	0	4	1
<i>Derbyia</i>	0	3	1	1
<i>Punctospirifer</i>	2	0	0	0
<i>Juresania</i>	0	1	0	0
<i>Antiquatonia</i>	0	0	0	1
<i>Linoproductus</i>	0	0	0	0
<i>Echinaria</i>	0	0	0	0
<i>Reticulatia</i>	0	0	0	0
<i>Palaeolima</i>	0	0	0	0
<i>Astartella</i>	0	0	0	0
<i>Aviculopecten</i>	0	0	1	0
<i>Straporollus</i>	0	0	0	0
Trilobites	0	0	0	0
Branched bryozoa	6	0	0	0
Encrusting bryozoa	0	0	0	3
Fenestrate bryozoa	0	0	0	0
Echinoids	0	0	0	0
<i>Stereostylus</i>	0	0	0	0
Crinoids	12	10	7	23
Fusulinids	0	0	0	1
Shark teeth	0	0	0	0
Sponges	0	0	0	0

APPENDIX B: GUILD RELATIVE ABUNDANCE PERCENTAGES FOR EACH SITE

	Guild abbreviation*	Witches Hill	OH 682	McDougal	Amesville	Caldwell	Belle Valley	I-70
1	LLSFR	46	40	45	18	75	70	71
2	LLSFS	29	43	20	75	0	2	2
3	LLSFC	2	2	0	0	1	1	2
4	LLSFSR	1	1	1	1	4	4	1
5	LLSFE	0	0	0	0	1	0	0
6	LLSFB	0	0	0	0	0	0	0
7	EG	2	1	1	0	0	0	0
8	LLSFBB	1	2	1	0	7	11	2
9	LLSFEB	3	3	1	0	0	1	1
10	LLSFFB	0	0	0	0	1	0	0
11	LLSFAS	0	0	0	0	0	0	0
12	EPP(S/PP)	0	0	0	2	0	0	0
13	HLSFS	9	6	19	3	10	11	20
14	ERG	6	2	11	0	0	0	0
15	PAP	0	0	0	0	0	0	0
16	EDF	1	1	0	0	0	0	0

*Guild abbreviations are explained in Fig. 14.

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