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CHARACTERIZING AND QUANTIFYING HABITAT HETEROGENEITY, EXTINCTION, AND PERSISTENCE OF HABITAT PREFERENCE IN PHANEROZOIC REEFS

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ABSTRACT

Habitat heterogeneity is understood to be a primary driver of taxonomic diversity in modern reefs, and is assumed to have acted similarly throughout the Phanerozoic history of reef-building. However, there is no established methodology to measure heterogeneity in fossil reefs, and the rock record presents many challenges to doing so, including issues of preservation, exposure, and time-averaging. Here, I present five quantitative and semiquantitative methods that can be applied to fossil reefs in order to characterize heterogeneity. These include the complexity and diversity of reef-builder morphotypes involved in reef construction, the number of distinct reef facies, the scale of relief the reef achieved in life, and a Structural Complexity Index (SCI) calculated using the dimensions of framework elements encountered along a transect. These metrics are applied to Ordovician and Pleistocene reefs, and biases of each metric are discussed in detail. These metrics are then applied to reefs across the middle-Paleozoic to assess how heterogeneity changed over the interval, as reefs became more diverse. Through this interval, reefs became larger, exhibiting greater relief, a wider array of reef-builder morphotypes, and a higher diversity of reef facies. The final chapter addresses the identity of a cohesive reef fauna in deep time, using reef crises as natural experiments to examine extinction and persistence of reefal preference for reef-builders and reef-dwellers across the Phanerozoic. Reefal taxa exhibit lower extinction than nonreefal taxa, consistent with having more eurytopic environmental distribution. Reef-builders and reef-dwellers do not exhibit significant differences in extinction, but reef-builders express significantly higher rates of persistence in reefal habitats. Reef-builders and reef-dwellers do not exhibit consistent responses to episodes of reef crisis, perhaps due to variation in the drivers of each reef crisis. Nevertheless, reef-builders and -dwellers do not respond to perturbations in similar ways, and should be addressed separately when analyzing diversity dynamics of reefal taxa.

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INTRODUCTION

Reefs--defined here as rigid, biologically-constructed or -facilitated buildups that achieve significant local topography above the surrounding seafloor— are deeply complex oceanographic and biological structures, hosting an incredible faunal diversity in a relatively small geographic area. The wide variety of habitats, both within and around reefs, plays an integral role in supporting that diversity by providing habitat heterogeneity—a habitat quality widely recognized as a driver of both alpha and beta diversity in the marine realm (Tews et al. 2004; Hewitt et al. 2005; Williams et al. 2010). Habitat heterogeneity in reefs includes not only the complex topography and array of cavities and crevices created by reef builders (Edinger and Risk 2000), but also the wide variety of habitats that reflect changing light, wave-energy, and nutrient conditions across the reef. This variation in habitat allows for high faunal diversity through fine-scale environmental partitioning.

Habitat heterogeneity is not only understood to be deeply important in the reef system today (Roberts and Ormond 1987; Wilson et al 2007); it has been proposed for reefs in the fossil record as a reason for their exceptional faunal diversity (Wood 1999; Kiessling 2002), and their role as evolutionary cradles in the marine realm (Kiessling et al., 2010). However, there are no established methods for examining heterogeneity in fossil reefs, and test these proposals. Moreover, the rock record presents many challenges for the identification of heterogeneity, from issues of exposure and preservation to concerns over time-averaging.

In Chapter 1, I propose five quantitative or semi-quantitative metrics for identifying heterogeneity in fossil reefs, informed by extensive field observation of dozens of Paleozoic and Recent reefs. These metrics include the identity and diversity of reef-builder morphotypes that comprise the reef structure, the diversity of facies present, the scale of relief exhibited by the reef during life, and a direct measure using straight-line transects, akin to modern rugosity metrics. Through Chapter 1, the limitations of these methods are discussed, and they are each applied to exemplar reefs from the Ordovician and Pleistocene. Despite limitations, these metrics are robust, and are a promising step towards identifying habitat heterogeneity at different scales and understanding its effects on the reef fauna.

These metrics are useful in their broad applicability, relying on features readily identifiable in the field, and commonly identified in the literature. It is in this light that we can apply these methods to examine habitat heterogeneity across the middle Paleozoic, as addressed in Chapter 2. The middle Paleozoic, particularly the Silurian and Devonian, was a 'heyday' of reef-building, in which reefs achieved their greatest latitudinal range, abundance, and global volume of the Era (Kiessling et al 1999; Kiessling 2002;2005). Moreover, reefs became far more taxonomically diverse as the interval continued, potentially related to changes in heterogeneity (Kiessling et al 2000; Kiessling 2002). With proposed methods for quantifying habitat heterogeneity, we can ask how, and at what scales heterogeneity changed between the Late Ordovician and Late Devonian. To do so, I applied the proposed heterogeneity metrics from Chapter 1 to 155 middle Paleozoic reefs of Laurentia, using field notes and data from the literature. I find that reefs do increase in heterogeneity, observable through the diversity of reef-builder morphotypes, facies diversity, and scale of relief. The changes in heterogeneity are fundamentally similar to what is observed during the individual growth of a reef, in which increasing relief encourages reef zonation, and ecological succession results in more diverse substrata and a greater diversity of reef-builder morphotypes.

Chapter 3 diverges from the idea of heterogeneity, and directly addresses the concept of a 'reef fauna'. Reefs are fundamentally reliant on reef-builders, and the fate of reefs is likely tied to the fate of the taxa that build them. However, the reef fauna consists of both reef-builders and reef-dwellers, and reef-dwellers may not be as fundamentally tied to the reef environment as reef-builders. Reefal taxa are observed as sensitive to perturbation throughout the fossil record (Copper 1994a; Brayard et al. 2011a; Erwin 2001; Wood 1999), but little nuance has been afforded for variation in reef-association. These perturbations, particularly reef crises, in which global reef volumes decrease dramatically (>70%) (Flügel and Kiessling 2002), offer an ideal natural experiment to ask how the extinction and incumbency dynamics of reef-builders and –dwellers differ, and how they relate to extinction dynamics of nonreefal taxa. Here, I examine genus-level occurrence data from the Paleobiology Database, addressing extinction of reefal and nonreefal taxa, and reef-builders and reef-dwellers, over reef crisis events and non-crisis events through the Phanerozoic. I further examine persistence of reefal preference among surviving taxa over those same interval. Reefal taxa, surprisingly, experience lower proportional extinction than nonreefal taxa, and although reef-builders and reef-dwellers do not differ in response consistently across crisis events, reef-builders do, indeed, exhibit a stronger tie to the reef environment, with reef-dwellers more flexibly occupying nonreef environments in stages following intervals in which they showed strong reefal affinity.

The work presented here encourages the separate analysis of reef-builders and reef-dwellers in deep time. Furthermore, it shows that there are viable methods to identify and quantify heterogeneity in fossil reefs, opening new avenues for exploration and questioning. For example, how does faunal diversity relate to heterogeneity in fossil reefs, and at what temporal and geographic scales does heterogeneity matter for influencing faunal diversity in reefs through time? Is the re-establishment of reefal habitat heterogeneity after major crisis or extinction events fundamental to faunal recovery? Methods presented here, although not perfect, are robust and relatively easily applied, hopefully giving paleoecologists another useful tool to help understand the development of the reef system through time.

CHAPTER 1

CHARACTERIZING AND QUANTIFYING HABITAT HETEROGENEITY IN FOSSIL REEFS: CASE STUDIES FROM THE ORDOVICIAN OF NEWFOUNDLAND, AND THE PLEISTOCENE OF FLORIDA

1.1 Abstract

Habitat heterogeneity is widely regarded as a fundamental factor in promoting biodiversity in the reef system and elsewhere, but little attention is paid to its influence on local and regional biodiversity in the fossil record. This situation is likely tied to the difficulty in describing and quantifying that heterogeneity. Here, I propose four semi-quantitative measures and one quantitative measure of heterogeneity, developed through extensive field observations of fossil reefs. Measures include: 1) the morphological complexity of reef-builders and the relative importance of open or compact reef-builder morphotypes; 2) the diversity of reef-builder morphotypes present; 3) the number of facies within the reef; 4) the order-of-magnitude scale of topographic relief; and 5) a Structural Complexity Index (SCI)--a continuous measure of heterogeneity, akin to 'rugosity' used in modern day habitats, using the intersection of straight line transects with framework elements. Field tests on Ordovician and Pleistocene reefs find that these four measures are broadly applicable to reefs of different time periods, but also come with limitations brought upon by exposure, preservation, and accessibility. Heterogeneity analysis, with proper understanding of these limitations, allows for greater insight into the paleoecology of fossil reefs, and can help us better understand how the reef system has developed through time.

1.2 Introduction

A positive relationship between biodiversity and habitat heterogeneity is well-established in the ecological literature, both theoretically and empirically (MacArthur and MacArthur 1961;

MacArthur, Wilson, and MacArthur 1967; Gilinsky 1984; Belmaker and Jetz 2012; Darling et al. 2017), and at many scales, ranging from local (mm to 10s of cm) to regional (km to 10s of km) (Hewitt et al. 2005; Archambault and Bourget 1996; Bourget *et al*, 1994). Habitat heterogeneity, referring to habitat variation and its temporal and/or spatial distribution in a landscape, can be defined along many different environmental conditions, such as substratum type, topography, water/wind stress, and distribution of resources. Positive relationships between habitat heterogeneity and biodiversity are thought to exist in ancient systems as well, but quantifying habitat heterogeneity in fossil environment is almost always more challenging.

Fossil reefs, which have been the focus of especially intense study for controls on biodiversity, are no exception. In outcrop, the entirety of a reefal body is rarely fully exposed unless it is small patch reef; exposures are 2- rather than 3-dimensional; considerable time-averaging of framework elements is common owing to variable growth rates between reef-builders, overgrowths of a complex topography, and post-depositional compaction; and diagenetic recrystallization, which can be rampant in such carbonates, can obscure the original outlines of framework elements. Post-mortem disintegration of reef structures by bioerosion also obscures original habitat complexity (Hubbard, Burke, and Gill 1998), although the debris can create additional habitats. Due to the challenge of directly applying heterogeneity measurements to the fossil record, habitat heterogeneity is rarely tested as a controlling factor on ancient biodiversity, with most studies focused at quite large, spatially coarse scales, such as contrasts between carbonate and siliciclastic settings, or between paleocontinents (Miller and Connolly 2001; Miller 1997; Kiessling and Aberhan 2007)

Here, I propose a robust, multi-fold approach to characterizing fossil reefs in terms of habitat heterogeneity, using a set of semi-quantitative and quantitative measures. To demonstrate the operational utility of this approach, it is applied herein to Ordovician-age patch reefs in western Newfoundland and to an exposure of a Pleistocene reef in the Florida Keys, both of which present distinct challenges with respect to exposure, diagenesis, and weathering. The applicability of this approach to many mid-Paleozoic reefs is also summarized. This wide suite of test cases reveals that although not all presented measures can be applied successfully to all reefs, the approach is useful in a majority of empirical examples. Wide-scale application of these metrics offers the potential to better understand habitat heterogeneity in the fossil record and to rigorously test the hypothesis that habitat heterogeneity was a direct control on biodiversity in reefs through deep time.

1.3 Background

1.3.1 Heterogeneity and biodiversity in the reef system

One proposed driver for the positive relationship between species richness and habitat heterogeneity is that heterogeneous environments exhibit a greater breadth of potential niche space that organisms can use and partition (MacArthur and MacArthur, 1961). In this case, finer niche partitioning allows for the maintenance of high local biodiversity. Although most historical work tying diversity to heterogeneity has been done in terrestrial environments (Pianka 1967; Wiens and Rotenberry 1981; Tews et al. 2004), there is a substantial literature identifying the effects of heterogeneity on local abundance and biodiversity in marine systems as well (Buhl-Mortensen et al. 2010; Bourget, DeGuise, and Daigle 1994; Hewitt et al. 2005), especially in reefs (Castro-Sanguino et al, 2016).

Reefs are defined here as rigid, biologically-constructed or -facilitated buildups that achieve significant local topography above the surrounding seafloor. Significant topography, in this case, is any local topography with enough prominence to affect local hydrodynamics and influence surrounding sediments. This definition omits the common criterion of “wave resistance”, as it is very difficult to determine in fossil buildups, and is irrelevant for buildups that do not occur in shallow water. This definition also does not prescribe a typical reef-builder and thus includes bioherms with either unclear or likely indirect biological construction, such as with mud mounds (Wood 2001; Riding 2002).

In the marine realm, reefs are widely recognized as centers of biodiversity--underwater cities that house a great variety of vertebrates, invertebrates, and algae within relatively small geographic areas. Although local biodiversity can be amplified by complex interactions between organisms (Erwin 2008; Bairey, Kelsic, and Kishony 2016), much of this high biodiversity may be attributable to the elevated habitat heterogeneity reefs provide through their complex physical form. The complex topography of reefs, as well as the extensive cavity networks within them, provides ample habitat for organisms with diverse niche requirements in terms of space, light, and water flow. This kind of habitat heterogeneity also leads to higher biomass of reef organisms, and seems to promote ecosystem recovery after disturbances (Graham and Nash 2012). Locally, heterogeneity of this sort and associated faunal diversity is mostly determined by the complexity of reef-builder morphotype (i.e. relative level of branching, and projection into water column), and the co-occurrence of multiple reef-builder morphotypes (Edinger and Risk 2000).

The hydrodynamic and sedimentological influence of reefs upon nearby habitats may also drive regional habitat diversity and, consequently, biological diversity on somewhat larger scales. This increase in heterogeneity can occur through the creation of novel sedimentary habitats, either associated directly with or adjacent to the reef framework, or associated with more distant backreef lagoons and protected shorelines. Elevated habitat heterogeneity at this spatial scale and higher is commonly associated with increased beta diversity (Hewitt et al. 2005; Adjeroud 1997).

1.3.2 Measurement of habitat heterogeneity in modern reefs

Although multiple qualitative and semi-quantitative methods for identifying heterogeneity have been proposed (e.g., Polunin and Roberts 1993; Wilson *et al.* 2007), quantification of heterogeneity in modern reefs is typically limited to direct measurement of rugosity. In taking traditional measurements, a chain or rope is laid across a section of reef (McCormick 1994; Graham and Nash 2012), and rugosity is recorded as the ratio of true chain length to effective horizontal distance covered when draped. In recent years, remote sensing and digital scanning have been used to obtain similar information (Brock et al. 2004; Zawada and Brock 2009; Storlazzi et al. 2016). Heterogeneity, measured in this fashion, is primarily driven by vertical growth of framework. This measure does not necessarily capture the full variability of spaces made available for use by reef occupants—for example, the prevalence of overhangs and cavities-- but it combines all features into a convenient, single metric. This metric focuses on projection into the water column, and is especially useful when the organism of concern is one that occupies the projecting structure, particularly fish.

Beyond the framework of 'rugosity', heterogeneity in modern reefs is also acknowledged in the literature in the variety of substrates present in sampling arrays. This application would include the registering of coral framework, rubble, and patches of sand or mud in a given area (Henry et al, 2010). This type of heterogeneity captures diversity of habitats more explicitly than rugosity as it is a distinct record of the number of broad habitat types present. Each measure captures a different type of habitat heterogeneity, and all measures are important for understanding reef diversity and ecology.

1.3.3 At what scales is heterogeneity important?

Heterogeneity, defined here as variability in local physical environment, is a concept tied to scale of observation. If one identifies habitats at the kilometer resolution, one patch of shallow sea floor may not differ from a neighboring patch of sea floor. However, at meter, or even centimeter-scales, heterogeneity may appear on that sea floor in the form of small rock cavities, patches of shell debris, and even variable sediment size. The scale that a study focuses on, when describing heterogeneity, depends on authors' prior assumption of the scales that matter for the biological phenomenon of interest (Meager and Schlacher 2013; Tews et al. 2004). For example, studies concerned with population connectivity in marine invertebrates or regional faunal distribution may identify heterogeneity at the kilometer or tens-of-kilometer scale, identifying distribution of coastal features and substrate type (Williams et al. 2010; Archambault and Bourget 1996). Others looking at the establishment of larvae on hard substrates may note heterogeneity at the millimeter to decimeter scale, identifying cracks, ridges and cavities that might influence settlement strategies of larvae and ultimate community composition (Bourget et al 1994; Mallela 2018). Ultimately, heterogeneity matters at the scales in which an organism interacts with its environment throughout all life stages.

1.4 The challenges of identifying habitat heterogeneity in deep time

Given the apparent importance of heterogeneity on biodiversity and biomass in modern reefs, can the same influence be detected in ancient environments? Complex structures in the past would likely provide the same kind of heterogeneous habitat as complex structures in the present, and so it seems likely that the organisms occupying the reef environment would respond similarly. Interpreting the effects of heterogeneity will be most straightforward where morphologically analogous reef-builders and reef-dwellers exist in the fossil record, and caution should be applied with the great diversity of non-analogous reef-building styles present through the Mesozoic and Paleozoic, such as those with significant structural contribution of mud or microbialite. Even if two reefs have similarly complex habitats, different modes of growth and interactions between reef-builders (i.e., symbioses, contact points that suggest non-contemporaneous growth) should also be explicitly taken into account in interpreting the use of those habitats as they are presented in the fossil record.

1.4.1 The taphonomic limitations on identifying heterogeneity in fossil reefs

The fossil record presents a unique challenge in reconstructing snapshots of specific physical environments because deposited sediment and organismal remains are not necessarily static in time. Sediment can be disturbed and reworked, and local substrate provided by carbonate-producing macro-organisms is subject to significant bioerosion. Furthermore, individual reef-builders in a fossil reef horizon, even if they are preserved *in situ*, may not have grown contemporaneously. The irregular growth surface ensures spatial overlap of different reef-builder cohorts in a given horizon, introducing significant time averaging of reef-builders identified (Edinger *et al*, 2001). As a result, subenvironments identifiable in fossil reefs are generalized for energy level, water depth, and sediment type, reflecting average environmental conditions over time. Only in rare situations are extensive paleo-surfaces preserved *in situ*, along with their occupants. Such snapshot preservation is enabled by rapid cementation as in hardgrounds (Brett and Brookfield 1984), rapid burial, or in exceptional scenarios such as stranding during tectonic events (Searle 2006). Of the ecological community that occupied these paleosurfaces, primarily only encrusting and boring organisms will faithfully preserve their spatial context (Zuschin et al, 2000).

Fossil reefs can preserve hard substrates and feature sites of rapid cementation and in-situ preservation, but they only rarely preserve distinct, continuous depositional/growth surfaces that are reflective of topography and comparable to those of modern, living reefs. Some insights can be made upon reef topography using the topography of individual reef-builders, represented by continuous growth surfaces, and the interaction between the edges of reef-builders and surrounding sediment. Variations in water depth across a reef can also be inferred from morphological variation of reef-builders that reflect adaptation to particular light or water energy levels (Anthony et al., 2005; Hoogenboom et al., 2008; Kershaw 1998), or known physiological limits of component organisms, especially the light requirements of different phototrophs (Wray 1977). Local topography can also be inferred from directional cues, such as geopetal infilling, and the reorientation of particular reef-building organisms with respect to light or flow direction (Łuczyński 2009).

Reefs inherently have topography, and they present hard substrata for continued colonization, making the top of the reef a dynamic, ever-changing surface. It is typically impossible to define a continuous surface without an event marker, such as a sediment apron deposited by a storm (Tierney and Johnson 2012). However, preservation of such sedimentary deposits can be quite variable, and may be best identified in reef-adjacent lagoonal settings (Bonem 1988), and not on the skeletal core of the reef.

1.4.2 The limits of spatial scale in identifying heterogeneity in fossil reefs

Although heterogeneity may influence reef communities at multiple scales, the rock record determines the scales at which we can identify heterogeneity. The first major filter is rock exposure. If regional heterogeneity at the tens-of-kilometers scale is of interest, we would need appropriately sized, reasonably uninterrupted expanses of contemporaneous rock in both longitudinal and latitudinal directions. Although in many cases workers can map individual lithologic units over such distances, it is rare to encounter truly uninterrupted and continuously accessible exposures of that scale. If there are spatial gaps in exposure, researchers can resort to interpolation, but in doing so, they must assume that extreme variation will not occur at the scale of the gaps presented. If a unique, isolated habitat, such as a patch reef or pinnacle reef, can be fully contained between distant exposures, evidence of that fossil habitat can be completely obliterated or obscured. Examinations of regional-scale heterogeneities will be strongly hindered by exposure limitations, especially in regions with significant plant cover or human alteration. Continuous outcrop exposure may place a practical upper limit upon observations of heterogeneity to changes at the facies scale (~10s of meters and finer), with coarser-scale exceptions possible with exceptional exposure. Methods for characterizing heterogeneity are best designed to take advantage of exposure at these smaller scales.

Fortunately, within an individual outcrop, facies-scale and finer heterogeneities are usually readily accessible. Decimeter- to meter-scale variations in physical habitat, through changes in sediment and framework structures, are typically available in outcrop, with some exceptions owing to patchy preservation. The lower limit of scale available for heterogeneity analysis is that of microfacies and microtopography (≤cm-scale) using petrographic thin-sections, although its applicability may be limited by the increased effort and costs associated with fine-scale sampling across a reef. Although microtopography and small scale heterogeneity are important for recruitment of reef-builders and the development of complex modern reef ecosystems, it is not a scale favorable to field examination. As a result, field-based assessments of heterogeneity, presented here, were designed to take advantage of the scales which outcrop and preservation allow access to—from local, decimeter-scale heterogeneity, to the meter- to the scale of facies.

1.5 A new protocol for measuring habitat heterogeneity in fossil reefs

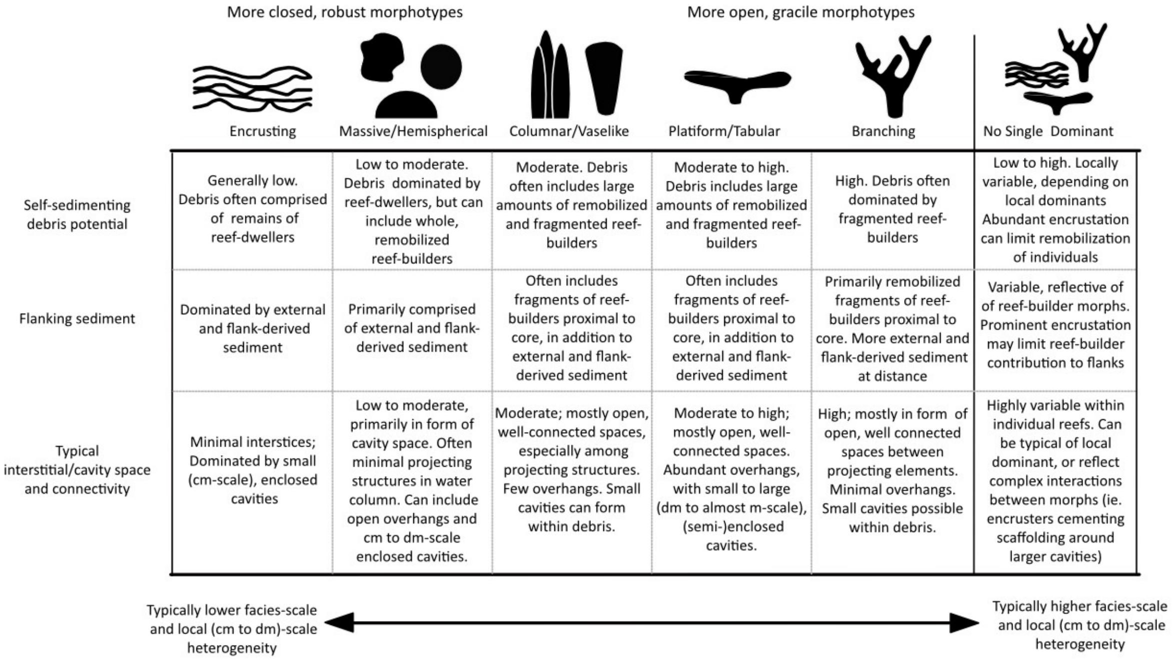
I propose that heterogeneity in fossil reefs can be quantified through five measurable traits: (1) the physical complexity of the reef-builder morphotypes that dominate the reef framework, with morphotype categories ranging from compact, encrusting reef-builders to more open, skeletal branching types; (2) the number of reef-builder morphotypes present; (3) the number of distinct facies present on or around a given reef; (4) the original magnitude of topographic relief above the surrounding sediment; and (5) the local rugosity, created by the variable sizes of, and spatial relationships between, component framework builders. The first four of these traits are semi-quantitative, categorical measures that can be applied to a majority of fossil reefs, even using the level of descriptions typically provided in the literature (see Chapter 3). The final measure, rugosity, is a fully quantitative, continuous measure that can be determined for a fossil reef given adequate exposure and preservation.

1.5.1 Trait 1: Reef-builder morphotype as a measure of local heterogeneity

Local heterogeneity, operationally defined here as decimeter to meter-scale heterogeneity, is a product of the modular structures that collectively build a reef. The morphotype of individual reef-builders influences the types and abundance of cavities and gaps, promotes the production of different kinds of debris, and may strongly influence neighboring sedimentary environments, contributing to facies diversity.

Although there are myriad descriptors for morphology in modern coral research, the morphology of reef-builders, coral or otherwise, are generalizable as one of the five broad morphotypes recognized here (Table 1.1): (1) encrusting, in which growth adheres and follows the contours of a substrate, with no characteristic three-dimensional shape achieved through organismal growth; (2) massive/hemispherical, which encompasses reef-builders with naturally domed growth forms, and irregular growth forms that are not constrained by the contours of a substrate; (3) columnar/vaselike, in which growth is primarily in the vertical direction, and the reef-builder remains unbranched or minimally branched; (4) platiform/tabular, in which growth is primarily in the form of a flat plane or multiple platelike elements, with new growth not limited to encrustation of a substrate; and (5) branching, in which ramiform or branching elements are a defining morphological character.

Table 1.1 : Hypotheses for the influence of dominant reef-builder morphologies on factors underlying local and facies-scale heterogeneity, particularly local sediment potential, contribution to flanking sediment, and the promotion of particular kinds of cavity space. Reef-builder types are broadly categorized into 5 generalized morphologies: 1) encrusting, in which framework builders grow outwards across a surface, consistently adhering to that surface; 2) massive and spheroidal morphologies; 3) columnar and vaselike morphologies, in which typical growth is predominantly vertical; 4) platform and tabular morphologies, in which typical growth is predominantly horizontal, and new growth is unattached to a substrate; and 5) branching morphologies. Dominance, as presented here, is where individual morphologies comprise ≥60% of local framework, by volume. For situations in which there is no single dominant builder morphology, effects on sediment and cavity formation will blend attributes expected from each morphotype present, or it will vary with localized dominance.



	Encrusting	Massive/Hemispherical	Columnar/Vaselike	Platiform/Tabular	Branching	No Single Dominant
Self-sedimenting debris potential	Generally low. Debris often comprised of remains of reef-dwellers	Low to moderate. Debris dominated by reef-dwellers, but can include whole, remobilized reef-builders	Moderate. Debris often includes large amounts of remobilized and fragmented reef-builders	Moderate to high. Debris includes large amounts of remobilized and fragmented reef-builders	High. Debris often dominated by fragmented reef-builders	Low to high. Locally variable, depending on local dominants Abundant encrustation can limit remobilization of individuals
Flanking sediment	Dominated by external and flank-derived sediment	Primarily comprised of external and flank-derived sediment	Often includes fragments of reef-builders proximal to core, in addition to external and flank-derived sediment	Often includes fragments of reef-builders proximal to core, in addition to external and flank-derived sediment	Primarily remobilized fragments of reef-builders proximal to core. More external and flank-derived sediment at distance	Variable, reflective of of reef-builder morphs. Prominent encrustation may limit reef-builder contribution to flanks
Typical interstitial/cavity space and connectivity	Minimal interstices; Dominated by small (cm-scale), enclosed cavities	Low to moderate, primarily in form of cavity space. Often minimal projecting structures in water column. Can include open overhangs and cm to dm-scale enclosed cavities.	Moderate; mostly open, well-connected spaces, especially among projecting structures. Few overhangs. Small cavities can form within debris.	Moderate to high; mostly open, well-connected spaces. Abundant overhangs, with small to large (dm to almost m-scale), (semi-)enclosed cavities.	High; mostly in form of open, well connected spaces between projecting elements. Minimal overhangs. Small cavities possible within debris.	Highly variable within individual reefs. Can be typical of local dominant, or reflect complex interactions between morphs (ie. encrusters cementing scaffolding around larger cavities)

Typically lower facies-scale and local (cm to dm)-scale heterogeneity ◄——► Typically higher facies-scale and local (cm to dm)-scale heterogeneity

Reef-builder morphotypes can influence local reef environments in many ways, summarized in Table 1.1. The effects range between two end-member morphotypes: (1) compact, robust forms such as encrusters and massive morphotypes, and (2) gracile, open skeletal forms that extend outward into the water column, such as branching morphologies. Reef-builders in the former group are less likely to promote large, open-cavity networks than do other reef-builders. They tend to be more robust to physical disturbance, and have relatively low potential for sediment production, or 'self-sedimentation'. Most sediment in reefs of these types is produced either by reef-dwellers, in their remains or through their bioerosive activities, or from organisms occupying the water column above a reef. The lower sediment potential of massive forms limits their impact upon neighboring (flanking) environments so that flanking facies are composed mostly of flank-sourced sediment. As a result, both local and facies-scale heterogeneities are likely to be relatively low in reefs dominated by compact forms compared to reefs built by more open, projecting morphotypes.

Reef-builders with more open skeletal frameworks, such as branching and platiform morphologies, are more likely to create large, open-cavity networks and shelter voids (Riding 1977), and are less robust to physical disturbance because more delicate forms project into the water column (Marshall 2000). Internal sediment is likely derived from reef-builder debris, and there are more opportunities for the development of complex cavities and overhangs within that debris. These reef-builders are also more likely to contribute to neighboring reef facies due to their debris potential. Flanking facies are not limited to flank-sourced sediment, but rather can contain higher concentrations of reef core facies debris proximal to the skeletal reef core. This situation will produce spatial variation in habitat, and perhaps multiple kinds of flanking facies. As a result, reefs built primarily by complex, open skeletal frameworks should exhibit relatively high local- and facies-scale heterogeneity.

1.5.2 Trait 2: Diversity of reef building morphotypes

Of course, many reefs do not have a framework dominated by a single builder morphotype. For cases in which particular reef-builders occupy distinct zones on a reef, local dominance can still be achieved, providing grounds for certain habits of cavity forming and debris production within and adjacent to those zones. If local dominance is not achieved, interaction between the different morphotypes will alter expectations for sedimentation and cavity production. For example, abundant encrusters can cement large debris produced by more open-framework reef-builders. This encrusting may reinforce the complex cavities and structures formed through scaffolding, but may also reduce the potential for production and remobilization of debris. Each distinct morphotype will contribute to reef heterogeneity individually, as described earlier, but in combination will compound heterogeneity further through their interaction. Thus, the number of distinct morphotypes present among reef-builders would directly relate to expected heterogeneity, both at the local, decimeter- to meter-scale, as well as the larger facies-scale.

1.5.3 Trait 3: Facies-variation as a measure of reef heterogeneity

The most direct analogue for habitat heterogeneity at the meter- to tens-of-meters-scale is the differentiation of biosedimentary facies. Reef facies represent local environmental conditions at the time of sediment deposition, and also reflect variation in sediment source— the suite of reef organisms that either create biomineralized skeletons or manipulate and break down skeletal material. Boundaries between facies can be defined along any number of sedimentary or biological characteristics, but the recognition of multiple facies nevertheless represents real ecological or environmental variation (Weinstein et al., 2015). Variation in facies that are distinguished by sedimentological and biological characteristics, and not by diagenetic or other post-burial preservational characteristics, will parallel variation among habitats.

The number of distinct facies in a given area or over a given reef is thus a reasonable metric for heterogeneity at the meter to tens-of-meters scale, and suitable for first-order comparison of heterogeneity between individual reefs. At its coarsest application, facies variation will distinguish traditional reef zones, perhaps even more faithfully than modern reef surveys due to the smoothing of year to year variation in their boundaries (Edinger et al., 2001). It will also often capture subenvironments within reef zones, particularly those defined by clustering of specific reef building organisms. If such subenvironments do not preserve well, facies diversity will be undersampled, thus providing a conservative estimate of original habitat heterogeneity.

The application of facies variation as a means of comparing heterogeneity among reefs of different construction and of different time periods requires careful consideration of bias in preservation. The preservation potential of reefs varies through the Phanerozoic due to increases in bioerosion and durophagous predation (Wood 2011). Although some deterioration of reef preservation is evident within the Paleozoic, related to the rise of durophagous predators (fish) in the Devonian, a much larger decline in preservation can be associated with the evolution of grazing, bulldozing, and boring organisms across the Jurassic and Cretaceous (Wood 2011). In addition, increasing predation of attached epifauna, also in the Mesozoic, should have reduced the ability of reef-dwellers to contribute to the stabilization of reef sediment. Finally, the appearance of live borers and modern reef fish between the Eocene and Miocene dramatically increased bioerosion in reefs, leading to debris-dominated reefs that characterize the latest Cenozoic and present day (B. Morton 1990; Wood 2011). In contrast, erosion in Paleozoic reefs was dominated by abiotic, physical processes, and so habitat conditions would likely preserve with greater fidelity than they do in geologically younger reefs. Thus, comparisons between reefs of different ages should take into account the potential for overrepresentation of facies diversity in Paleozoic reefs.

1.5.4 Trait 4: Original topography above surrounding sediment

Topography above the sea floor allows a reef to affect local water flow, and thus sediment and nutrient distribution, within and around a reef. This feature leads to the development of complex depositional facies, distinguishing forereef and backreef sedimentary environments, and zones proximal and distant from a reef core. Topographic relief also causes variation in hydrodynamic and light conditions, promoting the differentiation of reef habitat based on environmental preferences of reef-builders. This feature contributes to local heterogeneity through the physical relationships between framework elements, but also encourages facies differentiation due to differentiation of preferred habitat among reef-builders. Topographic relief is thus not a direct measure of heterogeneity, but rather is a measure that influences or covaries with the development of heterogeneity at multiple scales.

Topography is difficult to measure directly in the fossil record, as relationship to the surrounding sediment can be exaggerated by differential compaction, and the relationships between neighboring facies can be obscured by limited exposure. Nevertheless, some insight can be gained through those spatial relationships, and via known depth requirements of component organisms, local geopetal infilling of cavities, and both paleoecological and sedimentary indicators of water energy (Wood 1999). Exact topographic relief is not obtainable in most instances, but scale of relief is easier to distinguish. Reefs can be reliably assigned to one of six categories: no distinguishable relief (N), that is ≤ 5 cm-scale microrelief; low relief (L), with vertical growth ≤ 0.5 m; moderate relief (M) of ~1 m, that is within the range of 0.5-2.5 m; and three levels of high relief, at ~5 m scale (H, 2.5 – 7.5 m), ~10 m scale (H2, 7.5 – 25 m), and >25 m (H3). Although many reefs achieve relief far greater than 25 m, the expected imprecision of relief estimates due to limited exposure at large vertical scales makes subdivision beyond this limit questionable.

1.5.5 Trait 5: Potential rugosity measured using stretched-line transects--adapting a Structural Complexity Index (SCI)

Direct measurements of heterogeneity can be obtained through “transect-intercept” methods, where framework elements are identified and mapped along a straight-line transect, and the calculation of a Structural Complexity Index (SCI). In the forest ecology literature, SCI scores habitat heterogeneity based on an assortment of attributes defined by each particular study, often including tree height, nearest-neighbor spacing, tree diameter, species diversity, and various metrics related to foliage cover and stratification, with scores for each attribute either accumulated or averaged together (McElhinny et al. 2005). The calculation of SCI is thus not a standardized practice, and attributes that are included in its calculation will vary based on applicability to different habitats and the valuation of important attributes. In its simplest applications, SCI is a rugosity metric, concerned with the vertical distribution of tree crowns, and the distance between neighboring trees. It is calculated as the ratio produced when the area of the triangle defined by the crowns of three nearest-neighbor trees is compared to the horizontal planar area of the triangle defined by the corresponding three trunks (Zenner and Hibbs 2000; Zenner et al. 2015). Such measures are analogous, but not equivalent, to the (two-dimensional) rugosity measures applied to living reefs (Risk 1972; McCormick 1994), and can be made on fossil reefs given proper vertical exposure. With acknowledgment of the potential biases imparted by time averaging and compaction, an SCI based on framework dimensions and proximity should provide insight into local (decimeter to meter-scale) heterogeneity.

In order to measure SCI, a line transect (10 m) is laid roughly parallel to bedding, starting from a randomly chosen endpoint (Fig 1.1). Across the transect, framework elements that are likely *in situ*, or not significantly removed from their original positions, are identified and measured for length and height within the plane of exposure (Fig 1.1, line 2). The heights and midpoints of framework elements are used to calculate a Structural Complexity Index (SCI), which imitates a calculation of rugosity, using every intercepted framework element. This measurement can be applied to the identified reef mound alone if it is smaller than the transect distance, although this approach limits comparability between transects (Fig 1.1, line 3a), or it can be calculated over a standard distance (10 meters) for uniform comparison (Fig 1.1, line 3b). Finally, the distribution of framework and gap space can be used to characterize relative amounts, size ranges, and clustering of interstitial space within the reef framework in lieu of more thorough 2-dimensional mapping (Fig 1.1, line 4). Although this gap=space metric does not impact the calculation of SCI, it can help inform its interpretation.

Through application to fossil reefs, these measurements would present a maximum potential for topographic complexity of in-life framework. These measures are a maximum representation because the framework elements are removed from their relationship with the sediment, disassociating reef-builder size from true relief and elevating the perceived vertical topography.

Further. any given transect will cut through a time-averaged slice of a reef, and is thus likely to cut through more framework elements than were truly present at any single time point, given continuous colonization of open substrate during reef growth, and vertical compaction after burial. Thus, topographic complexity should be strongly elevated from a rugosity measurement taken on a living surface.

Due to that time averaging, the total amount of gap space between framework elements in an outcrop should be less than what was present in a single time-slice, and the sizes of individual gaps will skew smaller than what might have originally been present. Preservation of original sizes of true (roofed) cavities within this framework should not be significantly biased, and thus should be noted when present. If there are cavities within individual framework elements (coral heads, stromatoporoids), such as through boring activity, these cavities would be ignored when locating the center of intercepted framework elements for the purpose of SCI calculation, but their presence would suggest further complexity than what is recorded through SCI. Such transect measurements should provide a rugosity-like measure that is comparable among fossil reefs of varied ages, and also provide an estimate of framework content within reefs.

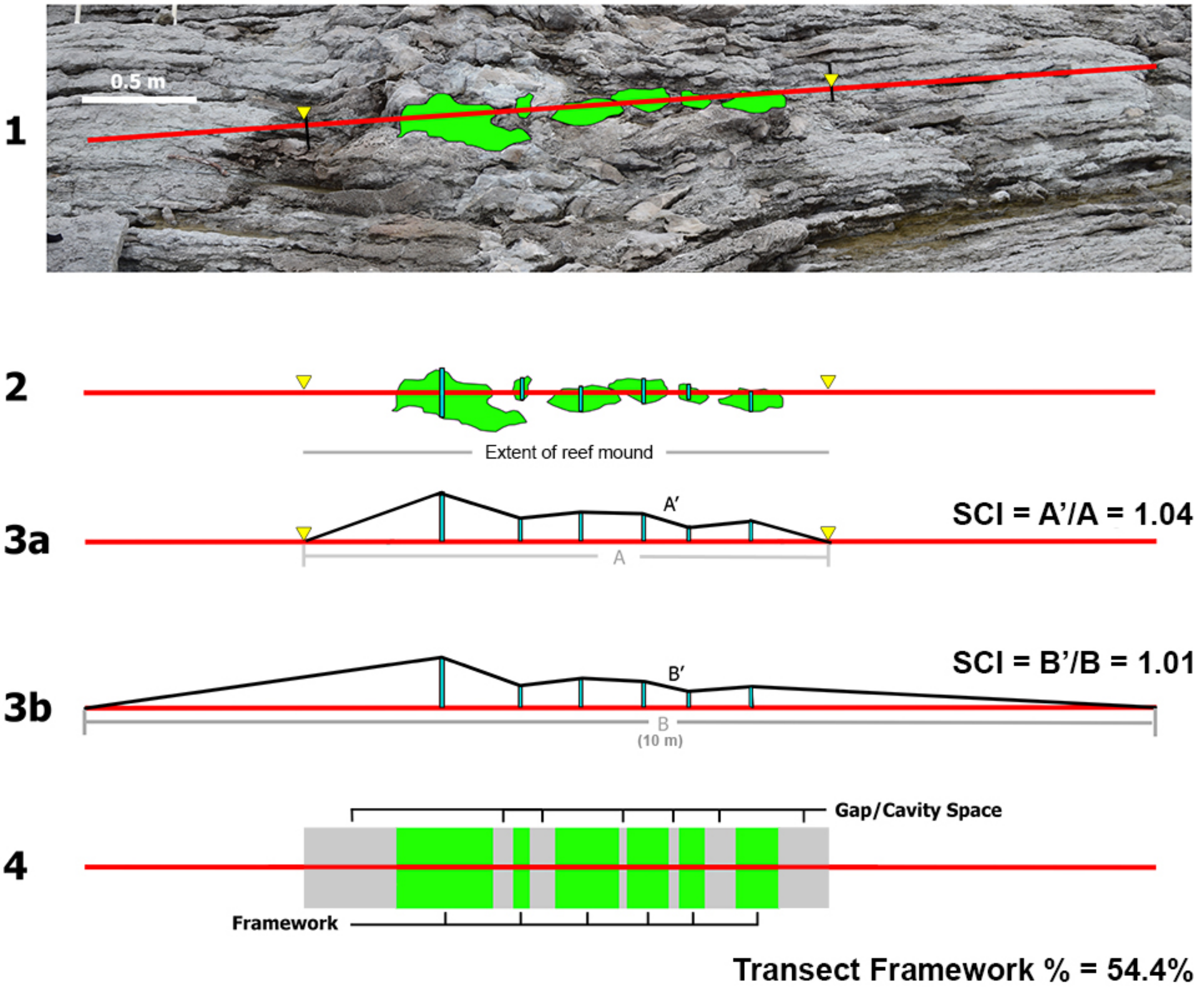


Figure 1.1: Example of transect-intercept measurements, using an Ordovician patch reef (Lourdes Formation, Long Point, Newfoundland). 1-3b: steps in the estimation of rugosity, a 2-dimensional analogue to the Structural Complexity Index used to forestry (see text). For a given stretched-line transect parallel to bedding (1), framework elements intercepted by the transect (2) are projected to rest along a single datum (3); the length of the hull connecting their high-points yields length A′, with rugosity defined as the ratio of A′ to A where A is either the full width of the bioherm (3a) or a standard length such as 10m (3b). The same transect can be used to quantify the relative amounts, size ranges, and clustering of interstitial space within the reef framework; 4). Values of SCI and framework % for this exemplar reef are provided.

1.6 Results: Application of the protocol to Ordovician and Pleistocene case studies

1.6.1 Heterogeneity in Ordovician patch reefs

Upper Ordovician reefs from Laurentia are typically small patch reefs with relatively few distinct reef facies (Webby 2002). The full range of lateral facies is not commonly identified in the literature, with descriptions frequently limited to identification of a single core facies and a single flanking facies. The diversity of reef facies is more usually described along vertical sections. Such upsection changes have been of great interest as potential examples of ecological succession (K. R. Walker and Alberstadt 1975; Copper 1988). Core framework varies widely in construction, with reefs built primarily by stromatoporoids, lithistid sponges, bryozoans, corals, and many different kinds of algae, including receptaculitids. Reefs may contain a combination of these reef-builders, and there is some evidence that patch reefs built through echinoderm-bryozoan affiliation may also exist (Dr. Jackie Wittmer, pers. comm.). Although no single reef can fully represent the variety of bioherms present at this time, we can look to exceptional examples to illustrate general habits.

The patch reefs of the Upper Ordovician (Sandbian Stage) Lourdes Formation on Long Point, Newfoundland offer readily accessible and well-exposed examples of reef-building in the Late Ordovician. The western shoreline of the Long Point peninsula offers a 12-km long exposure of Lourdes Formation limestones, with particular prominence of the Black Duck Member. The Black Duck Member comprises nearly horizontal, thin to medium bedded floatstones and grainstones, punctuated with a series of small patch reefs. These patch reefs are typically less than 3 meters across, and 8 meters thick, but can be up to 12 meters across and 15 meters thick (Batten Hender and Dix 2006). The host rocks and reefs are exposed from the lowest tide line to nearly 10 meters higher on the shoreline, where the unit is unconformably overlain by highly burrowed and locally karstic argillaceous packstones of the Beach Point Member of the Lourdes Formation. The reefs are constructed primarily by the tabulate coral, *Labyrinthites chidlensis*, with rare occurrences of other tabulate corals, *Eofletcheria sp., Aulopora sp. ,* and *Lyopora sp.* (Batten Hender 2007). Non-coral contributors to reef-building include rare stromatoporoids (*Labechia sp.*), demosponges, and algae. The reef mounds may be isolated features, but are often clustered within 5-10m of each other, and are surrounded by skeletal rudstones and grainstones. The reef cores are primarily coral framestone/rudstone, with occasional microbial boundstones.

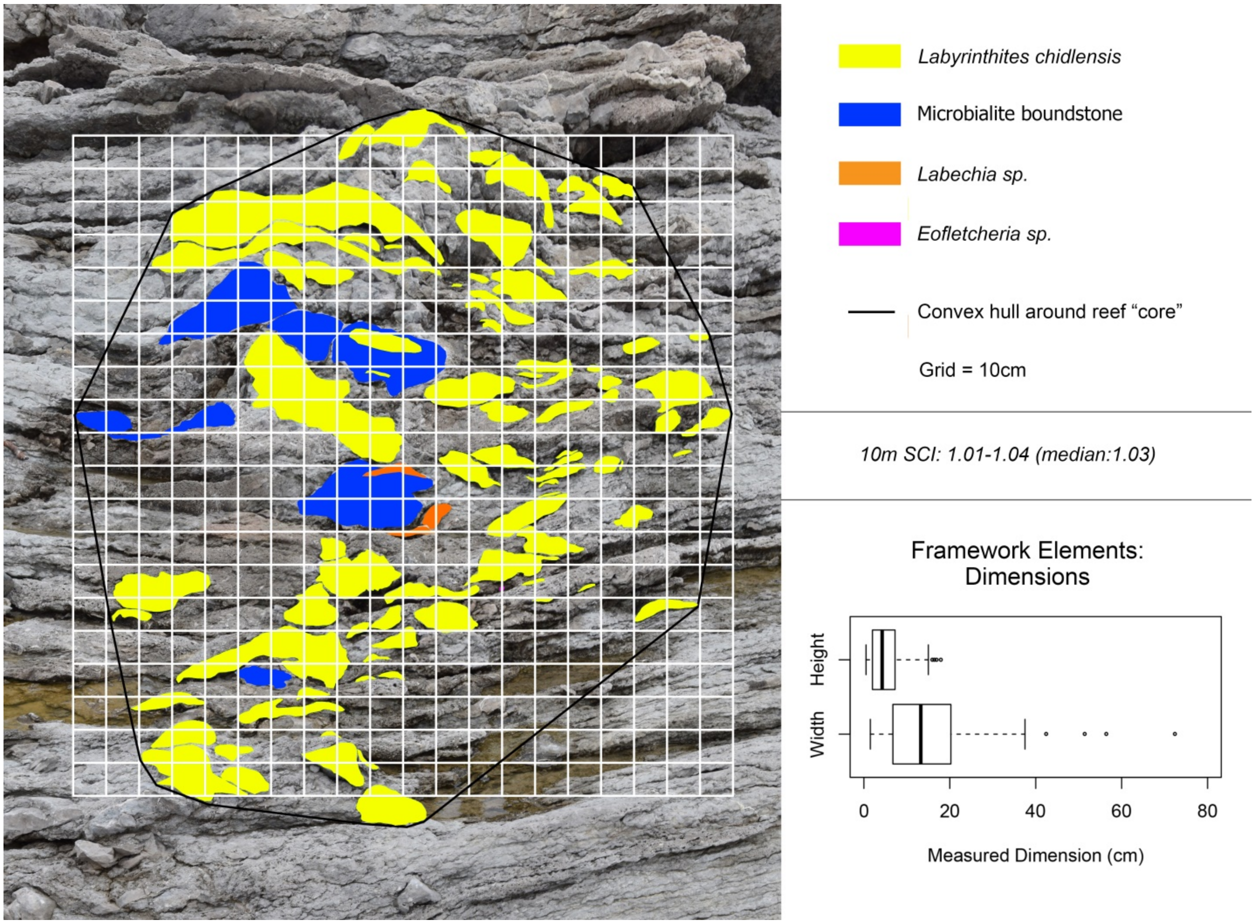


Figure 1.2: Grid map of a Late Ordovician patch reef on Long Point, Port au Port, Newfoundland. Reef-builders are low in faunal diversity, dominated by tabulate coral, *L chidlensis*. Individual corals are typically irregular or hemispherical, and much wider than tall—typically under 25cm wide and 7cm tall. Most are *in situ*, with only scattered individuals overturned. The image is of a sloped surface, which has been scale- and distortion-corrected using three known 0.5m^2 grid sections. Projected grid is 2 x 2 meters, and convex hull covers 3.25m^2. The box plot illustrates the width and height of component framework elements.

Two adjacent patch reefs (-58.879205 °W, 48.709903 °N) were mapped and photographed during the lowest low tide of June 2014. Heterogeneity measures were made across the reefs, and framework elements were mapped with 0.5m x 0.5m PVC grids (Fig 1.2). Percent framework was calculated in ImageJ (Rasband, n.d.) using area measurements for reef-builders and the area of the "reef core", which was operationally defined as a convex hull around identified framework builders. Framework builders make up 30.3% of the 3.25 m^2 area designated as the reef core: 24% as *L.*

chidlensis, 6% as microbial boundstone, and 0.3% as *Labechia sp*. An individual *Eofletcheria sp.* coral was identified from the example section, composing <<0.01% of the fossil reef core.

Individual reef-builders exhibit three of the morphotypes defined above—hemispherical, encrusting, and tabular, with hemispherical being the dominant morphotype. Reef-building corals tend to be low in profile, ranging from 3-76 cm across, and 1-18 cm tall, but typically less than 20 cm across and 7 cm tall (inset plot, Fig 1.2). Hemispherical and tabular morphotypes provided overhangs, either over original void space, or where sediment was eroded out from under them--a feature made evident by the uncommon presence of encrusting bryozoans on the underside of *in situ* coral heads. Millimeter-scale borings (*Trypanites*) can be seen on the tops of coral heads as well, potentially indicative of infrequent hiatal surfaces (Batten Hender 2007). Shelter voids between framework structures are often occupied by microbial boundstone, further suggesting that these reefs provided substantial three-dimensional habitat space, despite their small size.

The vertical relief these patch reefs obtained was probably no more than a meter, and likely less than half a meter for small reefs such as the mapped example presented. There are four distinct facies identifiable in these patch reefs: two core facies—(1) a coral-dominated framestone and (2) a microbial boundstone; (3) a flanking facies of bryozoan and crinoid debris grainstone/packstone facies with minor hardground development; and (4) an interreef, crinoidal, thinly bedded packstone/wackestone. Batten Hender (2007) suggested a fifth facies—a laminated interreef mudstone to packstone-- that also infilled shelter voids. This laminated facies was not observed in the reefs mapped herein, but may be more prevalent in larger reefs in the Long Point Formation observed by Batten Hender and colleagues.

Structural Complexity Index was calculated from 10 m partitions of a 20 m transect, repeated 20 times with a lateral shift of 0.5 m each time in order to ascertain the variation expected from the choice of starting point. The median SCI was 1.03, with a minimum and maximum of 1.01 and 1.04. If SCI were calculated from the full 20 m transect, the measure would be 1.02, very similar to results obtained with 10 subsections, suggesting that 10 m is a sufficient distance for quantifying SCI along this transect. The low SCI measures suggest very little potential rugosity at that scale, driven by relatively low-profile reef-builders (maximum height: 0.24 m). If a transect is limited to a 1.86 m stretch of just the reef core, the corresponding measurement is 1.20, which is the equivalent measurement one would get with a singular 0.7 m-tall structure in that same length.

1.6.2 Heterogeneity in a Pleistocene barrier reef

Applying this method to modern-style reefs requires more thorough assessment of potential biases because the nature of reef preservation is dramatically different from Paleozoic analogues. Buried and preserved modern reefs tend to be debris-dominated due to the prevalence of more fragile reef-builders (i.e. *Acropora*), and high levels of biological and physical disturbance (Hubbard *et al*., 1998). Rapid turnover and high growth rate of branching corals also result in over representation of such corals over their more robust counterparts**.** The abundance of debris reduces the apparent amount of framework, and reduces the size of existing framework such that SCI measurements would be greatly understated, relative to original topography. The appeal to such measures should be inferred as a minimum potential SCI, even if time averaging allows for more framework elements encountered per transect than existed at one time. Variation in the sizes of neighboring elements is what most strongly influences SCI, and thus fragmentation and (bio)erosion will ultimately reduce that variation.

The Pleistocene reef at Windley Key Fossil Reef State Park, in Windley Key, Florida (-80.595783 °W, 24.950724 °N), is associated with a former barrier reef complex, and is composed primarily of *Orbicella* [formerly *Montastrea*] *annularis*, *Montastrea cavernosa*, *Porites asteroides, P. porites*, *Diploria strigosa and D. labyrinthiformes* (Hoffmeister et al. 1964; S. M. Stanley 1966). The reef is exposed along vertical quarry walls, both parallel and perpendicular to paleoshoreline, providing ideal exposures for direct measurement of local reef structure in cross-section. The exposure has been interpreted as part of a larger reef tract, although it is unclear if it is the seaward reef tract, or a lagoonal patch reef tract behind the seaward edge, with debate hinging on whether the absence of *Acropora palmata* is due to unsuitable environmental setting, or a true absence of *A. palmata* from the Keys at this time (Precht and Miller 2007). Whatever the case, the exposure represents a framework core facies within the larger reef, dominated by massive reef-builders that built upward, tracking the accumulation of reefal debris (personal observation).

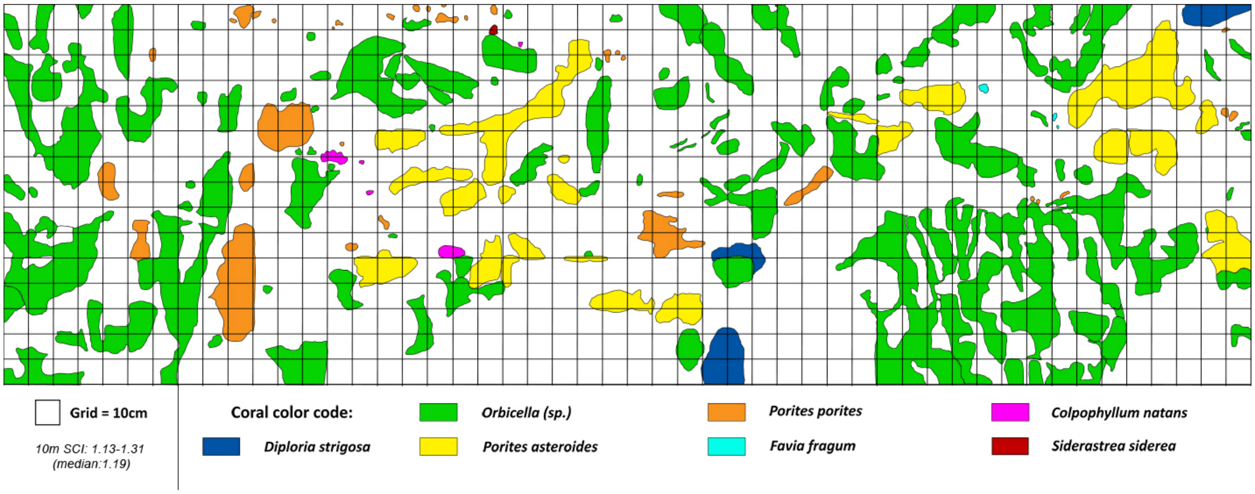


Figure 1.3: Section of mapped exposure of the Late Pleistocene reef at Windley Key Fossil Reef State Park. The 5m x 1.5m grid section here is from the coral-dense north wall of the quarry (24.9507°N, -80.5958°W), and features prominent, massively lobed *Orbicella* (formerly *Montastrea*), and large *Porites* heads, in addition to minor *Diploria*, *Colpophyllum*, *Favia*, and *Siderastrea*. Corals are typically irregular and massive, although columnar, branching, and tabular morphologies are also present, in addition to encrusting coralline algae.

Five twenty-meter horizontal transects were established across along-strike exposures of the reef (Appendix A). Starting points were chosen arbitrarily at three different exposures by blind throwing of a pebble towards the quarry wall. In addition, a 20 m x 1.5 m section was mapped in detail using half-meter grid squares to better assess the composition and two-dimensional structure of the reef, and to digitally recreate field measurements (Fig 1.3).

The exposure of the Windley Key Fossil Reef primarily reveals construction by the massive/hemispheroidal morphotype. Common *Orbicella, Porites*, and *Diploria* present as irregular, massive (and massively lobed) morphologies, with a minor component of columnar, platiform, and branching types. Encrusting morphologies are almost certainly present in the form of encrusting and binding coralline algae, although they are not primary reef-builders. The variety of reef-builder sizes is large, with recorded *in situ* corals ranging from 2 cm-tall recruits, to long-established colonies exceeding one meter in both height and width.

The facies diversity of this particular reef is unclear because its size substantially exceeds the available outcrop. The outcropping on Windley Key is a core facies of robust, framework corals, without strong zonation along sedimentological or faunal grounds across the exposure. Given the nature of modern reefs of the Keys, this barrier reef complex probably contained far greater facies diversity than can be identified from outcrop, owing in particular to the lack of exposure perpendicular to reef strike, which would reveal onshore-offshore differentiation of traditional reef facies.

SCI was measured from five 20-meter transects, three on the more coral-dense northern wall of the younger, west quarry, and two on the more coral-sparse southern wall. Ten-meter SCI measures were repeated at half-meter increments along each 20 m transect to assess potential variation due to starting placement. The median measured SCIs from 10 m subsections along the northern wall were 1.27 (range: 1.23-1.43), 1.19 (1.13-1.31), and 1.15 (1.09-1.30). The southern wall presented more modest SCI measurements of 1.14 (1.07-1.24), and 1.06 (1.02-1.10). If SCI were measured with full 20 m transects, values for those five sites would be, respectively, 1.24, 1.16, 1.16, 1.09, and 1.07—within the observed range of the 10 m measurements suggesting that 10 m measures are sufficient even for reefs built of larger framework elements. This expanded range of SCI in the Windley Key reef, in comparison to its Ordovician counterpart, is due primarily to that wide range of reef-builder size, with rapid fluctuations between heights of neighboring corals along transect along the northern wall. The density of reef –building corals is not especially high, with mapped areas of the coral-dense north wall containing 31.1% recognizable coral framework elements when viewed in outcrop (21.7% *Orbicella annularis*.; 5.8% *Porites asteroides;* 2.4% *P. porites*; 1.0% *Diploria strigosa*; 0.1% *Colpophyllum natans*; <0.1% *Siderastrea siderea* and *Favia fragum*), but the size range of components is great (1.17 x 1.47 m, to 0.02 x 0.06 m among corals of the first 20 m transect). This measurement is based on an overrepresentation of framework elements as well, because the corals are frequently riddled with boreholes from bioerosive reef-dwellers, reducing the framework to sediment even within the preserved outlines of individual corals.

1.7 Discussion

1.7.1 Limitations: When can and can't these measurements be made?

Where outcrop exposure is limited, not all types of heterogeneity measurements can be made. In the poorest exposures, all that may be identifiable are the broad morphological categories of reef-builders present, and a sampling of the facies present. In good exposures of well-preserved bioherms, transect measurements can be employed to describe the distribution of framework elements, and in suitably large exposures, the SCI can be calculated as well. SCI can be difficult to obtain if the distinct heights of framework elements are obscured by irregular morphologies. For example, boundaries of densely encrusting stromatoporoids may be difficult to identify without a microscope, and framework within an algal or bryozoan reef may not be resolvable to the scale of individual organism, but rather to the structures produced in accumulation. SCI, then, is most tenable in buildups composed of modular elements—individual organisms with distinct boundaries discernable in outcrop.

Ability to make these measurements also depends on preservation. In debris-dominated buildups, framework-builders will rarely be in life position. Also, in highly altered limestones, original textures may be obscured through large parts of a given exposure. As with the case of poor exposure, these situations may limit measurements to identification of reef-builder morphologies, and facies diversity.

1.7.2 Challenges in comparing Paleozoic reefs

The patch reefs at Long Point, Newfoundland offer an exceptional opportunity for detailed mapping and the application of each proposed heterogeneity metric, but the lack of ideal exposure, poor preservation, and nature of reef-builders in other sites will limit application of these metrics. Nevertheless, most reefs will present opportunities to identify and assess heterogeneity with one or more metrics, and thus provide useful points for comparison. Application of these methods on a selection of Middle Paleozoic reefs is summarized in Table 1.2.

Table 1.2: Potential for assessing heterogeneity in select Paleozoic reefs, and the Late Pleistocene reef of Windley Key, each examined in the field by the author. Measurement or category designation in parentheses, as explained in text. Whether quantitative or categorical, each metric has limitations due to exposure, access, preservation, builder morphotype, or scale. Very rarely will a fossil reef possess all necessary qualities for the proposed assessment. Only the Long Point bioherms mentioned above qualify, among the fossil reef sites listed.

Reef Site	Age	Potential for Field Measurement				Potential for detailed mapping
		Morphotypes	Facies	10-m SCI	Relief	
Green Head, Newfoundland (Pratt and James 1989)	Early Ordovician	Low; dependent on preservation and thin sections for identification. (Encrusting dominant; unclear inclusion of other morphotypes based on field observation)	Moderate; requires extensive microfacies analysis. (3 observed)	Very Low; dominant microbial component; reef-builders lack discrete morphologies. (NA)	Low; unclear relationship with neighboring sediment; limited to internal sediment cues. (L)	Low; variable preservation across reef
Isle La Motte, Vermont (Pitcher 1964)	Late Ordovician	High; well preserved, extensive exposure across horizontal plane, local vertical exposure. (Encrusting dominant, with massive/hemispherical, and columnar morphotypes)	High; well preserved, although limited in exposure. (3 observed in Crown Point Fm; 2 in Day Point Fm; and 2 in Valcour Fm)	Low; facies specific measurement possible in limited vertical exposures; unclear boundaries between dominant encrusting stromatoporoids in Crown Point Fm. (NA)	Moderate; limited by exposure. Local topography visible. Large-scale topography not observable. (L)	Moderate; planar exposure limited by lichen and turf coverage; uncommon and laterally restricted vertical exposure of particular facies
Chicoutimi, Quebec (Harland, et al, 1987)	Late Ordovician	High; well preserved, extensive exposure along bedding plane. (Massive/hemispherical dominant, with encrusting morphotypes	Moderate; well preserved, although reef interior or vertical changes in facies inaccessible. (2 observed)	Low; no vertical exposure. (NA)	High; affected by erosion, but likely no higher than tallest builder. (L)	Very high only along bedding plane; there is no vertical exposure

Table 1.2, continued…

Long Point, Newfoundland (Batten Hender and Dix 2006)	Late Ordovician	Very high; excellent exposure and preservation. (Massive/hemispherical dominant, encrusting, tabular, and branching morphotypes	Very high; excellent exposure and preservation. (3 observed)	Very high; extensive vertical and lateral exposure. (1.01-1.04)	Very High; clear relationships between reef-builders and surrounding/ Internal sediments. (L)	Very High; excellent exposure and preservation
Port aux Choix, Newfoundland (James and Klappa 1989)	Middle Ordovician	High; locally-poor preservation conditions, but extensive exposure. (Encrusting, massive/hemispherical, columnar, and tabular morphotypes)	Moderate; extensive exposure of m-scale reefs. Internal facies difficult to identify in outcrop, but reefs small enough for comprehensive thin section analysis. (3 observed)	Low; extensive exposure, but framework elements difficult to discern from matrix when viewed in outcrop due to preservation. (NA)	Moderate; small mounds distinct from surrounding sediment. Relief likely limited to size of indiv. reef-builders. Internal structures invisible. (L)	Very low for internal reef structures; High for distribution of patch reefs across extensive lateral exposure
LeRoy, New York (Lindemann 1989)	Early Devonian	High; excellent exposure and preservation; less robust morphologies inferred from debris. (Branching dominant, with massive/hemispherical, columnar, tabular, and encrusting morphotypes)	Moderate; excellent exposure in LeRoy quarry, although the reef continues beyond the exposed area; likely under-sampled. (7, from Lindemann 1989)	Moderate/Low; reef is debris-dominated, and more complex elements are broken down; SCI will strongly undersample framework; eroding quarry walls leaves significant gaps. (NA)	Very low; exposure is insufficient for reef size; local topography not preserved in debris; possible to assess indirectly with stratigraphic relationships. (M)	High; Locally possible due to excellent preservation and vertical exposure; local gaps due to erosion of quarry walls
Formosa, Ontario (Fagerstrom 1961)	Early Devonian	High; locally poor preservation, but extensive local exposure of different reef facies. (Tabular dominant, with massive/hemispherical, branching and encrusting morphotypes)	High; good local exposure of different facies, although km-scale gaps between outcrops. (4 observed)	Moderate/Low; good lateral exposure allows for measuring individual reef facies, although patchy recrystallization blows out boundaries between framework and matrix. (NA)	Moderate/Low; exposure insufficient for the scale of reef; local topography observable in relationship between large reef-builders and surrounding sediment. (M)	High; Extensive local exposure—facies specific mapping possible, with gaps for recrystallized portions and weathered cavities.
Windley Key, Florida (S. M. Stanley 1966)	Late Pleistocene	High; abundant, massive corals *in situ*, while more delicate morphotypes known from debris; significant bioerosion affects preservation potential. (Massive/hemispherical, branching, columnar, tabular, and encrusting morphotypes present)	Moderate; excellent exposure, but not large enough to examine facies changes onshore or offshore from the reef crest (NA)	Very high; excellent horizontal exposure and access; reef elements are large enough to occasionally be truncated by the vertical limits of the outcrop (1.02-1.43)	Low; modern reefs can inform depth of the preserved community, but there is no avenue to assess relief above surrounding nonreef environments given the exposure. (NA)	Very high; excellent exposure and access. Extensive boring, alteration, and encrustation can obscure exposed corals, but they remain identifiable

Ultimately, preservation and exposure are inconsistent between the listed Middle Paleozoic reefs. Identification of reef-builder morphotypes and facies diversity can be done fairly consistently, but SCI, however, can be applied only where conditions allow for sufficient lateral exposure and clear preservation of framework structures. This metric cannot be applied to microbe-dominated reefs or reefs with poor preservation, and debris-dominated reefs present a challenge in interpretation. For such reefs, heterogeneity is most consistently inferred from reef-builders and facies diversity.

1.7.3 Challenges in comparing reefs between time periods

These concerns over preservation and exposure hold for comparison between Paleozoic reefs just as they do for comparison with Mesozoic and Cenozoic reefs. However, reefs of similar time intervals generally exhibit a level of consistency in their construction, and the identities of their reef-builders that allows for easier comparison, providing exposure and preservation are similar. When comparing between disparate time intervals such as the Ordovician and Pleistocene, that assumption does not apply. The development of more debris-dominated reefs in the Cenozoic should cause relative underrepresentation of *in situ* reef framework in the Pleistocene, despite the inclusion of overlapping cohorts. Even with this bias, the heterogeneity of the Pleistocene reef example in Windley Key is distinctly higher than its Paleozoic counterparts as measured by reef-builder morphotypes and SCI, despite similar framework abundances in the studied outcrops. Greater heterogeneity is mostly a product of the larger reef size of the Pleistocene example, with more framework elements encountered in each transect. Where corals were sparse in the Windley Key reef (Transects 4 and 5; Appendix A), SCI was still high due to the larger sizes of the reef-builders, themselves. Thus, although caution is still needed regarding over preservation and exposure, differences in preservation do not prevent reasonable comparison.

1.7.4 Potential utility across non-analogous reefs and adaptation to nonreef framework carbonates

Heterogeneity measurements can be deeply useful for paleoenvironmental reconstruction and in understanding paleoecology, even outside the reef system. The repurposing of widely utilized observations and measurements, as well as the application of new methods to understand heterogeneity, can and should be applied to reefs of different builder types. They can also be applied to nonreef framework carbonates so long as differences in preservation are understood. Nonreef communities with substantial framework producers, such as coral and skeletal sponges, can offer very complex environments for use by the local community, but the lack of a cemented framework will permit greater post-burial compaction of sediment. Framework elements of the original environment will be subject to a greater level of time averaging when viewed in outcrop, and proximity in outcrop can closely resemble a true framestone without close examination of displacement of matrix material.

Such environmental settings are likely to exhibit SCI measurements similar to reef environments, though, due to the presence of similar reef-builders and the measurement's ignorance of true topography. This measurement could still legitimately indicate locally complex environments, but the absence of facies-scale heterogeneity would differentiate them from reefal counterparts.

1.8 Conclusions

Habitat heterogeneity is a vital factor for understanding modern reef communities, but is often ignored in fossil assemblages. Reefs are deeply complicated systems in life, and that complexity can be compounded in ancient examples by erosion, burial, and diagenesis. Despite that inherent complexity, there is still information we can obtain from fossil reefs that can aid our interpretations of heterogeneity. Although imperfect, the application of qualitative and quantitative methods proposed here can improve our understanding of the heterogeneity of fossil reef environments and better inform our paleoecological interpretations of such buildups. It can provide a starting foundation for direct comparison of individual reefs throughout the fossil record.

Reef-builder morphotypes and facies diversity data are readily accessible from the literature and from outcrop, and should be considered in a quantitative fashion in tracing the development of complex reef systems. The Structural Complexity Index described herein can be simply obtained in the field, and more such measurements are needed to explore sensitivity of this metric in reefs of more varied construction, including those dominated by branching reef-builder morphotypes, or built by organisms other than corals and stromatoporoids. Applying even simple, metrics to environments as complex as reefs can be remarkably useful in assessing heterogeneity in the fossil record. Collection of these data, in addition to the development of more sophisticated measures, should be strongly encouraged in order to establish a deeper understanding of habitat heterogeneity in deep time.

CHAPTER 2

FACIES DEVELOPMENT AND INCREASING HABITAT HETEROGENEITY IN MIDDLE ORDOVICIAN TO LATE DEVONIAN REEFS: A RECAPITULATION OF INDIVIDUAL REEF-BUILDING DYNAMICS

2.1 Abstract

Increasing biological diversity within Laurentian reefs from the Middle Ordovician to the Late Devonian is long-assumed to have coincided with an increase in habitat heterogeneity. Using data from 155 reefs in this interval, I test for change in three key factors that should contribute to the physical complexity of reefs: (1) the number and types of reef-builder morphotypes present, (2) the number of distinct reef facies present, and (3) topographic relief. I find that reefs transitioned from typically low-relief, encruster-dominated buildups with low facies diversity in the Late Ordovician, to higher-relief structures with higher diversity of both reef-building morphotypes and facies over the rest of the middle Paleozoic. As a consequence, habitat heterogeneity would have increased both at the local scale (i.e. more complex cavities, overhangs, attachment surfaces) and at the facies scale (subdivision of reef into distinct zones, more biological differentiation within core and debris facies). Over geologic time, the increase in facies diversity per reef recapitulated the increase in facies diversity that an individual reef would acquire through autogenic sedimentary dynamics, which includes both vertical facies differentiation by ecological succession and lateral facies arising from topographic relief and its ecologic correlates.

2.2 Introduction

The middle Paleozoic can be considered the ‘heyday’ of Paleozoic reef building. During this interval when continents were flooded by warm seas, reefs – defined here as biologically-constructed or -mediated buildups that achieve significant local topography above the surrounding seafloor –

achieved their greatest latitudinal range, abundance, and global volume of the Era (Kiessling et al 1999; Kiessling 2002;2005). The global reef system of the Silurian through Late Devonian (Frasnian) was dominated by frame-building corals and stromatoporoids – a reef-building fauna that emerged from the earliest metazoan reefs of the Middle Ordovician. Although global reef volume declined at the Ordovician/Silurian boundary, the style of reef-building and the identities of dominant reef builders changed very little; most subfamilies and genera of corals and stromatoporoids within early Silurian reefs were also present in Late Ordovician reefs (Copper 1994). Given the consistency in the faunal groups building reefs, this Middle Ordovician to Late Devonian interval has been identified as a distinct period of global reef-building (Wood 1999; Kiessling et al 1999; James and Bourque 1992).

Despite consistency in reef-building fauna, reefs became far more species-rich across this interval (Kiessling 2009). While detailed studies of large Ordovician reefs commonly note <40 invertebrate taxa (e.g., Chazy reef at Isle La Motte by Kapp 1975, others), similarly thorough studies of Devonian reefs can include >125 taxa (Fagerstrom 1961). This rise in taxonomic richness might be related to the evolution of new reef-specific guilds and/or diversification within existing reef-specific higher taxa, but surveys of Silurian reefs suggest that the gain in richness instead results from high redundancy within already-established guilds and greater species packing without the creation or proliferation of a reef-specific fauna (Watkins 1993; 1997; 2000).Reefal taxonomic diversity is high, but selected from the same species pool as the surrounding nonreef environments.

Greater species packing can be achieved through increased vertical tiering of fauna above or below the sediment-water interface (Ausich and Bottjer 1985). However, increased biodiversity across individual reefs might also derive from a third variable, namely a concomitant rise in spatially variable habitat, that is, “habitat heterogeneity”, allowing for finer partitioning of space. Modern studies suggest that habitat heterogeneity is fundamentally linked to higher biodiversity in reef communities (Roberts and Ormond 1987; Wilson et al 2007). Previous workers have also suggested that facies-scale heterogeneity increased between the Ordovician and Devonian, due to increasing reef size and debris potential (Kiessling et al 2000; Kiessling 2002). Nonetheless, habitat heterogeneity has not yet been measured across fossil reef environments, a critical step to testing its possible role in the long-recognized rise in taxonomic richness.

Heterogeneity can be difficult to measure consistently among fossil reefs owing to differences in exposure and preservation, but several aspects of heterogeneity can readily be observed, even under poor conditions. Here, I focus on three measurable factors contributing to habitat heterogeneity within reefs: (1) the number and types of reef-builder morphologies present, (2) the number of distinct reef-associated facies, and (3) the scale of topographic relief that the reef exhibited in life, distinct from its total preserved thickness. These factors are commonly described in published reports of fossil reefs, by both paleontologists and geologists. Combined, such data provide fertile ground for exploring how within-reef heterogeneity has changed over the critical, middle Paleozoic interval of reef development, and for assessing its role in driving the taxonomic diversification of reef systems. For example, the number of reef-builder morphotypes and the dominance of complex forms (e.g., vertical, branching) implies the presence of complex gaps, cavities, and surfaces for attachment within reefs, reflecting sub-meter-scale habitat heterogeneity. Distinct reef facies -- operationally defined as meter-scale-and-larger subdivisions of a buildup that are distinguished by unique depositional fabric, grain size, and/or characteristic faunal composition -- directly relate to similarly-scaled biological and physical environments present in the once-living reef (Weinstein et al 2015). In addition, the robustness of different reef-builder morphologies will influence the production of sediment by fragmentation, creating further heterogeneity via the creation of distinct sedimentary environments. Finally, topographic relief will influence the range of hydrodynamic and/or light environments available across a reef, potentially affecting both the identity of reef builders and distribution of sedimentary facies.

Here, I combine new field observations with published data in order to test for temporal trends in spatial heterogeneity at local (patch) and facies (landscape) scales over the Middle-

Ordovician to Late Devonian history of reefs in Laurentia. What role did changes in the morphology and taxonomy of framework producers play in the increase in reef-facies diversity observed over this interval? Were these changes associated with new core facies and/or the development of novel flanking facies? How did relief influence facies diversity, and how distinct was that influence from that of reef size more broadly (e.g., preserved thickness and breadth)? To what extent do changes in habitat heterogeneity over geologic time recapitulate those observed during the development of an individual reef through such processes as ecologic succession, taphonomic feedback, and other biological modification of the local sedimentary environment (autogenic sedimentary dynamics, *sensu* Olszewski 2016)?

2.3 Background

2.3.1 Autogenic sedimentary dynamics and spatial contingency

Between the initial establishment, or 'pioneer' stage, of a reef and its ultimate, 'climax' stage, we can expect changes in the number and identities of distinct reef facies. Their accumulation is an expression of the autogenic sedimentary dynamics of the reef system, that is, how organisms change their local sedimentary environment due to intrinsic biological feedback (Olszewski 2016). Examples include (1) the stabilization of loose sediment by encrusters, which promotes colonization by other epifaunal colonists, and (2) the expansion of coral-rich debris facies through the introduction of fragile, branching corals, creating habitat for organisms preferring or requiring physical cavities. The new set of fauna or sediment producers facilitated by the first set creates, in turn, yet newer environmental conditions, and the process continues. Such facilitation of novel colonists and influence on physical environmental conditions underlies autogenic ecological succession and will manifest as up-section changes in facies (Copper 1988). Along with such factors as regional physical oceanography and topography, including proximity to shore, autogenic dynamics also promote lateral variation in depositional facies, a phenomenon widely recognized in living systems as reef zonation (Goreau 1959; Stoddart 1969; Davidson-Arnott 2010).

Some differentiation of reef facies can be expected from increased relief alone, although facies also become differentiated by the effects of particular reef builders in conjunction with geographic and bathymetric context. Initially, a reef will have a single facies composed of its particular builders. As topographic relief increases, it can affect local hydrodynamics and accumulate flanking sediment, either from neighboring sediment or from self-sedimentation of reefal debris. Further increases of relief can lead to subdivision of flanking deposits in terms of grain size and sorting, due to both proximity to the reef core and any gradient in water energy related to change in bathymetry. For example, flanking sediment may contain a proximal coral-rich packstone facies and a more distal, pelmatazoan-rich packstone/wackestone facies, which may grade further seaward into deeper forereef facies, landward into backreef lagoonal facies, or along strike into inter-reef or channel facies. Further subdivisions along the flank or within the core may occur through the preferences of reef inhabitants for particular environments or through competitive exclusion from some habitats. Over time, environmental subdivisions can be expected to arise from the ways in which those organisms alter environmental conditions, perhaps through their vertical growth, their stabilizing effects, or the type of sediment they produce.

Further facies diversification depends on large-scale reef architecture—a product of how relief, developed by organisms and interacting with water depth and lateral extent, affects hydrodynamics at a more regional scale. As shallow reef mounds grow larger, they are more likely to connect and form barrier and fringing reefs. The maturation into complex reef architectures produces many new reef zones, driven by changes in local hydrodynamics. Forereef and backreef zones become more sharply differentiated than what is possible with simple reef mounds, and the creation of novel lagoonal and reef flat facies becomes more likely. These environments can be further subdivided on sedimentological and faunal grounds. There is no minimum amount of relief needed to achieve such milestones, as they are contingent upon local water energy, depth, and proximity to shore or to other reef mounds.

2.4 Methods

Data on the reef-builder composition, facies-level heterogeneity, and original topography of reefs were derived from original field observations on 25 reefs and published descriptions of an additional 130 reefs, spanning the Middle Ordovician through the Frasnian stage of the Late Devonian (Appendix B1).

A reef, as the term is used here, is a biologically-constructed or -mediated buildup that is sufficiently rigid to achieve significant local topography above the surrounding seafloor given the ambient hydrodynamic regime. This definition omits the common condition of wave-resistance in order to reflect a modern understanding of reefs, which encompasses deep-water rather than solely shallow-water phenomena (Roberts et al 2006; Hovland 2008). In addition, this definition excludes wave- and current-generated buildups composed entirely of loose skeletal debris, even though their accretion may be promoted by preferential recolonization.

Data collected for each reef includes the identity and morphology of reef builders, the number and types of facies present, estimates of vertical relief in life, and overall dimensions as preserved in the rock record. In the literature, these types of data are described at varying levels of detail and with inconsistent terminology, arising from the diverse geological and paleobiological objectives of authors. For example, although biologists and paleobiologists employ highly specific terminology to describe growth forms, particularly of corals, non-specialists often use familiar shapes (i.e., ‘bowl’, ‘stick’). Language for facies descriptions also varies depending on the scale of observation (e.g. thin section sampling, hand samples) and on the choice of classification system (e.g., Embry and Klovan 1971; Folk 1959). Microfacies classifications that rely on diagenetic as well as sedimentary features likely over-split reefs compared to the environmental variability important to living organisms. Finally, reported reef dimensions and topographic relief are often order-of magnitude estimates from indirect evidence, such as variation in water depth inferred from variation in sedimentary fabric and species composition thought to signify variation in wave energy and light levels. This inconsistency in description hinders direct comparisons among reef descriptions by different authors. Here, I resolved such issues by simplifying over-split facies descriptions to reflect in-life environmental variation, and by using categorical classification for reef-builder morphologies and relief attributions (for more detail, see previous chapter).

2.4.1 Reef builder morphotypes

Reef builders are defined here as the taxa that produce rigid biological structures that fundamentally contribute to the elevation of a reef above the surrounding seafloor. The term encompasses the traditional reef guilds of “constructor”, “binder”, and “baffler”, as members of each guild can be considered rigid elements that contribute to the accretion of a given reef (Fagerstrom 1991). Reef builders were categorized into five general morphotypes: encrusting, massive, columnar/vaselike, tabular/platelike, and branching (Fig. 2.1; Appendix B). Although stromatactoid mud did not exhibit a distinct growth morphology, it frequently contributed to the rigid cores of middle Paleozoic biogenic buildups, and so was included in my analyses as a sixth category of reef-builder where present, equivalent to the five other morphotypes in Figure 2.1.

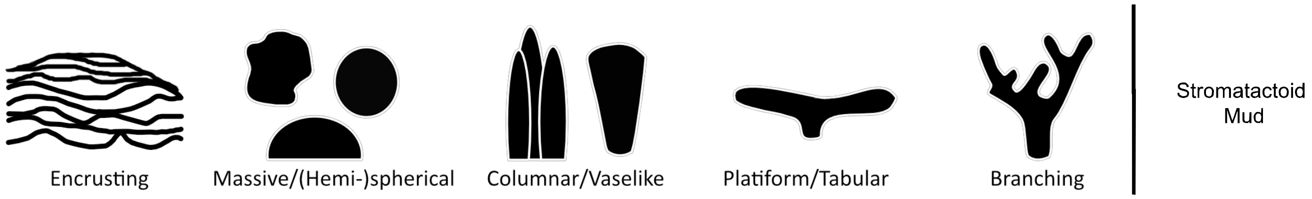


Figure 2.1: Five reef-builder morphotypes used to describe reef builders. Stromatactoid mud, although not a distinct reef-builder morphology, is treated as a morphotype -equivalent when identified as a major contributor to the three-dimensional reef structure

For literature-derived data, the original author's morphological description was taken *prima facie*, and I assigned it to one of the five morphotypes recognized here. If the author's morphologic description referred to the preserved form, and that description was inconsistent with the form assumed in life, then I assigned it to a corrected category. For example, a "columnar" stromatoporoid would be better characterized as hemispherical if that was the form of its growth surface during life, with the columnar form created only by persistent upward growth of the colony in response to an aggrading seafloor. In instances when reef-building species were listed without morphological description, I avoided categorization unless a single, characteristic form could be assigned to that species or genus using the *Treatise on Invertebrate Paleontology* as an authority (Selden 2015; Hill 1981).

Morphologies that fell between two categories were assigned to the more complex form, where branching is judged to be more complex than columnar or tabular forms, which are in turn more complex than massive, which is more complex than encrusting. Thus a coral with delicately branching plates would be assigned to the branching category, and one with digitate growth extending from an encrusting base would be assigned to the columnar category. Non-discrete frame builders, such as stromatolites and thrombolites, were classified as encrusting unless a characteristic macrostructure (decimeter scale or larger) was explicitly described (e.g., "columnar branching thrombolite"). Reef-builder data could be obtained from 134 of 155 examined reefs.

2.4.2 Facies description and facies diversity

For this study, facies were distinguished on the basis of sedimentological and biological features that could be observed at the scales of hand samples and outcrops, such as fabric (e.g., "boundstone", "rudstone"), grain size and sorting, major taxa, and spatial context (e.g. relationship to reef core). Where taken from the literature, facies were defined and counted as the author(s) originally presented them. The only exceptions were facies subdivisions based on microfacies work:

these characterizations were simplified as explained above, ignoring facies that were distinguished on the basis of diagenesis and preservation alone. Although facies descriptions vary widely in the literature, I assume that fabric classification schemes, the effort expended by authors in bioclast identification, and their sensitivity to facies splitting are all unbiased with respect to geologic time. Facies data were obtained from 101 out of 155 reefs included in this study (Appendix B).

2.4.3 Relief

The original topographic relief of a reef is typically inferred from environmental cues of reef components, in addition to the relationship between the reef and its surrounding sediment. Evidence includes the onlap of the reef 'core' by flanking beds, the presence of reef talus in those flanking beds, geopetal infilling of large cavities, and paleoecological and sedimentological variance that reflect environmental gradients linked to changing depth (Wood 1999). Precisely estimating the paleorelief of a fossil reef is challenging in outcrops with poor or limited exposure, and/or with uncertain amounts of compaction of surrounding sediment.

I devised a categorical scale to maximize the data that could be obtained from different sources. Each reef was assigned to one of six categories: no distinguishable relief (N), that is ≤ 5 cm-scale microrelief; low relief (L), with vertical growth ≤ 0.5 m; moderate relief (M) of ~1 m, that is within the range of 0.5-2.5 m; and three levels of high relief, at ~5 m scale (H, 2.5 – 7.5 m), ~10 m scale (H2, 7.5 – 25 m), and >25 m (H3). Although many reefs likely achieved relief far greater than 25 m, the expected imprecision of relief estimates at large scales makes subdivision beyond this limit questionable. Relief data were obtained from 92 out of 155 reefs included in this study (Appendix B).

2.4.4 Final Notes on Literature-Based Data

Regional reef surveys (e.g., monographs on the reefs of a particular age in a particular terrain) were treated as a single entry into the database unless the survey described individual reefs in detail, comparable to a research report. Data on builder morphology, facies, and relief were all based on the most detailed description in the publication, which in some instances is an idealized reef diagram. Where dimensions of multiple reefs were described, I used the largest values of reef size and relief presented. Finally, although many reef descriptions lacked one of more types of data, each was included in the data set as even partial data can contribute to documenting changes in the reef system of the middle Paleozoic.

Analyses of literature and field data were completed using base functions and the "vegan" statistical package in R (R Core Team 2015), including NMDS analysis to characterize reef-builder morphologies by time interval.

2.5 Results

2.5.1 Occupancy and taxonomic associations of reef-builder morphotypes

Reef builders of each morphological category were present in reefs across the entire study interval, but their frequency of occurrence changed (Table 1). Encrusters, including stromatoporoids, bryozoans, and microbes, were nearly ubiquitous in Ordovician reefs (50 of 56 reefs [89%]). Hemispherical and massive stromatoporoids, sponges, corals, and receptaculitids were present in almost half of all Ordovician reefs (43%), with tabular (bryozoans, corals) and branching forms (corals) present in ~20%. 8 of 56 Ordovician reefs (14%) lack massive, tabular and branching forms entirely. Finally, mud-dominated bioherms are rare through the Ordovician (5%).

In contrast, by the Devonian, encrusters became less common, present in just over half of the reef sites (21 of 38 [55%]). Bryozoa and cyanobacteria are the main taxa taking this form. Hemispheric and tabular stromatoporoids and favositid corals became the most frequent reef builders (84% and 74% of reefs, respectively), and branching corals, such as *Alveolites* and *Thamnopora*, and the branching stromatoporoid *Amphipora,* were almost as widespread (71% of Devonian reefs). Mud-dominated mounds were slightly more common (13%) in the Devonian than in the Ordovician, but the difference is not statistically significant given the sample size.

Table 2.1**:** Proportional occupancy of all reef sites by reef builders of each morphological category. Most reefs contained multiple reef-builder morphologies, with encrusting and massive elements the most common. Strong increases in branching, tabular and massive morphologies, along with a loss of encrusting reef builders, marked the transition between the Ordovician and the younger Silurian and Devonian records.

	Mid/Late Ordovician (n=56)	**Silurian (n=40)**	**Devonian, pre-Famennian (n=38)**	**Total (n=134)**
Stromatactoid Mud	0.05	0.10	0.13	0.09
Encrusting	0.89	0.63	0.55	0.72
Massive/Hemispherical	0.43	0.80	0.84	0.66
Columnar/Vaselike	0.36	0.28	0.34	0.33
Tabular/Platelike	0.20	0.48	0.74	0.43
Branching	0.23	0.65	0.71	0.49

	Mid/Late Ordovician	**Silurian**	**Devonian, pre-Famennian**
Encrusting	*Cyanobacteria (Thrombolites, Stromatolites), Bryozoa*, Stromatoporoidea	Cyanobacteria (Stromatolites), Tabulata	Stromatoporoidea, Tabulata, “Algae”(Cyanobacteria?)
Massive/ Hemispherical	*Tabulata, Stromatoporoidea,* Receptaculitidae, Demospongiae	*Tabulata Stromatoporoidea*, Receptaculitidae	*Tabulata, Stromatoporoidea,* Rugosa
Columnar/ Vaselike	Rugosa, Stromatoporoidea	Rugosa	Rugosa, Stromatoporoidea
Tabular/ Platelike	Tabulata, Stromatoporoidea, Bryozoa	Stromatoporoidea	*Tabulata, Stromatoporoidea*
Branching	Thrombolites, Bryozoa	Tabulata, Bryozoa	Rugosa, Tabulata, Stromatoporoidea

Table 2.2: Taxonomy of reef builders by morphotype among reefs of each study interval. Common dominant reef-building groups in italics. Dominant reef builders include fewer taxonomic groups in later intervals.

Although each reef-builder morphotype was present in reefs within each increment of the middle Paleozoic study interval (Table 2.1), the number of morphotypes per individual reef increased from the Middle Ordovician to the Late Devonian (Fig. 2.2). A typical Late Ordovician reef had few reef-builder morphotypes, despite the large diversity of faunal groups engaged in reef building at this time (Table 2.2). In contrast, Silurian and Devonian reefs had greater average diversity of reef-building morphotypes but a narrower taxonomic range (primarily large corals and stromatoporoids).

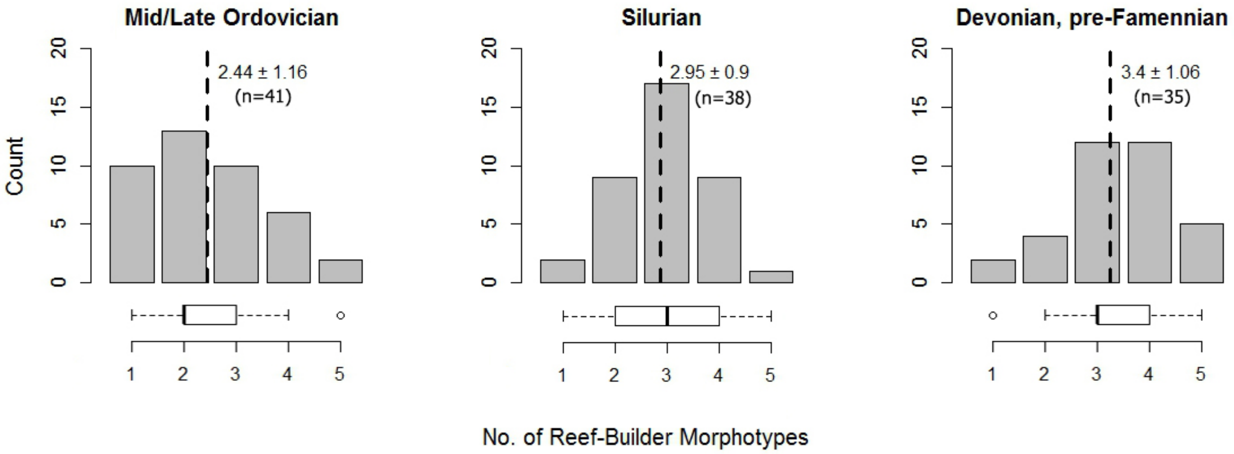


Figure 2.2 : Frequency distribution of the number of distinct reef-builder morphologies present per reef, by study interval, with mean and standard deviation. Box and whisker plots indicate median (heavy line), first and third quantiles (box), and extreme data points no further than 1.5x the IQR (whiskers). In Ordovician reefs, the presence of two reef-builder types is most common, and reefs are rarely constructed of more than three types. Silurian and Devonian reefs tend to include builders of 3 or more morphotypes, and rarely by a single type.

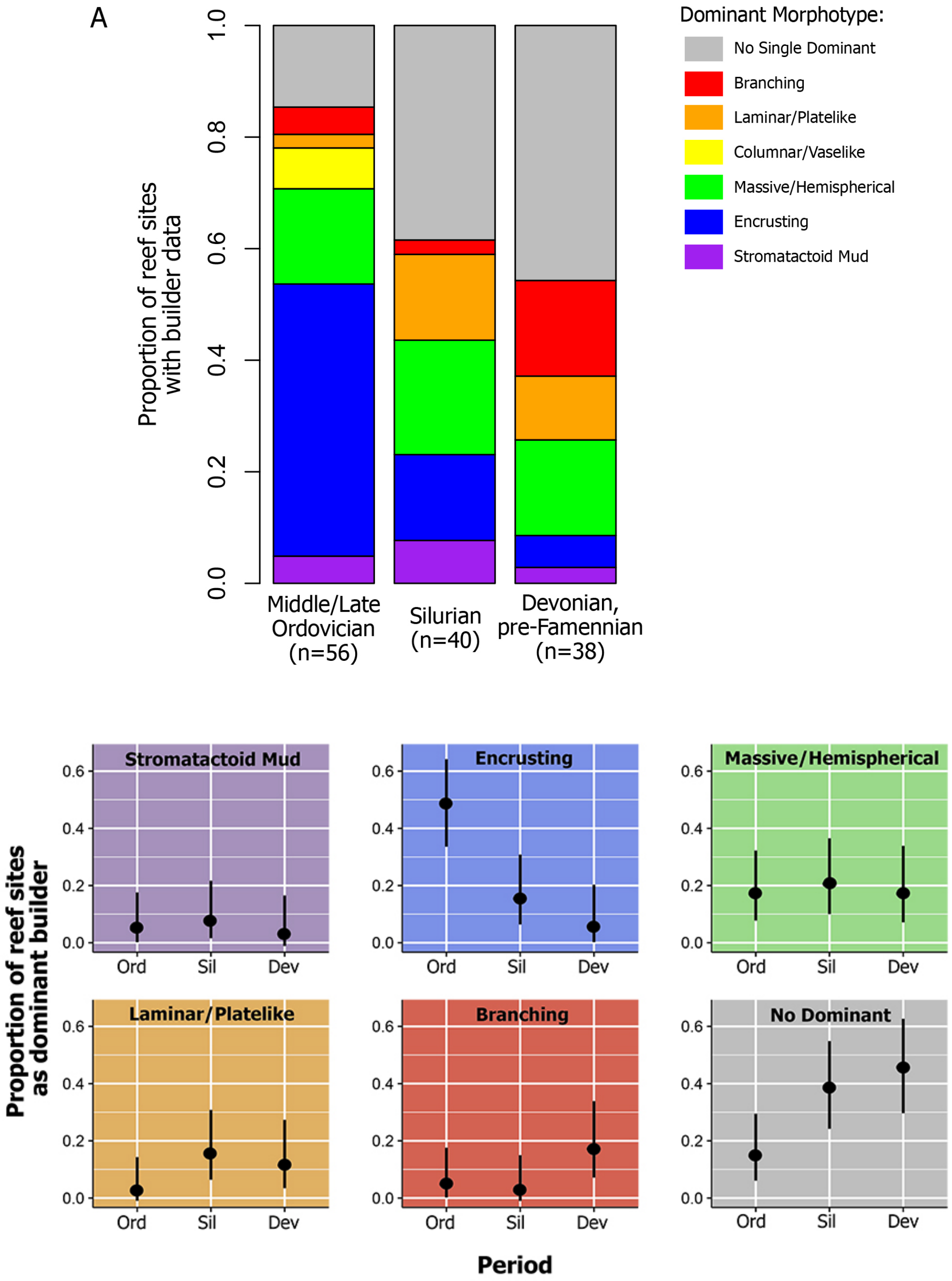


Figure 2.3 **:** (A) Stacked bar graph of primary reef-builder morphotypes among reefs of each period, and (B) subdivided more finely by individual reef builder morphotype with 95% adjusted Wald confidence intervals. Columnar dominance omitted because they do not dominate reefs younger than Ordovician age.

2.5.2 Dominance by single reef-builder morphotype

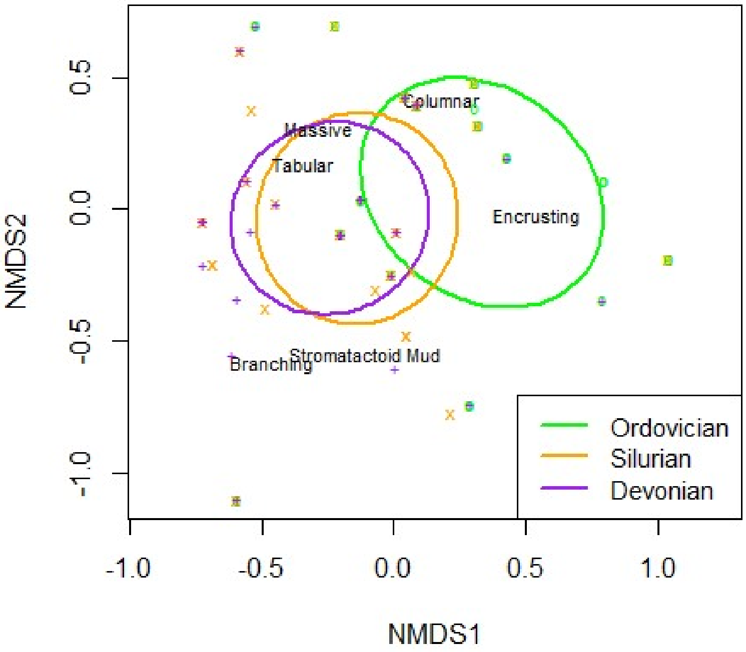
Although multiple morphotypes were present in most reefs in the database, one type usually dominated (Fig. 2.3a). From the Middle Ordovician through the Frasnian stage of the Devonian, massive morphotypes were steadily present as dominant reef builders in about 20% of reefs. These massive builders were usually stromatoporoids and tabulate corals, and created reef-core boundstones, framestones, and rudstones throughout the study period. Variation among periods arises in the number of reefs dominated by morphotypes other than massive builders, particularly encrusting, tabular, and branching forms.

In the Ordovician, encrusters were the dominant morphotype in 50% of reefs, present as both microbial and metazoan encrusters, particularly stromatoporoids, and bryozoans. Despite the globally-recognized change in taxonomic composition of reef builders from microbes to metazoans through the Middle Ordovician (Adachi et al 2011; Webby 2002), the data in Fig. 2.3 show that encrusters, as binding organisms, retained their prominent role in reef-building throughout the Ordovician. Microbial boundstones persisted through the reefs of the Late Ordovician, but are replaced in prevalence by the expansion of bryozoan and stromatoporoidal boundstone reefs. Reefs dominated by encrusters become significantly less common in the Silurian and Devonian (down to ~5%; Fig. 2.3a), concomitant with the decreasing *occurrence* of encrusting morphotypes (from 89% to only 55% of reefs, Table 1). Encrusting algae continued to maintain a presence in reefs through the Silurian and Devonian, but the proportion of microbial carbonate in reef rock dropped sharply at the end of the Ordovician and remained so until the Late Devonian (Frasnian/Famennian; Riding 2006).

Tabular and branching builders increased in importance as dominant reef builders through the Silurian and Devonian, although neither increase is significant given the limited sample size. Dominance by branching forms rose from ~5% in the Ordovician, mostly in the form of thrombolitic reef mounds, to ~19% in the Devonian, when corals were the dominant branching reef builders. Silurian and Devonian reef cores contained fewer boundstone facies owing to rarer dominance by encrusters, and usually consisted of abundant framestone and rudstone facies composed of fragmented reef builders. Furthermore, boundstone core facies in Devonian reefs included fabrics akin to the 'coverstones' of Tsein (1981), which are characterized by sedentary, tabular organisms (e.g. corals, stromatoporoids) that cover and stabilize loose sediment. This coverstone fabric is distinct from the boundstones common to Ordovician reefs that are created through cementation of framework elements or debris by encrusting algae, bryozoans, and stromatoporoids.

2.5.3 Reefs that are not dominated by a single morphotype

Reefs lacking a single reef-builder morphotype were present throughout the middle Paleozoic, but this state increased substantially (although not significantly) between the Middle Ordovician and the Devonian (Fig. 2.3b). Such reefs may have had multiple reef-builder morphotypes thoroughly admixed, or exhibited lateral or vertical zonation of dominant reef-builder types. All six Ordovician reefs in the database that lacked a single dominant builder morphotype had fairly uniform core frameworks in which multiple reef builders occupied the same core facies, none achieving even local dominance. Silurian and Devonian reefs in this category include examples without local dominants, like their Ordovician counterparts, but some (6 of 28 such reefs) exhibited strong lateral and/or vertical zonation of reef-builder morphotypes across their reef core. Different builder types were locally dominant in adjacent habitats within the reef.



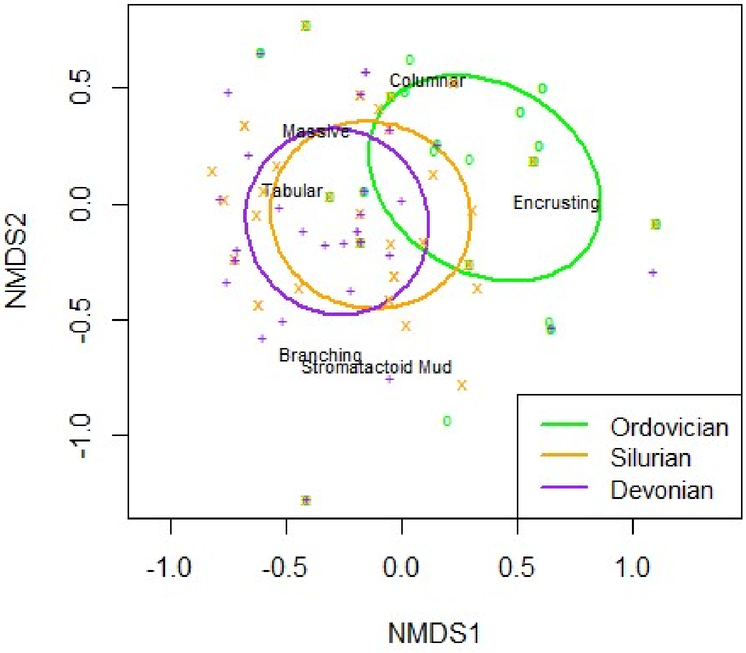


Figure 2.4 **:** Non-metric multidimensional scaling (NMDS) using dominance (top graph) and presence/absence alone (bottom graph) of reef-builder morphologies, showing general separation of Ordovician from Silurian and Devonian assemblages, likely influenced by affinity for encrusting reef builders. Ellipses denote one standard deviation for reefs, color-coded for the time period. Stress values are 0.06 for dominance/presence/absence, and 0.03 for presence/absence

2.5.4 Multivariate associations of reef builders

Multivariate, non-metric multidimensional scaling (NMDS) analysis of dominance/presence/absence and simple presence/absence data for builder morphotypes indicated that reefs of the Middle to Late Ordovician are readily distinguished from those of the Silurian and Devonian (Fig. 2.4). All builder morphotypes were present in many of the same combinations across time, and so the separation is not strong – the standard deviation ellipses of the three study intervals substantially overlap. Ordovician reefs were primarily distinguished by the commonness of combinations that feature encrusters and, to a smaller extent, simple vertical elements such as column and vase morphologies. In contrast, Silurian and Devonian reefs commonly had reef-builder combinations that included branching and tabular morphotypes.

These analyses reveal that some morphotypes occupy similar areas in NMDS space, indicating commonality in their occurrences. Tabular and massive morphotypes are closely related in NMDS space, as are branching types and stromatactoid mud.

2.5.5 Original topographic relief and preserved thickness

Over the middle Paleozoic, reefs expanded to greater scales of relief above the paleo-seafloor, based on mean and median categorical values (Fig. 2.5). Relief increased most strongly between the Ordovician and Silurian, from a median categorical value of Low ($z < 0.5m$) to Moderate ($0.5m < z < 2.5m$). Relief then remained high through the Devonian.

Original relief inferred from physical stratigraphic and other evidence is positively correlated with the total preserved thickness of a reef (Fig. 2.6). Overlap between reef thickness and different scales of relief is expected because reefs of greater preserved thickness can include reefs with greater ranges of relief, up to the measured total thickness.

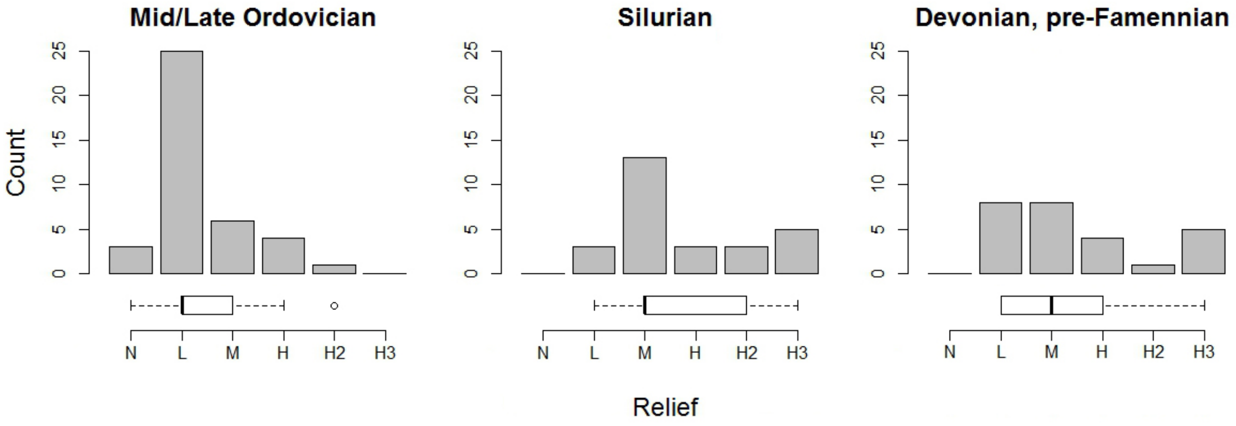


Figure 2.5 **:** Frequency distribution of topographic relief (z) of reefs over time. N=no appreciable relief (z<0.1 m); L = z<0.5m; M= 0.5m<z<2.5m; H= 2.5m<z<7.5m; H2= 7.5m<z<25m; and H3= z>25m. Plotting conventions as in Figure 2.2.

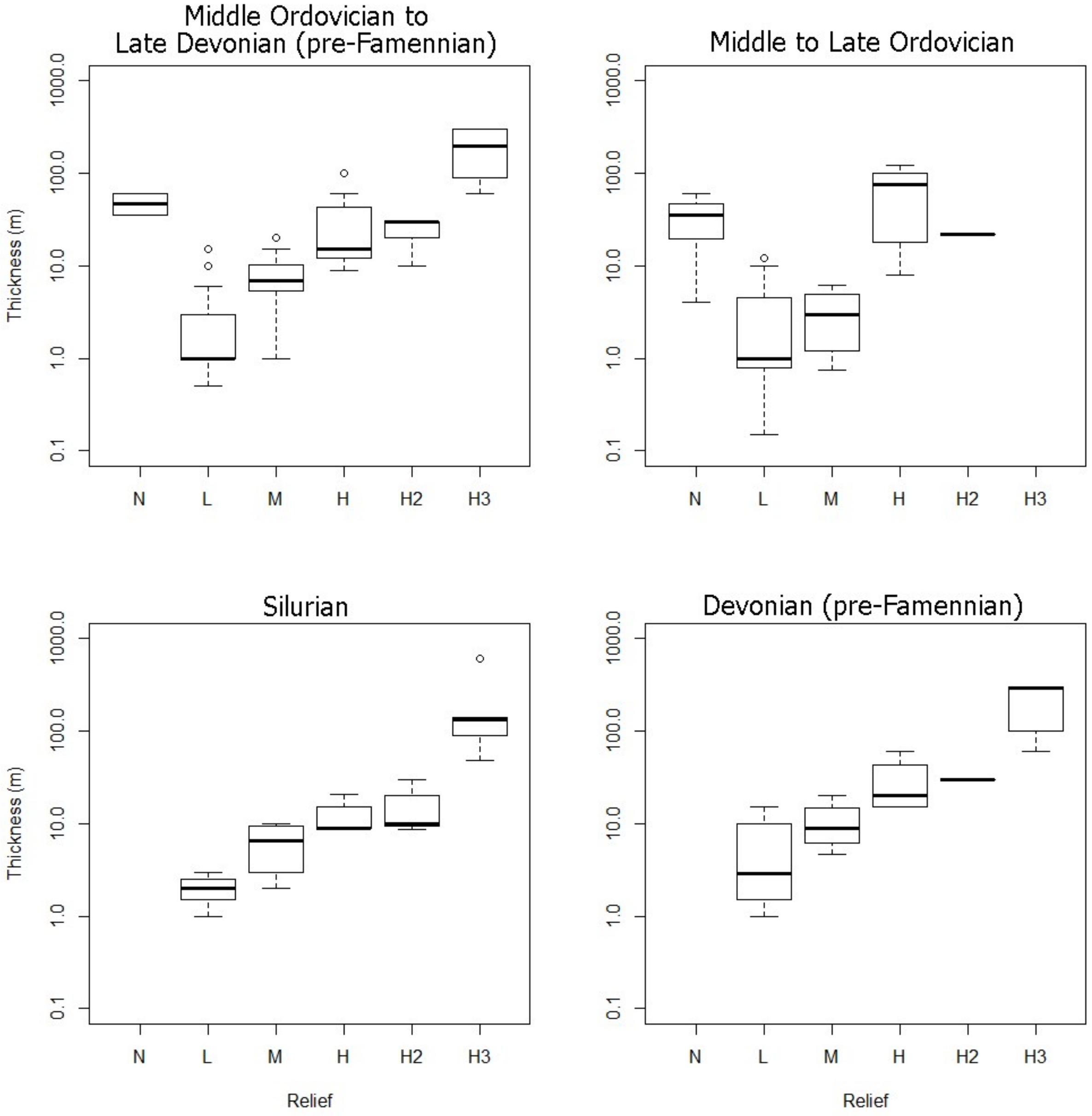


Figure 2.6: Positive relationship between original relief and preserved thickness of reefs in the entire study interval (upper left) and within the Ordovician, Silurian, and Devonian study intervals. Note logged thickness scale. N=no appreciable relief (z<0.1 m); L = z<0.5m; M= 0.5m<z<2.5m; H= 2.5m<z<7.5m; H2= 7.5m<z<25m; and H3= z>25m.

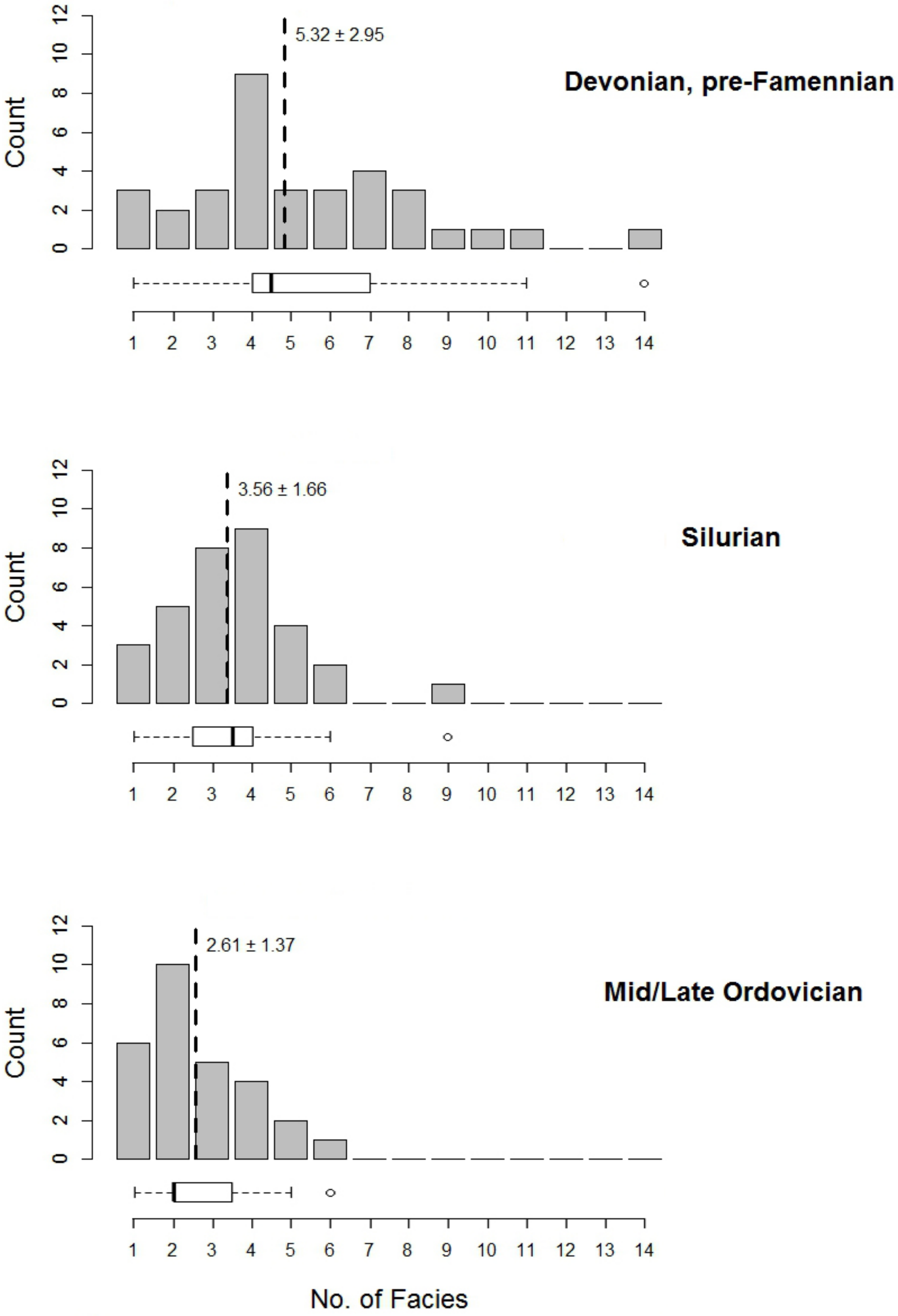


Figure 2.7: Frequency distribution of facies diversity within reefs, Middle Ordovician through Devonian, pre-Famennian, conventions as in Figure 2.2.

2.5.6 Lateral and vertical facies variation within reefs

Ordovician reefs typically had few distinct facies, a median 2.6, compared with younger reefs (Fig. 2.7). Most common were small patch reefs with one or two core facies, and a simple (lithologically homogeneous) and undifferentiated flanking facies surrounding them (as in the Chicoutimi reefs of Harland et al, 1987). Ordovician reefs with higher relief and/or greater lateral extent typically exhibited more complex and diverse facies, which are typically recorded in up-section facies changes (e.g., Lake 1981; Pitcher 1964) that some authors have attributed to ecological succession (Walker and Alberstadt 1975; Alberstadt et al 1974). Vertical variation in facies within a reef could reflect the shifting of original lateral facies variation over time. However, the Ordovician literature contains few Laurentian reefs where significant horizontal differentiation of core facies was suggested, even when vertical variation was evident (one notable exception being the Chazy reefs of Pitcher 1964). This situation contrasts starkly with the higher facies diversity of Devonian reefs (median 5.3, Fig. 2.6). Devonian reefs commonly featured both laterally differentiated debris facies along reef flanks, and lateral as well as vertical facies variation within the core.

2.5.7 Relationship between facies diversity and the original relief and preserved size of reefs

A strong positive relationship existed between reef relief and facies diversity in each time interval, but was strongest when data were pooled across the entire middle Paleozoic study interval (Fig. 2.8). Furthermore, facies diversity was highest in the Devonian, particularly in the highest-relief category, but through the Silurian and Devonian, there was also an upward expansion in facies diversity expressed by low and medium-relief reefs. Reefs with complex reef architecture—including pinnacles and true barrier reef morphologies -- also became more common across Laurentia during the Silurian and especially the Devonian (Copper and Scotese 2003; Copper 2002), likely creating the strong skew in the data.

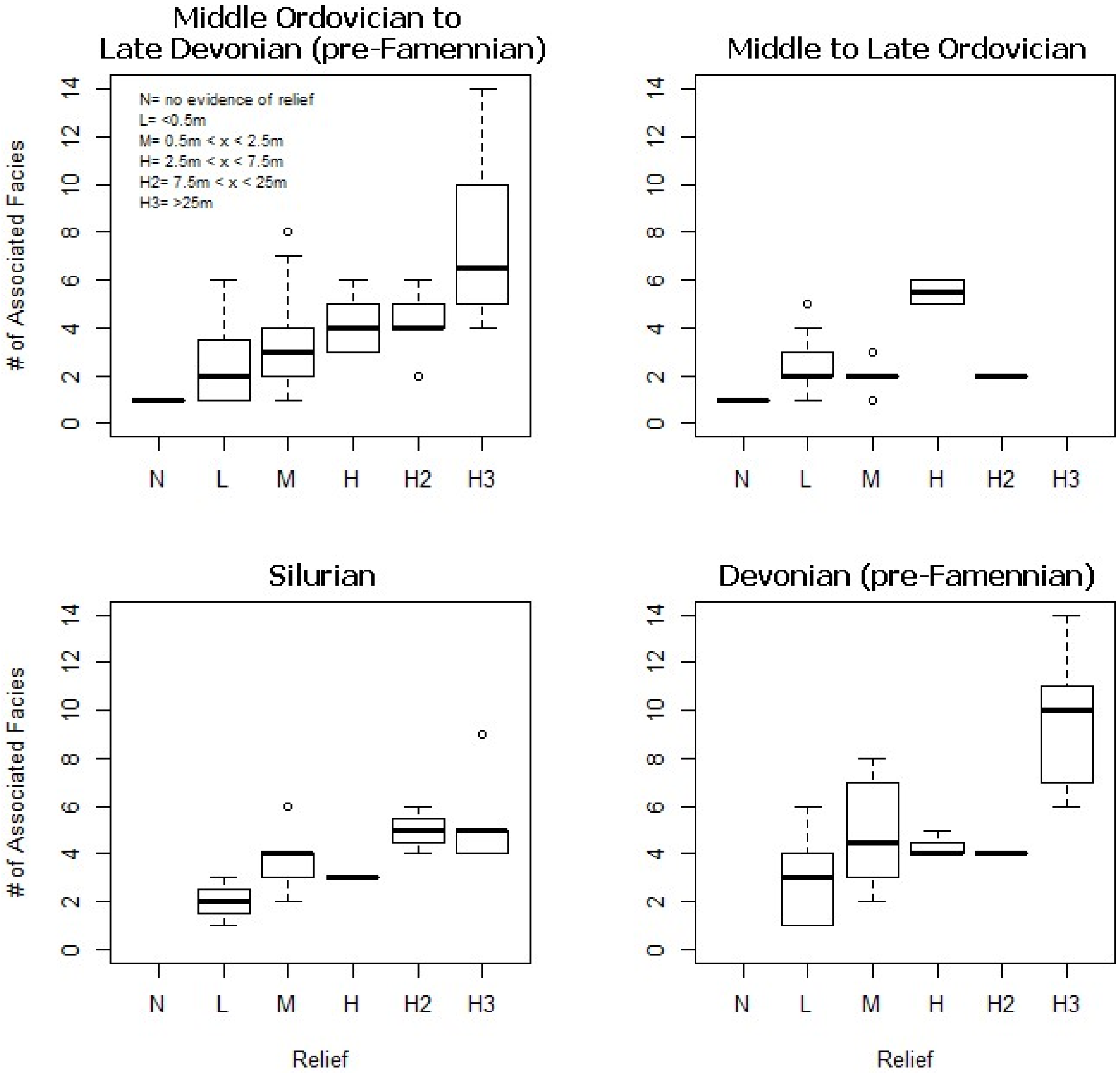


Figure 2.8: Box plots of variation in facies diversity as a function of reef relief. A consistent positive relationship exists between facies diversity and relief in pooled data from the study (upper left), and is broadly exhibited within each study interval (other graphs). Note increase in abundance of low relief, high facies diversity reefs in the Devonian.

Despite this overall positive relationship between facies diversity and reef relief , some small, low-relief reefs did have multiple, laterally differentiated facies, even in the Ordovician. For example, the patch reefs at Long Point, Newfoundland, were fairly complex mounds, each generally less than

10m wide, with cores up to 4m across, but they only achieved roughly a half-meter of relief in life. These reefs could nonetheless be partitioned into four distinct facies— both coral framestones and stromatoporoid/microbial boundstones within the reef "core", a pelmatazoan-dominated grainstones with hardground development along the reef flanks, and inter-reef, fine crinoidal packstones and wackestones between individual mounds. Other workers have identified a fifth facies composed of intra-reef laminated sediment, presumed to be internal cavities (Batten Hender and Dix 2006). This complexity is surprising for small reef mounds, and rivals some higher-relief reefs from the Ordovician.

2.5.8 Relationship between facies diversity and reef-builder morphologies

Heat maps reveal, within each interval of the middle Paleozoic, a positive relationship between facies diversity and the diversity of builder morphotypes (Fig. 2.9). However, no strong relationship exists between reef relief and the dominant morphotype (Fig. 2.10). Encrusters were solely responsible for the highest relief reefs in the Ordovician, but encrusting, massive, and tabular morphotypes, as well as combinations thereof, formed the highest relief Silurian reefs. The highest relief reefs in the Devonian had no single dominant morphotype.

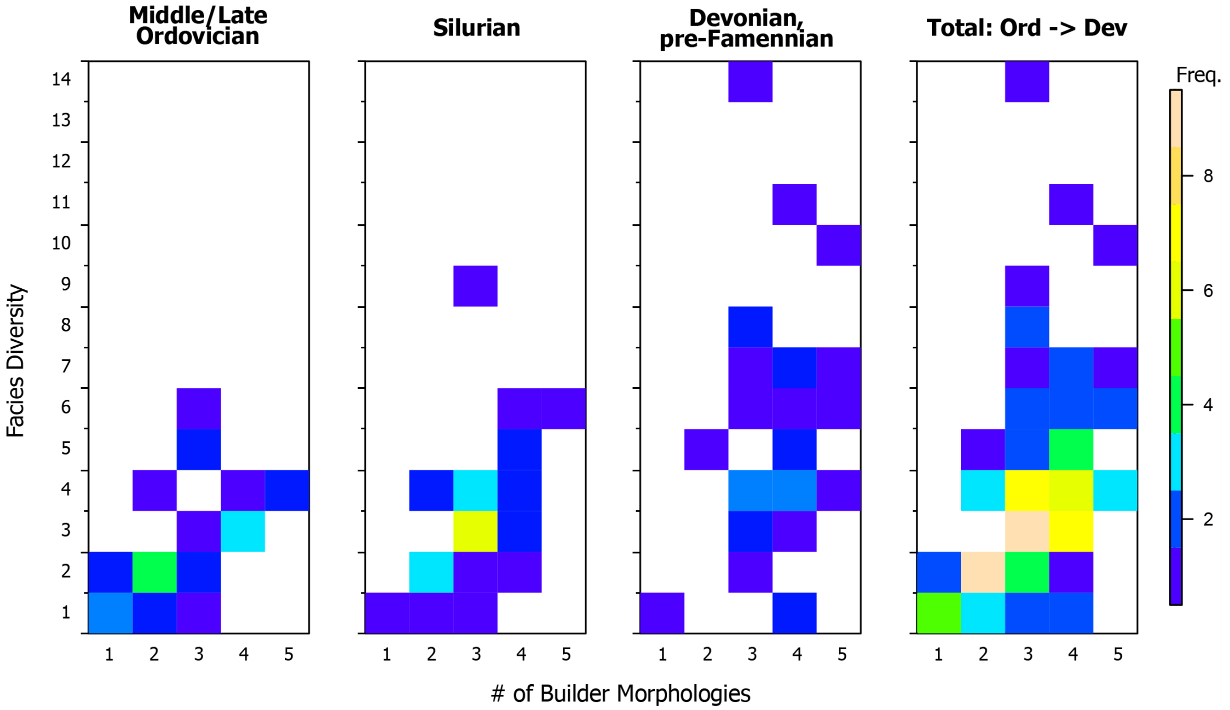


Figure 2.9 : Heat maps showing a consistent positive relationship of facies diversity to reef-builder morphotypes, Middle Ordovician through Frasnian stage of the Devonian

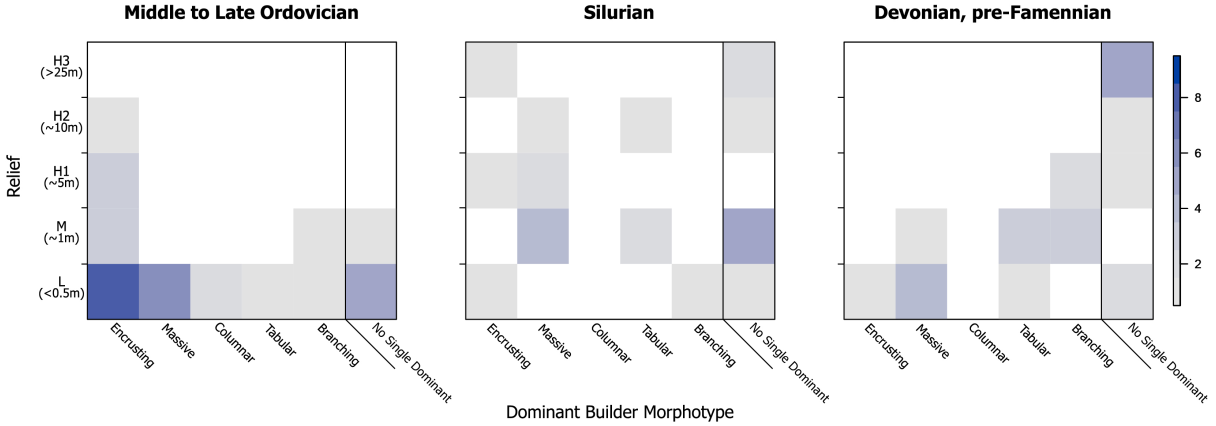


Figure 2.10: Heat map of variation in original reef relief and dominant reef-builder morphotype, showing no consistent pattern, although massive and encrusting reef-builders dominate the highest-relief Ordovician reefs, whereas assemblages with no single dominant morphotype compose the highest-relief reefs in the Silurian and Devonian.

2.6 Discussion

2.6.1 Impact of literature bias

Analysis is only as good as the data used, and understanding biases in the data can help constrain what can be inferred. Firstly, while some reef descriptions are extremely detailed, with lists of species present and reef-building guilds occupied, many others are products of long-ranging exploration of remote territories, providing only cursory biological detail. Biological observations in those cases may focus only on the most visually obvious reef-building elements, such as branching corals or massive stromatoporoids. A reporting bias towards such large and striking reef builders is thus expected. Meanwhile, encrusting bryozoans, and algae that do not produce large stromatolites/thrombolites, may be overlooked due to difficult identification in outcrop. Unless authors include thin-section work, encrusting elements are seldom reported as playing a primary role in reef building, and may not be reported at all. Encrusting and microbial elements are thus expected to be underreported, whereas the absence of discrete, three-dimensional builders in a report likely reflects true absence of those primary reef-builder morphologies. My finding that massive, tabular and branching elements increase over time among reefs is thus likely a robust pattern.

Secondly, reef facies diversity is broadly under-sampled in all time periods due to coarse facies identification and lack of exposure, biasing data away from high facies diversity in the Devonian, in particular, due to the increase in large-scale reefs. Reef descriptions that include extensive microfacies analysis skew facies diversity upwards due to fine differentiation of facies, even when microfacies data are filtered to reflect only environmental variation during life. However, fine-scale, microfacies analysis may be unfeasible with large and/or poorly exposed reefs due to limits on time, access, and manpower. Thus, facies diversity will likely be under-reported for reefs included in regional geological surveys, especially in remote areas such as the Canadian Arctic, within which facies are often generalized as “core”, “forereef”, or “backreef lagoon”. Facies diversity will also tend to be underestimated where reef descriptions rely entirely upon core or geophysical, subsurface observations. Vertical resolution of facies is high for individual cores, particularly when described through microfacies analysis, but lateral resolution is poor.

Such over-splitting of facies can be compensated for by coarsening the analysis to macroscopic observations, as is done in this study, but publications that lump together potentially diverse facies cannot be corrected *post hoc*. This bias will depress measured facies diversity, particularly when it comes to finer-scale partitioning by reef fauna. Because this bias towards under-sampled facies diversity will be greatest for larger reefs, facies diversity is likely more under-sampled in the Devonian than in the Ordovician. Large Devonian reefs were also often described from remote locales, particularly the Canadian Rocky Mountains and Arctic, compounding the under-estimation of facies diversity in younger rocks. Thus, the reported trends should be robust: true facies diversity should skew even further towards high facies diversity in the Devonian than documented here.

2.6.2 Taxonomic membership of morphotypes: change over time, and relevance to patch-scale habitat heterogeneity

Encrusting reef builders in middle Paleozoic reefs include the clotted and laminar microbial fabrics that dominate Early Ordovician reefs, but these taxa became less common as primary reef builders over the course of the Late Ordovician (Adachi et al 2011; Webby 2002), when bryozoans and stromatoporoids were more likely to be dominant encrusters. The modest decrease in encrusters observed from the Ordovician and through the Silurian and Devonian is primarily due to the decline of stromatolitic and thrombolitic fabrics in reefs. There are good examples of Silurian reefs with substantial microbialite (Clough and Blodgett 1989; Kahle 1994) and it may play a role in maintaining global metazoan reef building at this time, but the presence of large sections of reef built by stromatolites and thrombolites was rare among Laurentian reefs of this time, and the overall percentage of microbial reef rock is low (Webb 1996). That said, encrusting elements that play a role in cementation, particularly cyanobacteria and calcifying algae, were frequently observed in the Silurian and Devonian reefs that were examined with thin section microscopy. Considering the lack of detailed microscopy in many reef entries of the data set, this trend likely reflects a reduction in microbial and algal structures that are recognizable in outcrop, rather than a true loss of reef occupancy by encrusters.

The increase in dominance into the Silurian and Devonian (Fig. 2.3) by more complex morphotypes tracks the general expansion of corals and stromatoporoids toward more complex forms (Kershaw 1998, Hill 1981). Perhaps the most notable addition is the branching and columnar stromatoporoid, *Amphipora*, a common constituent of Devonian reefs alongside tabular and massive reef builders.

The reduction in encrusting dominance allowed for more complex habitats to be made by organisms with distinct, three-dimensional forms. This change also promoted greater debris production, enhancing patch scale heterogeneity as debris facies become more interspersed across a reef, filling the cavities and crevices created by non-encrusting reef builders. The development of complex morphologies among the newly dominant reef-building fauna of the Silurian and Devonian ensured that this rise in local, patch-scale heterogeneity became widespread across Laurentia.

2.6.3 Reef builder morphotypes in combination, and relevance to patch-scale habitat heterogeneity

Combinations of reef builder morphologies can create more complex reef architecture than what is likely with a singular morphology, and so it is worth examining the common suites of co-occurring morphologies and how they contribute to patch-scale heterogeneity. The two most prominent morphotype combinations are the pairing of stromatactoid mud and branching organisms, and the pairing of massive and tabular morphologies (Fig 2.4).

Most reefs (7 of 12) composed primarily of stromatactoid mud included branching organisms, typically bryozoans or corals, as secondary reef builders. The taxonomic identity of these mud-associated reef-builders varied from reef to reef, suggesting the absence of close biological associations among taxa. These mud-dominated mounds might indicate calmer environments that would favor more delicate branching organisms of any group; in the case with bryozoans as secondary reef builders, greater water depth might be indicated because these taxa could tolerate cool waters or low light conditions.

Although stromatactoid mud was capable of building large-scale (tens to hundreds of meters), stable, three-dimensional structures, it is unclear how stromatactoid mud contributed architecturally at the patch level (meter-scale). Thus, its particular interaction with co-occurring reef-building structures, and presumed contribution to patch-scale heterogeneity through such interaction, is suspect. Rather, it may have had more influence upon facies-scale heterogeneity, because mud-dominated buildups may have had facies distinguished by the presence of branching organisms, particularly as flanking debris, distinct from a mud-dominated core facies. Alternatively, mud and branching organisms may have co-occurred locally where branching organisms (such as fenestrate bryozoans) were sufficiently abundant to act as bafflers, trapping mud. This may have defined an individual buildup as the core facies, or formed an additional, distinct facies from any surrounding debris-dominated facies or sponge-bearing mud facies. The literature reveals no consistent facies association or organization for the co-occurrence of stromatactoid mud and branching reef builders.

The frequent co-occurrence of tabular and massive morphotypes in NMDS space, and the presence of stromatoporoid or coral representatives of both morphotypes at such reefs, albeit in different parts of the reef, could reflect ecophenotypy within particular reef building fauna. For example, photosymbiotic organisms that would normally grow into bulbous shapes may grow into flattened shapes when at depth and in need of maximizing light intake (Graus and MacIntyre 1976). They may also take on this ecomorph at shallow depths, when exposed to high water energy (J.

Morton 1974). Variation in builder morphology may also be a function of growth relationship with the surrounding sediment. For example, massive growth forms may functionally assume this shape along a growing surface when growth simply keeps up with accumulation of surrounding sediment. The co-occurrence of these two builder morphotypes can thus result from two separate types of organisms with distinct morphotypes building a reef, but ecomorphological variation exhibited by a single reef builder is likely common enough to explain the co-occurrence in NMDS space.

The co-occurrence of tabular and massive morphologies across a reef contributed to patch level heterogeneity in the definition of alternate facies that may relate to wave energy, or light level. Where they co-occurred at a local (patch) scale, morphologies did not appear to interact to form novel structures or cavities, especially when one reef building organism was responsible for both morphologies (pers. obs.), and when the particular tabular forms that were present did not exhibit elevation from the sediment-water interface beyond that of their hemispherical counterparts (e.g. the Formosa reefs of Fagerstrom 1961).

2.6.4 Development of habitat heterogeneity at the facies (landscape) scale

The greatest influence of reefs on facies-scale habitat heterogeneity was likely through the creation of relief. High-relief reefs will include habitats that cover a greater variety of hydrodynamic regimes and depths, from reef flat to distal fore-reef zones. From an ecological standpoint, this allows for differentiation of space by reef builders with different environmental tolerances. From the sedimentological angle, the variety of hydrodynamic regimes will also encourage diverse sedimentological regimes across a reef, allowing for multiple types of flanking and interreef sedimentary facies.

Ordovician reefs tended to be small and low-relief, and may not have exhibited such facies variation precisely because they did not reach significant enough sizes to significant impact local hydrodynamic regimes.

Increasing reef relief in the Silurian and Devonian conforms to the idea that reefs became much larger in the rock record, but the number of high-relief reefs is low. The scarcity of high-relief reefs in the data set was likely a product of poor exposure of the largest reefs, many of which were known only from cores. The presence of relief could be inferred, but in such scenarios, estimates of relief were rarely made, as the exposure did not allow for detailed observation. Nevertheless, the reduction in frequency of low relief reefs is probably a real signal, in line with the reduced frequency of small patch reefs.

2.6.5 Reef development underlies facies-scale heterogeneity within reefs

So, do the autogenic sedimentary dynamics of reef systems change between the Ordovician and the Devonian? I argue that it is highly likely, but primarily due to effects of builder diversity and favorable spatial relationships. The physics responsible for the impact of relief on facies diversity – i.e., the influence of a large obstacle upon water flow and wave energy, controls on sediment transport -- did not change between periods, but the reef builders and the kinds of sediment (mud, coarse debris) being acted upon by hydrodynamic variation across the reef changed dramatically. In addition, even low relief reefs achieved fairly wide lateral extent in the Devonian, allowing for perhaps broader effects on local hydrodynamics. The effects are likely exhibited in Figure 2.8; Devonian reefs with even low and moderate levels of relief exhibited a much greater range of facies diversity than comparable, earlier reefs. Those facies distinctions primarily relate to zones of particular reef fauna and distinct faunal debris.

The increase of landscape-scale habitat heterogeneity through zonation over geologic time, documented here, could reflect a secular change in how reef builders of different morphotypes interact with local environments, but it may also be due to a confluence of changes in reef size and builder morphological diversity through time. In principle, larger reefs provide greater opportunity for variation in physical environments to manifest across a reef, and allow greater opportunity for identification of local variation in reef builders. Where multiple reef-builder morphotypes are present among reef building taxa, variation of reef building taxa within a reef is likely to synchronously reveal variation in dominant morphotype as well. To illustrate, one of the larger Ordovician reefs in the data set, located near Pulaski, TN (Alberstadt et al.,1974), shows a level of reef-builder zonation that smaller reefs do not exhibit. Encrusting algae, bryozoans, and stromatoporoids each dominate construction in different parts of the reef core. Although there is lateral (and vertical) zonation of reef-building taxa, there is still only one dominant reef-builder morphotype present. On the other hand, large Silurian and Devonian reefs also feature lateral zonation of dominant reef builders, such as corals and stromatoporoids, but those particular zones will be distinguishable through builder morphology as well, with massive corals and stromatoporoids dominant in one area and platelike or branching corals dominant in another. It is unclear if zonation is expressed at smaller scales in the Devonian than in the Ordovician, but the widespread occurrence of reef builders of different morphologies accents the diversity of physical environments created across a given reef.

2.6.6 Role of sea level change in reef trends

Because geographic and oceanographic contingencies promote or impede the development of complex reef architecture, we must ask whether such contingencies might have shaped the Silurian and Devonian reefs of Laurentia. Vertical reef growth is constrained by accommodation space, bound by the sea surface above, and the sea floor below. The ultimate controls on accommodation are eustasy and sea floor subsidence/uplift.

Widespread epicontinental flooding in the Silurian and Devonian, in conjunction with warmer water temperatures, greatly expanded shallow shelf habitat suitable for warm-water reef building (Copper 2002). This would have an obvious impact on reef latitudinal distribution and abundance, but individual reef size and relief should not necessarily increase with higher sea level. Rather, reef size is more influenced by the relative stability of sea level, and the continued accommodation of reef growth through subsidence or continued sea level rise. Relatively stable sea level would allow for more continuous individual reef growth, limiting reef failure through drowning by rapid sea level rise, or stranding due to rapid sea level fall. Persistent or gradually increasing accommodation space would allow for greater accumulation of reefal carbonate and the development of thick reef sequences in the rock record. Although major variations in sea level occurred during the Silurian and Devonian, these periods were still relatively stable in comparison to the Late Ordovician, during which increasing continental glaciation caused fairly rapid and dramatic changes in sea level (Haq and Schutter 2008). Perhaps then, it is expected for Silurian and Devonian reefs to obtain larger sizes through duration. Duration of time available for reef growth should affect thickness and lateral extent of reefs, as well as potential to develop into broad platform, and barrier reefs. However, it does not address relief.

Relief in reefs comes about from disproportionate carbonate accumulation across a set area of the sea floor. This effect could derive from different growth rates among zones of reef builders, or simply relate to differential accumulation between framework and surrounding non-framework carbonates. It can also reflect exaggeration of underlying topographic heterogeneity, as growth rates of photoautotrophic and photosymbiotic reef builders that scale with light levels (Bosscher and Schlager 1992). The shallower the location, the more solar energy and wave energy it experiences, contributing to higher growth rates of constituent builders. Eventually, framework growth will approach an upper boundary--sea level--and accumulation of surrounding sediment will catch up, reducing local relief and broadening the reef platform. Although stable high sea level may reduce the risk of reef drowning or stranding, it might also reduce opportunity for high local relief to accumulate unless there is continued subsidence to maintain accommodation space and allow for further vertical distinction between reef and off-reef.

The Silurian and Devonian reefs in the database that feature the highest relief are primarily found in intracratonic basins of the Great Lakes region and in the open-shelf basins now in the

Canadian Rockies, respectively. Although these areas each experienced some level of thermal and/or physical subsidence during the time of reef growth (Heidlauf et al., 1986; Howell and Van Der Pluijm, 1999), neither region was particularly close to a then-active plate margin, where one might expect high rates of subsidence, and greater potential for the development of high reef relief. Some other combination of favorable conditions for carbonate production, particularly for reefal carbonates, may have existed in the midcontinent at this time in order to maintain sufficient differential accumulation and develop high relief, but those factors are unclear.

2.6.7 Examining biological controls on relief

The greater relief of Silurian and Devonian reefs relative to their Ordovician counterparts may not simply be a product of accommodation and water depth, but rather a product of other environmental conditions and the accumulation potential of the reef builders themselves. That said, it might be worth examining the relative ability of particular reef builders to create relief through growth rate, building habit, and cementation. For example, reefs built of cemented branching, tabular, and columnar morphologies can produce a scaffold effect, allowing greater vertical growth with less skeletal material than required for a reef with more robust or encrusting builders. However, one can also argue that greater debris production of a reef, perhaps due to the presence of less robust reef builders, could strongly reduce local topography, while robust forms should generate less debris and perhaps establish greater differentiation from the surrounding seafloor.

On a reef-by-reef basis, relief should be affected by the type of builders present, as they necessarily impact the style and rate of accretion, but the scale of effect on overall relief may be less than what could be revealed by the particular bin sizing used here. Models based on lagoonal reefs suggest a link between reef-builder morphology and overall reef morphology (Blakeway and Hamblin 2015). Fundamentally, reef-builder shape is less important than whether a given reef builder is prone to collapse or remain in place. The two factors are linked however, as delicate morphologies are more prone to breakage and collapse than robust morphologies. These types of model simulations seem like an ideal candidate to examine biological controls on relief.

2.7 Conclusions

The variety of individual reef-builder morphotypes in Laurentian reefs did not change dramatically between the Middle Ordovician and Late Devonian, but prevalence and abundance of reef builders in individual reefs changed. Encrusting metazoan and microbial reef builders did not disappear after the Ordovician, but they did relinquish their role as dominant reef builders to organisms with more branching and tabular morphologies. These morphologies, in addition to massive morphologies, became widespread in reefs at this time. Broadly, the transition from the Ordovician to the Silurian was a continuation of the trajectory reef building initiated between the Early and Latest Ordovician—a replacement of dominant, amorphous and encrusting reef builders by those with more defined, individual forms. Reefs became more modular at the scale of individual organisms, and at the facies scale. Increasing modularity would have contributed to increasing local heterogeneity within reefs, as they became more structurally complex at smaller scales due to greater debris production and increasingly complex gap and cavity space surrounding reef builders.

The scale of relief achieved by reefs also increases dramatically across this time interval. This compounded the effects of increased reef-builder types, and allowed for greater distinction of facies across reefs. The development of high relief in reefs, and perhaps more common complex reef architectures, was enabled by greater reef sizes in the Silurian and Devonian, allowing for the expansion of novel facies types and the creation of high facies-scale heterogeneity.

Although reefs of the Silurian and Devonian were primarily built of faunal groups that began building reefs in the Ordovician, the younger reefs present architectures and environments dramatically different from those of the Middle to Late Ordovician. The identification of a continuous middle Paleozoic reef interval has relied primarily on the identification of those dominant reef-building fauna, particularly corals and stromatoporoids. The variation of reef-building fauna active in the Ordovician, particularly the prominence of microbial reef binding, was responsible for variability in the attribution of the early bound for a middle Paleozoic reef interval distinct from that of the Late Cambrian/Early Ordovician (Kiessling 2002). Silurian and Devonian-style reef building can be seen in particular reefs of the latest Ordovician, but the broader reef system of Laurentia can be best described as in protracted transition between Early Ordovician and Silurian-style reef building, tied to both but distinct from either, individually. Finer distinctions might be possible within the global reef system, however, particularly with inclusion of paleogeographic regions with a greater record of Hirnantian stage reef building.

The method of inferring heterogeneity used here can be applied to reefs from other paleogeographic regions and different time intervals, mostly using data already in the literature. Moreover, inference of local and facies-scale heterogeneity can be used to inform interpretations of reefal diversity patterns. With respect to the advent of highly facies-diverse reefs in the Silurian and its continuation into the Devonian, detailed reef surveys can be used to account for the contribution of inter-facies beta diversity to perceived changes in overall reef diversity. A shift towards this level of environmental detail, along with an expansion to other paleogeographic regions, would provide greater insight into the development of the middle Paleozoic reef system, and offer parallels applicable to later expansions of the global reef system. Future applications can look towards recoveries of the global reef system after large-scale collapse. Are there predictive patterns in intra-reef heterogeneity observable through recovery intervals? How does recovery of global reef volume or abundance mirror the recovery of individual reef complexity? With more detailed individual reef surveys and greater understanding of the in-life impacts of complex reef environments on local paleoecology, we can obtain an important and novel level of insight into the development of the global reef system through time.

CHAPTER 3

ON EXTINCTION WITHIN THE REEF FAUNA DURING PHANEROZOIC REEF CRISES, AND THE VARIABLE PERSISTENCE OF HABITAT PREFERENCE AMONG REEF-BUILDERS AND REEF-DWELLERS

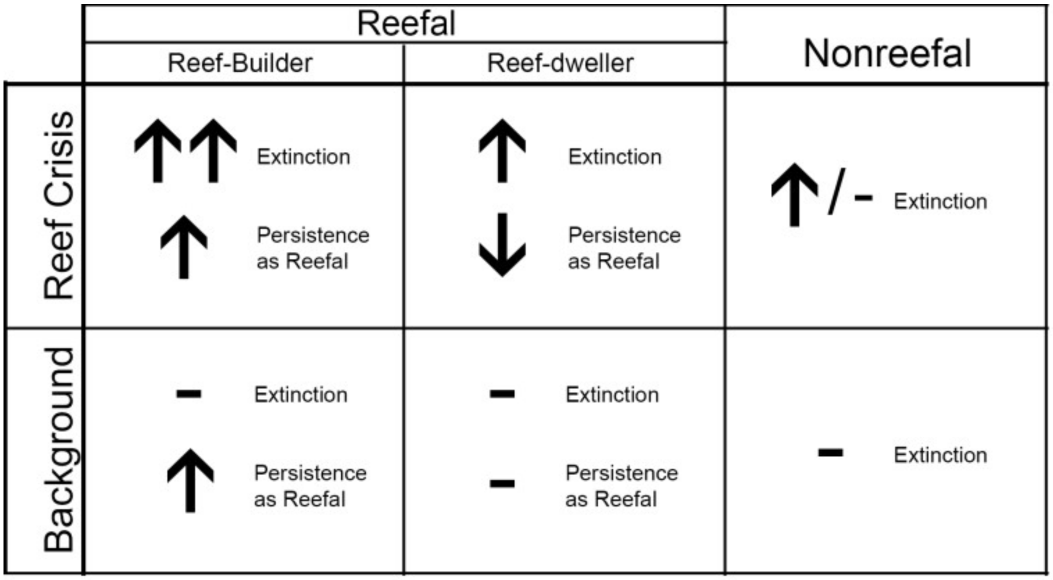
3.1 Abstract:

Episodes of reef crisis, defined by significant loss in the volume of reefal carbonate rock, are associated with dramatic turnover in clades of reef-builders, but little attention has been directed to reef-dwellers during these episodes. Do they exhibit the same extinction dynamics as reef-builders, or does their greater breadth of preferred habitat allow them to evade extinction? In recovery following crises, do they exhibit the same incumbency as reef-builders? To explore these questions, stage-level occurrences of 24,028 marine invertebrate genera, differentiated as reefal (reef-builders and reef-dwellers), and nonreefal genera, were compared during eleven reef crises and for intervening background intervals through the Phanerozoic. I find that reefal genera collectively often feature lower extinction rates than nonreefal genera, potentially tied to a more eurytopic habit than nonreefal genera. There is also a stronger persistence of reef habitat preference among reef-builders than reef-dwellers, but inconsistent responses in extinction. Reef crises are often tied to greater extinction of reefal taxa, particularly reef-builders, but reef crises and non-crisis intervals that are not otherwise linked to mass extinction events do not show significant difference between reef-builders and reef-dwellers. These results suggest Phanerozoic reefal genera are less susceptible to extinction than non-reefal genera, and that the reef-dwellers and reef-builders exhibit different levels of persistence in occupation of reefal habitat. However, that difference may not strongly impact susceptibility to extinction.

3.2 Introduction

Every taxon has a preferred environment or suite of environments, and their survival or extinction can be associated with the fate of their preferred habitat (Peters 2008), particularly so for organisms that are highly specialized (Munday 2004). Taxa associated with reefs are thought to be especially sensitive to habitat loss because they are seen as highly specialized for living in the reef environment. Furthermore, reefs themselves are especially sensitive to perturbation, declining or disappearing well before other ecosystems prior to broader mass extinction events (Copper 1994a), and exhibiting a delayed recovery during post-extinction intervals (Erwin 2001; Wood 1999; Brayard et al. 2011b). Reefal taxa are expected to disappear along with the reef environment, but large-scale paleobiological analyses of reefs rarely take into account nuances in reef dependence, such as the possibly different fates of reef-dwellers and reef-builders during crises (e.g. Kiessling et al. (2007), regarding the End-Triassic extinction).

Should reef-builders and reef-dwellers be expected to exhibit similar extinction dynamics, particularly during reef crises, when habitable reef area declines strongly? Reef-builders are, by definition, tied to the existence of reefs, and so if reef habitat disappears, it should be mirrored by a strong decline or total loss of reef-builders (Fig 3.1). Furthermore, the definitional ties of reef-builders to reef environments should result in a conserved preference for reef environments through the duration of a taxon, even after reef crisis events. In contrast, although reef-dwellers occupy reef habitats, they need not be obligately tied to them (Watkins 1997; Watkins 2000), and thus might not undergo the same – or any – significant decline with reef loss. Furthermore, as non-obligate reef taxa, reef-dwellers may not express that same environmental conservatism when reefs return to prominence post-crisis. Nonreefal taxa, having no reef association, are expected to exhibit lower extinction than reefal taxa during reef crises, but may suffer heightened extinction where reef crises coincide with broader mass extinction events.



	Reefal		Nonreefal
	Reef-Builder	Reef-dweller	
Reef Crisis	↑↑ Extinction ↑ Persistence as Reefal	↑ Extinction ↓ Persistence as Reefal	↑/- Extinction
Background	- Extinction ↑ Persistence as Reefal	- Extinction - Persistence as Reefal	- Extinction

Figure 3.1: Hypothesis table of expected extinction and reef persistence in reefal and nonreefal genera across crisis and background intervals. During reef crises, extinction is expected to be high for reefal taxa, particularly reef-builders, due to their fundamental ties to the reef environment. Nonreefal taxa may exhibit elevated extinction if the crisis event is linked to a broader mass extinction, but otherwise should show no difference with non-crisis events. Persistence in the reef habitat is expected to be high for reef-builders, but less so for reef-dwellers. Reef-dwellers are expected to exhibit reduced reefal preference after crisis events.

Here, using the eleven Phanerozoic "reef crises" identified by Flügel and Kiessling (Flügel and Kiessling 2002) and stage-level occurrences of macroinvertebrate genera from Cambrian to Recent rocks, filtered from a download from the Paleobiology Database (PBDB), I test for different levels of extinction between reefal and nonreefal genera, and between reef-builders and reef-dwellers, across reef crisis and background intervals. I further examine the persistence of reef occupation by reef-builders and reef-dwellers. Over the Phanerozoic, I find that reefal genera, surprisingly, exhibit lower proportional extinction than do nonreefal genera across non-crisis intervals, but reefal taxa exhibit higher proportional extinction during crises, as expected. Among reefal fauna, reef-builders and -dwellers do not exhibit a consistent difference in extinction overall, including no consistent difference during reef crises. However, reef-builders retain a stronger tie to the reef environment, with a higher proportion returning to reefs than seen among reef-dwellers. However, there is no statistical difference in retained reef preference between reef crisis and non-crisis intervals. These results suggest that reef-builders and reef-dwellers differ in their extinction dynamics and sustained habitat preference through time. However, the inconsistent impact upon extinction and reef habitat preference during reef crises may be indicative of the variety of different causes for reef crises, and is worth further exploration.

3.3 Background

3.3.1 Reef crises

The concept of a 'reef crisis' is historically linked to episodes of major reef collapse and reef gaps, in which reefs become scarce or fully absent from the known rock record. Crisis events were originally viewed through the lens of diversity crises, but studies implicitly assumed that the abundance and diversity of reef taxa were expected to rise and fall in concert with the size and geographic extent of reefs, both of which occurred in response to global stressors (Fagerstrom 1987; Kauffman and Fagerstrom 1993; Copper 1994b). Reefs were recognized as absent following each of the "Big Five" mass extinctions (Sheehan 1985), and the reef crisis literature was focused on the decline of reefs and reefal taxa leading up to the crisis interval and their delayed recovery afterwards. Long-recognized crises include the scarcity of reefs immediately prior-to and following the end-Ordovician extinction (Brunton and Copper 1994; Copper 2001), the loss of coral and stromatoporoid reefs at the Frasnian-Famennian boundary and their protracted recovery into the Carboniferous (Stearn 1987; Fagerstrom 1994; Copper 2002; Morrow, Harries, and Krivanek 2011), and the reef gaps following the end-Permian(Stanley 2003; Stanley 2010; Brayard et al. 2011), end-Triassic (Kiessling et al. 2007; Stanley 1988), and end-Cretaceous extinctions (Bryan 1991; Copper 1989).

Phanerozoic reef crises were first quantitatively identified, explicitly from the perspective of reef volume, by Flügel and Kiessling (Flügel and Kiessling 2002) using their Paleoreef database (Kiessling and Flügel 2002): reef crises were identified as stage boundaries over which preserved reef carbonate volume declined by ≥75%, corrected for differences in stage durations. Eleven stage boundaries met this criterion of a reef crisis, including those between: the Hirnantian and Rhuddanian (O-S), the Frasnian and Famennian (D), the Serpukhovian and Bashkirian (C), the Artinskian and Kungurian (P), the Guadalupian and Wuchiapingian (P), the Changhsingian and Induan (P-Tr), the Rhaetian and Hettangian (Tr-J), the Pleinsbachian and Toarcian (J), the Tithonian and Berriasian (J-K), the Berriasian and Valanginian (K), and the Cenomanian and Turonian stages (K).

In a more conservative analysis, Kiessling identified reef crises as statistical outliers, based on the frequency distribution of global reef-volume, stage by stage (Kiessling 2011). Seven reef-poor crisis stages were identified from boxplots (outliers were >1.5 times the interquartile range from the median value): the Fortunian Stage (Cambrian); the Dapingian Stage (O); the Rhuddanian and Aeronian Stages(S); the Famennian Stage (D); the Induan Stage (Tr); the Hettangian Stage (J); and the Toarcian Stage(J). Kiessling (2011) further argued that reef crises should be limited to skeletal metazoan reefs, or at least analyzed separately from microbial reefs, because they may respond to different environmental changes and exhibit different patterns of extinction and recovery. Through analysis of time-standardized volume changes among the subset of skeletal metazoan reefs, Kiessling (2011) identified five post-Cambrian reef crises. The post-crisis, reef-poor intervals were: the Famennian Stage (D); the Induan and Olekenian Stages (Tr); the Hettangian Stage (J); the Toarcian and Aalenian Stages (J); and the Ypresian Stage (Eocene Series).

Reef crises, defined by the drastic reduction of reef volume, do not have to be the cause or consequence of the extinction of reef builders (Kiessling and Simpson 2011). The extinction of reef builders is commonly expected to lead to a loss of reefs, but low-diversity reefs can maintain high carbonate production. Reasonable causes for reef crisis can include the removal of key fauna, but can also be tied to stressors that would limit carbonate production, in general. Kiessling and Simpson (2011), in addressing a definition of reef crises defined by carbonate production, suggest ocean acidification as a common cause for most of their identified reef crises, except for the crisis following the end-Ordovician extinction.

3.4 Methods

3.4.1 Data acquisition and filtering

Global occurrence data for all marine invertebrate genera for Cambrian to Recent intervals were downloaded from the Paleobiology Database (PBDB) (www.paleobiodb.org) in April 2018, including metadata on family and order-level taxonomic attributions, sedimentology, and stratigraphic context, and attributed paleoenvironment of the original fossil collections. To create an internally consistent dataset, the raw download of occurrences was filtered and corrected in the following ways:

(1) Occurrences were limited to those with stage-level or equivalent information tied to their collection. Regionally-defined stages were ignored unless they could be correlated with international stages recognized by the International Commission on Stratigraphy (April 2018 version; http://www.stratigraphy.org/index.php/ics-chart-timescale). Due to a lack of consistent stage attributions in the Cambrian, all Cambrian occurrences were split into the four Cambrian series recognized by the ICS (2018). Due to similar limitations of fine-scale dating, Silurian and Cenozoic time bins were distinguished by epoch, including the Pleistocene and Holocene. The final temporal span of data thus includes the entire Phanerozoic, split into 74 time bins.

(2) Genus, family, and order names were checked for consistent spelling, and each genus was checked to ensure consistent higher-level assignments: close spellings and entries that diverge in higher-level taxonomic assignments would otherwise appear as distinct, unique combinations. These errors, particularly at the genus level, most often result in the splitting of taxa and the creation of new “genera” with only one or two occurrences, thus biasing the dataset toward more taxa with shorter ranges and fewer occurrences. Such biases can be avoided in PBDB-based studies by omitting all generic singletons and doubletons, but due to concerns over low sample size, corrections were opted for in order to limit data loss from the automatic culling of these entries. Both tasks were completed line by line using a filter that identified unique Genus/Family/Order combinations, which were then reviewed. Data were corrected for spelling and consistent taxonomic grouping only: no attempts were made to correct for modern taxonomy. The final list of marine invertebrate taxa totaled 24,863 genera in 3,022 families and 471 orders (Supplementary file)

(3) To categorize occurrences as reefal and nonreefal, I used a similar procedure as Foote (Foote 2014), using the PBDB “environment” field associated with occurrence data. A reefal designation encompasses “basin reef”, “intrashelf/ intraplatform reef”, “slope/ramp reef”, “platform/shelf-margin reef”, “perireef”, and “reef, buildup or bioherm” assignments. Occurrences that lacked environmental data but included sedimentary information suggesting reef affinity (i.e. “reef rock”, “framestone”) were also given a ‘reefal’ attribution. Occurrences that lacked environmental data or were described as indeterminate, such as “marine indet” and “carbonate indet”, were left as “NA”-- not assigned to either reefal or nonreefal status. All other environmental attributions in the PBDB were categorized as ‘nonreefal’ occurrences.

This initial cleaning and filtering produced a dataset of 649,350 marine invertebrate occurrences, with 65,784 identified as reefal, 224,656 as nonreefal, and 358,910 as indeterminate. Across 74 time bins, these occurrences represent 65,152 unique genus/time bin combinations.

In order to label genera as reefal or nonreefal (detailed below), this subset was then iteratively culled of genera with too few occurrences with determinate environmental affinity in order to reduce volatility from chance attributions of a genus to a reefal or nonreefal environment. For example, genera with only one or two occurrences can erroneously be attributed to an environment based on the chance environmental attribution of a single occurrence; such genera cannot be determined to be reefal or nonreefal through statistical means, and thus singleton and doubleton occurrences should be excluded from analysis. At the other confident extreme, however, very few genera have ten or more occurrences in a single time bin: limiting the analytical dataset to genera with ≥10 occurrences leaves only 6,898 genus/time bin combinations, which is only ~10% of the total genera/stage combinations. That subset would provide little statistical power once records are parsed for each time bin into reefal and nonreefal taxa, and reefal taxa into reef-builders and reef-dwellers. Analyses were thus completed with subsets that included ≥4 and ≥8 occurrences attributable as reefal or nonreefal (15,323 and 8,541 genus/time bin combinations, respectively). The results presented here use an analytical dataset with ≥4 occurrences per genus per time bin, and equivalent figures using the more conservative cutoff can be reviewed in Appendix C.1.

3.4.2 Designation of genera as reefal, nonreefal, or indeterminate

Genera were identified as reefal if the proportion of reefal occurrences among all environmentally-assigned occurrences in an individual time bin was significantly greater than that produced by a random reassortment of collection-associated environmental data. To establish this assignment, environments were resampled 200 times, without replacement, using the distribution of environments, including indeterminate and unassigned environments, sampled in the cleaned PBDB collections of each geologic stage. Indeterminate environments were included to correct for bias in environment reporting: charismatic environments, such as reefs, are more likely to be positively reported, while nonreef environments are more likely to be placed in indeterminate category. Genera with reefal occurrences above the 95th percentile of what would be expected through re-sampling environmental data were formally designated as 'reefal' for that particular stage.

After filtering the dataset for ≥4 and ≥ 8 occurrences with qualifying environmental data, 4085 and 2219 genus/time bin combinations, respectively, could be designated as 'reefal' and 10,368, and 5,832 genus/time-bin associations could be designated as nonreefal. The remaining generic occurrences had indeterminate affinity in their respective time bins.

3.4.3 Stenotopy and geographic restriction

In order to identify relative stenotopy (narrow environmental range) and geographic restriction of reefal and nonreefal taxa, I first used a separate, but functionally-equivalent method to that used above, in order to distinguish whether a genus was reefal or nonreefal. Instead of manual shuffling of collection-level data, the 95th percentiles of reefal or nonreefal occurrences were calculated directly from the underlying proportion of reefal and nonreefal occurrences in each time bin.

For this study, a genus exhibits strong stenotopy if it predominantly occurred in solely reefal or nonreefal environments, and stenotopy was measured as the proportion of total occurrences in a genus's preferred habitat, between 0 and 1. For each time-bin, mean stenotopy was calculated for reefal and nonreefal genera.

Geographic range was determined from the subset of occurrences with paleolatitude and paleolongitude data, and geographic restriction of a taxon was defined as having a paleogeographic range that did not exceed 5 degrees in any cardinal direction. The proportion of geographically restricted reefal and nonreefal genera was calculated for each time bin. Binomial regression analyses were run on reefal and nonreefal taxa to test correlation between extinction risk and both geographic restriction and stenotopy.

3.4.4 Discrimination of reef-builders and -dwellers

Genera were categorized as reef-builders by their membership in 33 orders that include prominent reef-builders (Appendix C.2). These orders include stony corals, skeletal sponges, and reef-building bivalves such as rudists. Genera in these orders are compared with those from all other marine invertebrate orders, which are labeled as “reef-dwellers” when found in reefs. Although most—if not all--of these reef-building orders contain both reef-builders and -dwellers, they are comprise the most prominent reef-building genera, and should express variation in extinction and reef persistence, in comparison to orders that are more exclusively reef-dwellers, if such variation exists. Bryozoans, although capable of significant reef-building and demonstrably important in stabilizing reef sediment, are not typically responsible for framework-building (Ernst and Königshof 2008), and are especially difficult to generalize as reef-builders at the order level across the Phanerozoic. Thus, bryozoan orders were not included as reef-builders in this study.

3.4.5 Episodes recognized as reef crises

Reef crises were identified as in the more inclusive analysis of Flugel and Kiessling (2002), based on an arbitrary ≥70% decline in the preserved volume of reef rock. The eleven reef crises are the stage boundaries between the Hirnantian and Rhuddanian (O-S), the Frasnian and Famennian (D), the Serpukhovian and Bashkirian (C), the Artinskian and Kungurian (P), the Guadalupian and Wuchiapingian (P), the Changhsingian and Induan (P-Tr), the Rhaetian and Hettangian (Tr-J), the Pleinsbachian and Toarcian (J), the Tinthonian and Berriasian (J-K), the Berriasian and Valanginian

(K), and the Cenomanian and Turonian stages (K). All other stage boundaries are considered to be ‘background’ intervals.

The Cretaceous-Paleogene boundary is the only one of the “Big Five” extinction events that was not identified as a reef crisis by Flügel and Kiessling (2002).

3.4.6 Analysis of Extinction and of Persistence of Preference for Reefal Habitat

Extinction and persistence of reef preference were both examined across time bin boundaries. For each genus that could be identified as reefal or nonreefal in each time bin, the data were queried to identify the genera that made their last appearance in that particular time bin. This group of genera was labeled as “extinct”, without correction for potential under-sampling in later stages. Proportional extinction was calculated for both reefal versus nonreefal genera, and for reef builders versus reef dwellers, in each stage. Confidence intervals were calculated using the Wilson method (Wilson 1927).

For the persistence of reefal preference, the subset of surviving reefal genera in each time bin was analyzed to identify the genera that have a sufficient number of reefal occurrences to qualify as a reefal genus in either of the two subsequent time bins. These genera were labeled as persisting in their reefal preference. If a genus later appears in reefs, but does not have sufficient occurrence data to statistically determine affinity, then they were not categorized as persisting in their reefal affinity. For statistical power, persistence of reefal preference was only analyzed for reef fauna, that is including both reef-builder and reef-dweller subsets.

3.5 Results

3.5.1 Extinction of reefal and nonreefal genera

Considering all 74 time bins in the Phanerozoic dataset, reefal and nonreefal genera follow similar overall patterns of extinction (Fig 3.2a). During the 11 reef crisis events, the proportional extinction of reefal taxa are either significantly higher (2 intervals; Frasnian/Famennian and Pleinsbachian/Toarcian) or not significantly different (9 intervals) from those of nonreefal taxa (Fig. 3.2c).

During background, non-crisis intervals, reefal genera most often exhibit proportional extinction significantly lower than (25 of 62 boundaries), or insignificantly different from (34 of 62) nonreefal genera (Fig 3.2b). Reefal genera exhibit higher proportional extinction during 3 of 62 intervals, including the 2nd and 3rd Cambrian series, the Wuchiapingian/Changhsingian stages of the Late Permian, and at the Cretaceous/Paleogene boundary.

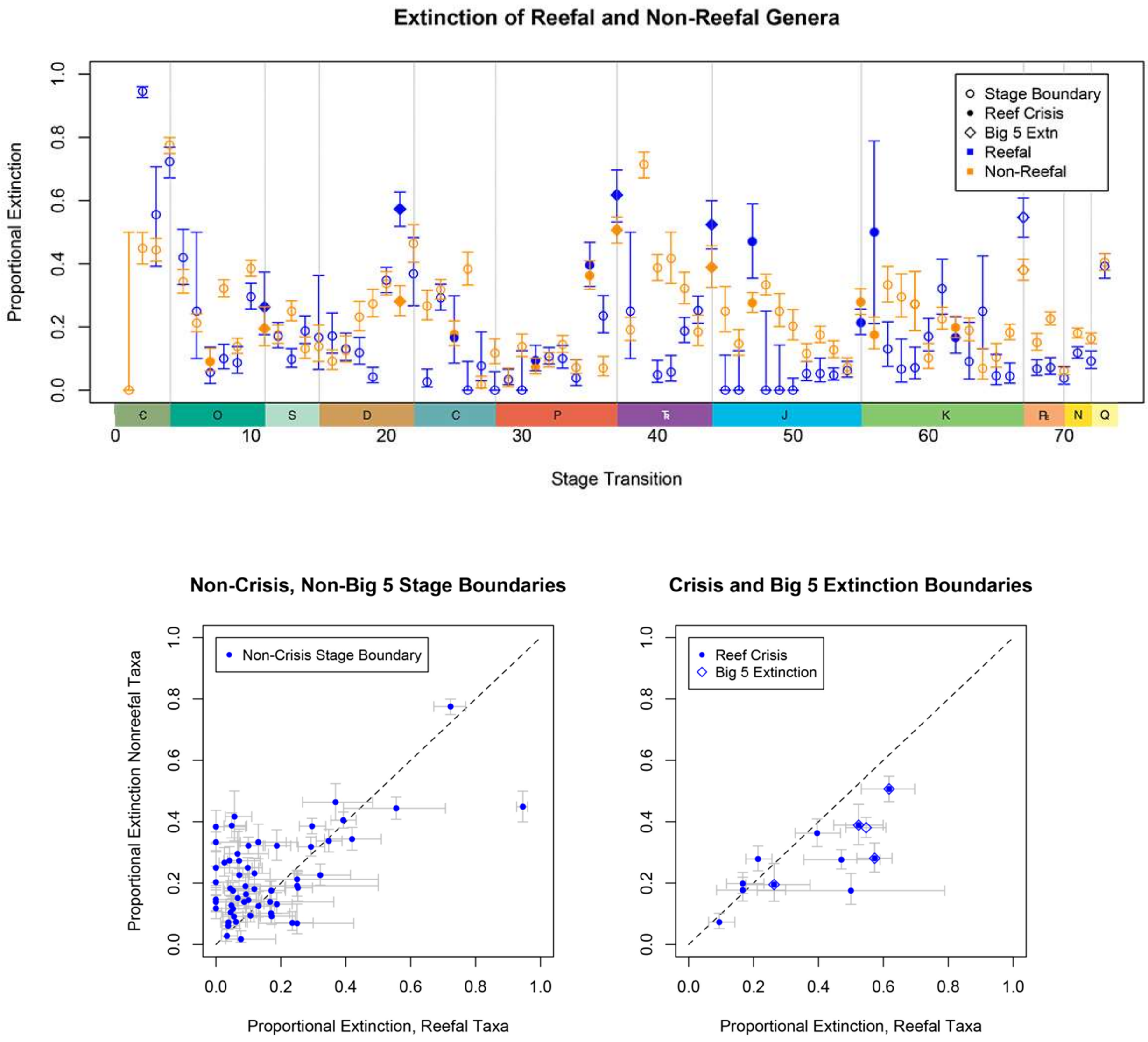


Figure 3.2: Proportional extinction of reefal and nonreefal taxa across time bin boundaries, using a ≥4 occurrence/time bin cutoff (upper graph, A). Reefal and nonreefal proportional extinction are plotted against each other for all non-crisis stage boundaries (data points in bottom left graph, B) and reef crisis and mass extinction events (bottom right, C). Extinction rates of reefal taxa are significantly higher than those of nonreefal taxa in only 3 of the 62 non-crisis stage boundaries; nonreefal taxa have significantly greater extinction than reefal taxa at 25 non-crisis boundaries. In contrast, during reef crisis events, the extinction rates of reefal taxa are either higher or not significantly different than those of nonreefal taxa.

3.5.2 Stenotopy and geographic restriction of reefal and nonreefal taxa

Contrary to stereotypes, reefal genera are more evenly distributed across both reef and nonreef habitats – i.e., are less stenotopic in that sense -- than nonreefal genera in the same time bin

(Fig. 3.3). Analysis finds that reefal taxa are rarely limited only to reef environments, whereas most nonreefal taxa are limited to nonreef environments. Binomial regression analysis indicates stenotopy is significantly correlated with extinction risk for both reefal (Coeff: 2.08 ± 0.22; Pr=<0.001) and nonreefal (Coeff: 2.71 ± 0.53; Pr=<0.001) taxa.

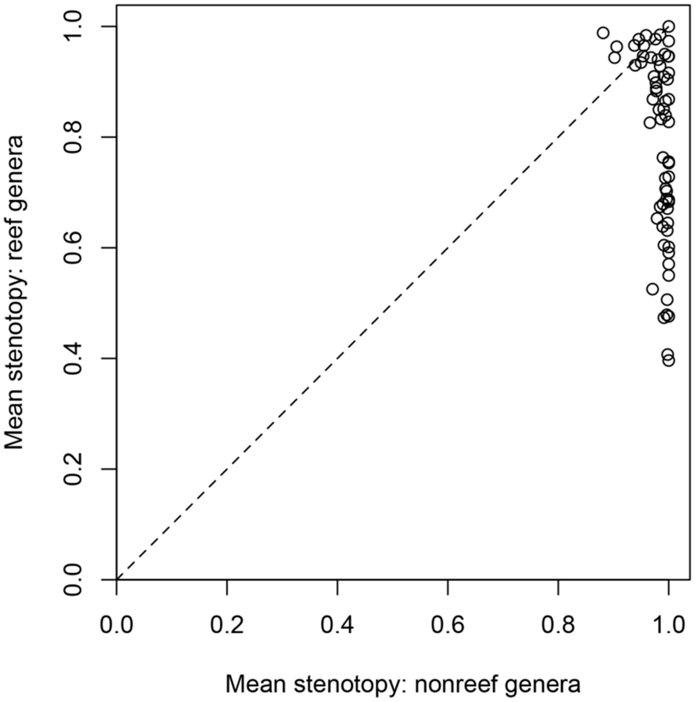


Figure 3.3: Stenotopy of reefal taxa and nonreefal taxa. Each point relates to the taxa within an individual time bin. The subset of taxa that are statistically reefal in a given stage are less stenotopic – are more likely to occur in both nonreefal and reefal habitats – than corresponding nonreefal taxa, which are overwhelmingly stenotopic and found only in nonreefal habitats.

Considering all 74 time bins in the data set, reefal genera are not significantly more geographically restricted than non-reefal genera (Fig. 3.4). Binomial regression analysis does indicate, however, that extinction negatively correlates with being geographically widespread across the dataset, for both reefal (Coeff: -0.74 ± 0.10; Pr <0.001) and nonreefal genera (Coeff: -1.07 ± 0.07; Pr=<0.001).

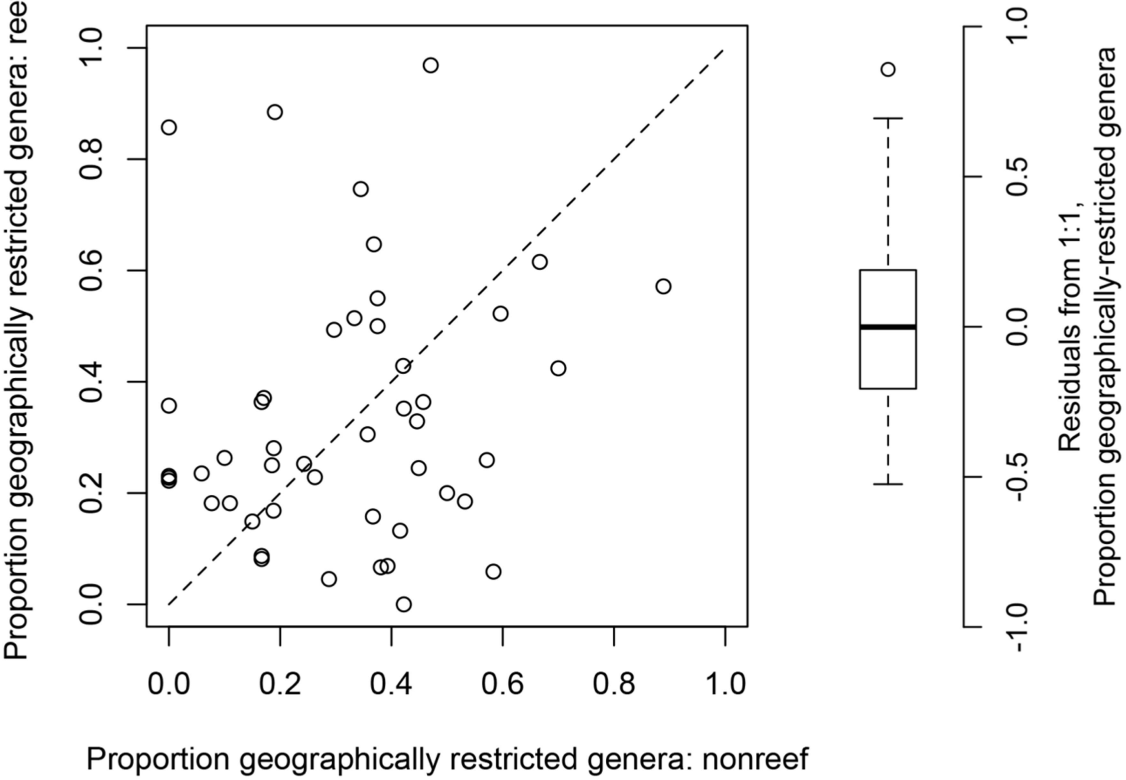


Figure 3.4: Proportion of reefal and nonreefal taxa that are geographically restricted in each stage, and distribution of residuals from the corresponding 1:1 line. Median: -0.01. Geographically restricted taxa are operationally defined here as having a paleogeographic range of less than 5 degrees of latitude or longitude. Reefal taxa are not more geographically restricted than nonreefal taxa.

3.5.3 Extinction of Reef-builders and Reef-Dwellers

Using the 63 stage boundaries where both reef-builders and reef-dwellers are present, the extinction patterns of reef-builders do not differ notably from those of reef-dwellers (Fig 3.5). Reef builders exhibit statistically higher proportional extinction in only two of 10 crisis events (20%; Pleinsbachian-Toarcian, Cenomanian-Turonian), and across 8 (15%) of 53 non-crisis boundaries, including the Cretaceous-Paleogene boundary (Fig. 3.5). Reef-dwellers exhibit higher proportional extinction for two crisis events (20%; Changhsingian-Induan, and Tithonian-Berriasian) and 9 (17%) non-crisis boundaries.

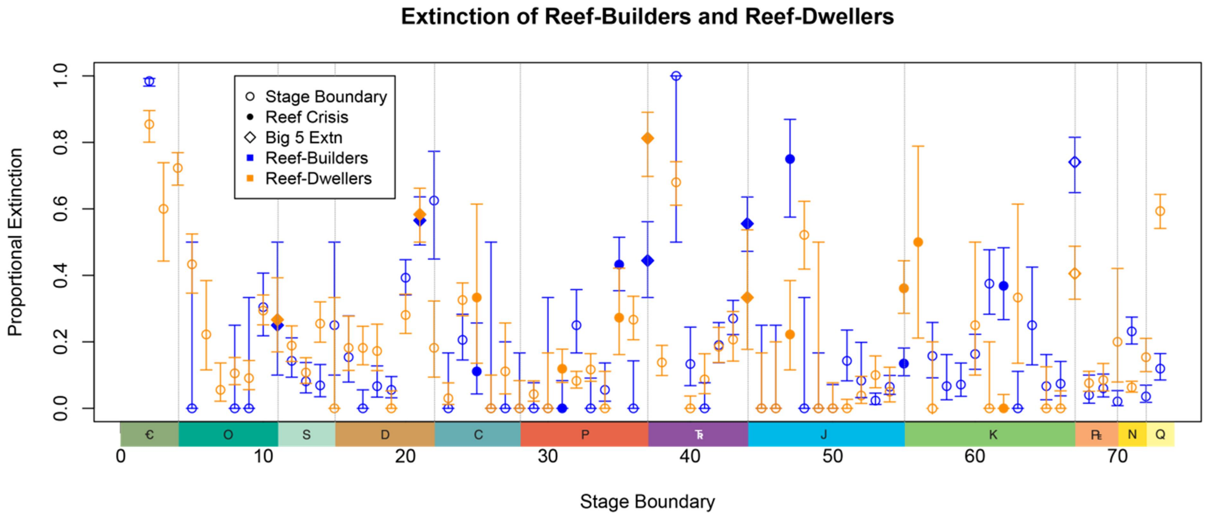


Figure 3.5: Proportional Extinction of reef-builder and reef-dweller genera, by stage. In the 63 boundary intervals where both reef builders and dwellers are present, reef builders exhibit significantly higher proportional extinction in only a few crisis (20%) and a few non-crisis intervals (20%), a rate closely matched by reef dwellers (15% and 17%, respectively).

3.5.4 *Persistence of reef habitat preference*

Persistence of reefal habitat preference ranges from complete turnover -- with zero reefal genera found in reef habitats in subsequent stages -- to nearly 90%, with almost all surviving genera retaining a reefal habit (Fig 3.6). High turnover across some stage boundaries is related to the extinction of major reef taxa, such as the loss of coral and stromatoporoid reefs across the Frasnian-Famennian boundary, or with the drastic loss of rudist reef-bearing carbonate platforms across the Cenomanian-Turonian. Other intervals with high turnover are synchronous to the introduction of new dominant reef-builders, such as the Dapingian-Darriwilian boundary, at which point reef building transitions from microbial to metazoan construction. Turnover in other intervals, though, is unrelated to major turnover of higher-order reef-building clades, but reflects turnover at lower taxonomic levels, or high turnover of reef-dwelling taxa (Fig 3.7), such as with the Roadian-Wordian (~8% of reef-dwellers persist as reefal) and Wuchiapingian-Changhsingian (~6% of reef-dwellers) boundaries. Overall, persistence of reef preference is very low across reef crisis events, including the Serpukhovian-Bashkirian (0 reefal genera persist as reefal), the Changsinghian-Induan (0 reefal genera), Rhaetian-Hettangian (~10%), Pleinsbachian-Toarcian (~11%), and Cenomanian-Turonian (~9%) intervals.

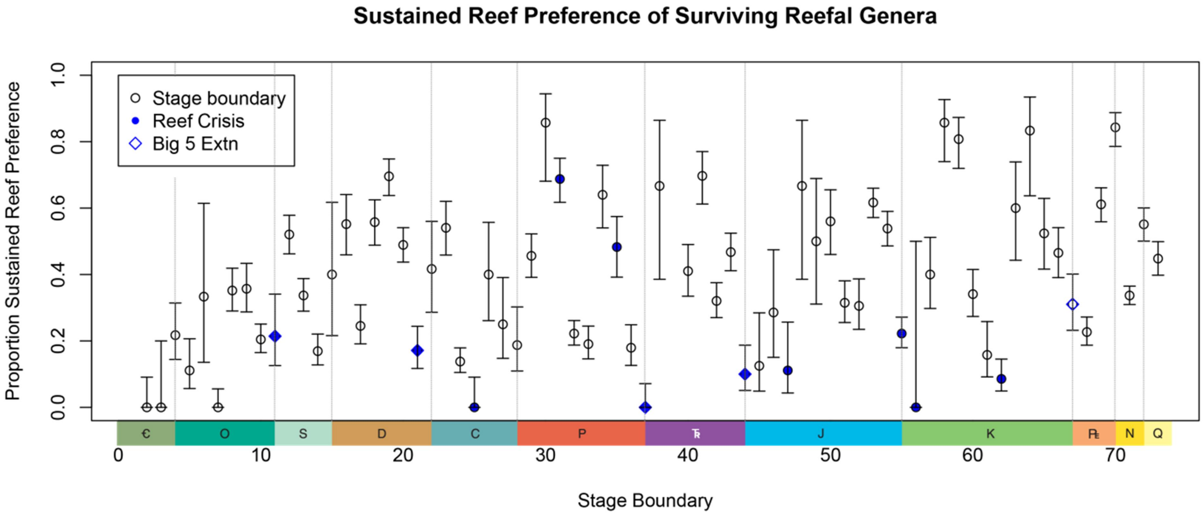


Figure 3.6: Persistence of reef preference among reefal genera, ≥4 occurrences per time bin, and limiting observation of reef preference to 2 time bins after the boundary of interest. Surviving reefal taxa are frequently identified as reefal in later stages, with very few occasions in which that isn't the case, particularly between the different Cambrian series, the Dapingian and Darriwilian stages of the Ordovician, the Serpukhovian and Bashkirian stages of the Carboniferous, and the Changhsingian and Induan stages at the Permian-Triassic boundary.

Reef-builders show significantly higher persistence in reefal habitats than reef-dwellers in 37 of the 62 (60%) time-bins where both sets are present (Fig. 3.7). Reef-dwellers return in a higher proportion than reef-builders across only one stage-boundary (Sakmarian-Artinskian), but the sample size of reef-builders there is so low (N=2) that the result is likely by chance. Although reef-builders could be replaced by new dominant reef-building taxa, the greater persistence of reef preference among surviving reef-builders is as expected. Although surviving reef-dwellers are able to return to the reef environment, they consistently return at lower proportions than reef-builders.

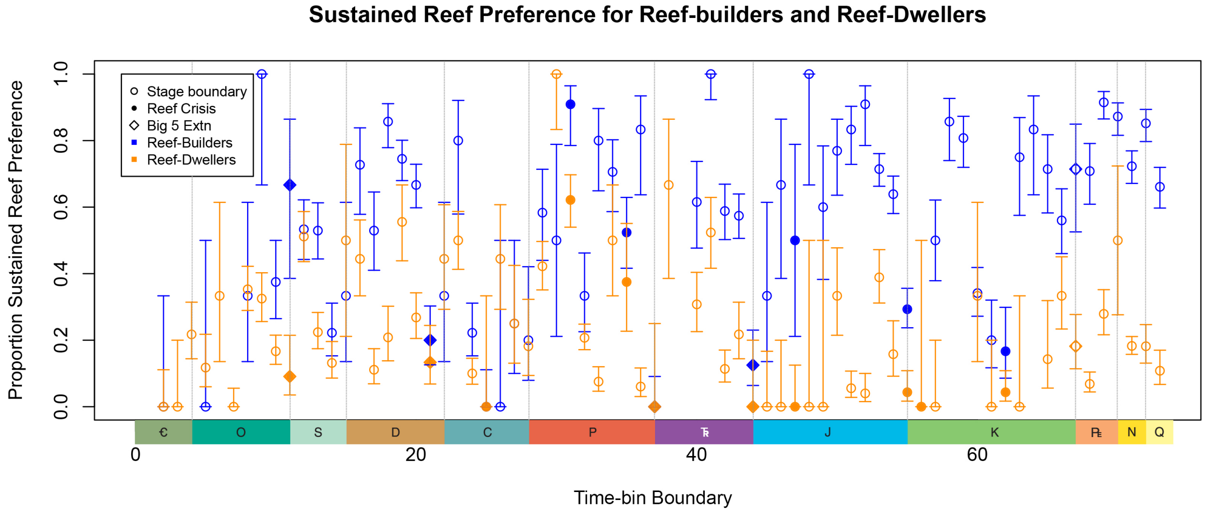


Figure 3.7: Persistence of reef preference among sets of reef builders and reef dwellers, based on ≥4 environmentally-identifiable occurrences. Of 62 boundaries where both reef builders and dwellers are present among surviving taxa, a higher proportion of reef-builders return to the reef environment than reef-dwellers in 37 (60%). Reef dwellers return in a higher proportion in only 1 instance, the Sakmarian-Artinskian boundary, where reef-builders comprise a very low sample size (n=2). The same pattern exists for the subset of reef crises, with 4 of the 10 qualifying crisis intervals exhibiting significantly higher persistence of reef preference by reef builders.

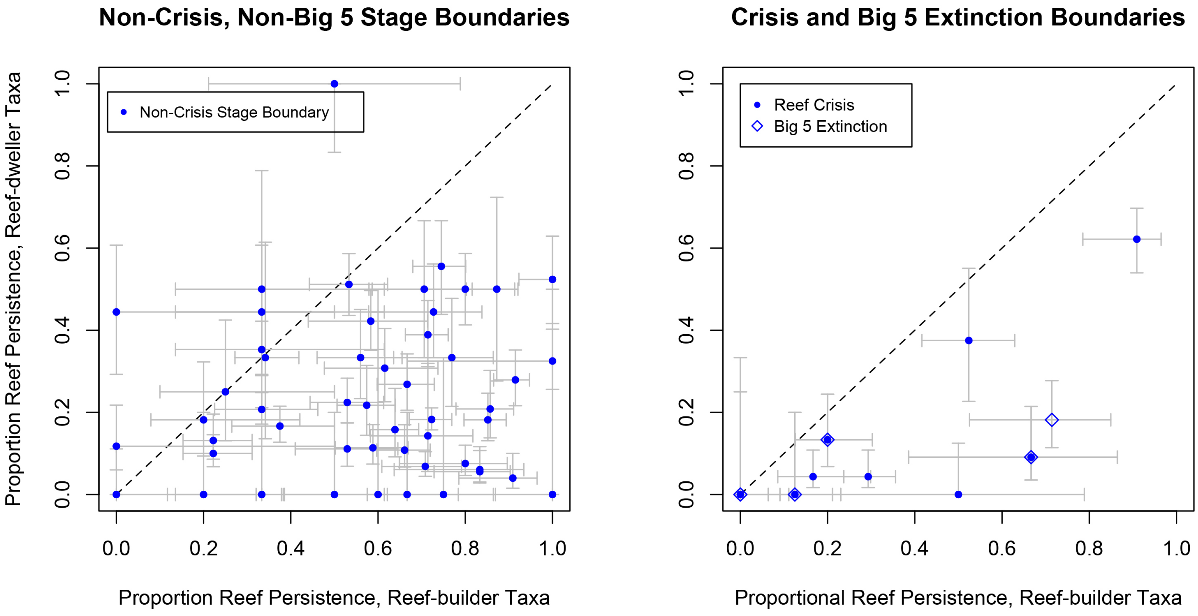


Figure 3.8: Persistence of reef preference for non-crisis events, and both crises and each of the "Big 5" extinctions. Reef-builders express much higher persistence in the reef fauna than dwellers, and crisis events fall in the same range as background intervals, with no consistent pattern.

In crossplot, background intervals display the general habit of reef builders to return to reefs most frequently (Fig 3.8). Reef crisis intervals exhibit a similar pattern, with reef-builders returning in either greater proportions or with no significant difference from the proportion of reef dwellers returning to the reef environment.

3.6 Discussion

3.6.1 Extinction of reefal genera

Reefal genera maintain low proportional extinction relative to nonreefal genera across most of the Phanerozoic, which could be related to the relative stenotopy of these groups. Habitat specialization contributes strongly to extinction risk (Munday 2004), and the stenotopy of nonreefal genera is consistent with what is observed here (Fig. 3.3). Further analysis of geographic range and extinction selectivity among the genera in the dataset is also consistent with previous work linking geographic restriction to extinction risk (Payne and Finnegan 2007; Jackson et al 1985; Jablonski 2005), but neither reefal nor nonreefal taxa are consistently biased towards geographically restricted genera through time.

The stenotopy of nonreefal genera is partially dictated by the method of identifying nonreefal taxa, but it isn't likely to bias the end result. In order to have nonreefal occurrences above the 95th percentile, a genus needs to have an overwhelmingly high percentage of nonreefal occurrences due to it being the most common environmental grouping in the data set. Reefs, being rarer in the data set, have a much lower proportional threshold for generic occurrences in order for a genus to be considered reefal. Previous analysis by Foote (2014) suggests that taxa that are not stenotopic for a preferred environment (carbonate/clastic, reefal/nonreefal carbonate) are rare, and that is also the case with this data set. Genera with ≥4 occurrences in a stage that cannot be identified as reefal or nonreefal are a very small proportion of the data set (14 of 4,085 genus/time-bin combinations). The addition of all unassigned taxa to the grouping of nonreefal taxa still produces the same pattern, with extreme stenotopy of genera that are not statistically overrepresented in reefs.

3.6.2 Elevated extinction during crises -- episodes of major turnover in reef-building

As suggested by Kiessling and Simpson (2011), there isn't necessarily a fundamental link between extinction of reefal taxa and loss of reef volume, but the intervals where proportional extinction of reefal genera increase include reef crises. This is the case at the Frasnian-Famennian and Pleinsbachian-Toarcian boundaries, where major groups of reef-builders, in particular, are subject to extinction. Reefs in subsequent stages are built by an entirely new suite of taxa; coral and stromatoporoid reef-builders wane at the Frasnian-Famennian (Webb 1998), with microbial reef-building returning to prominence. Similar turnover can be seen at the Pleinsbachian-Toarcian boundary, at which point heavy calcifiers such as corals and sponges face selective extinction (Dunhill et al. 2018), and the few remaining Triassic corals become extinct, making way for a new reef-building coral fauna that would radiate through the Upper Jurassic (Stanley 1988; Lathuilière 2011). This is also apparent, although not significantly in the presented data, at the end-Triassic, and at the end-Permian, the latter of which punctuates a major turnover of reefal taxa between the Paleozoic and Mesozoic eras (Pruss and Bottjer 2005).

The prime exception here, among major mass extinction-associated crises, is the end-Ordovician, when proportional extinction is not reported to be as high as in later extinction events. Reefs become rare in the first two stages of the Silurian, following the end-Ordovician extinction, but reefs are built by the same major clades--corals and stromatoporoids—although different groups of corals take on primary roles in reef-building (Copper and Jin 2012). Overall, reefs experienced little change over the Ordovician-Silurian boundary in comparison to other major extinction events (Wood 1999), similar to what is observed in nonreef benthic ecosystems of the time (Droser et al. 2000). Common reef fauna, including corals, undergo extinction of particularly stenotopic taxa, but return again in the Silurian in prominent ecological roles (Elias and Young 1998).

The most common drivers for the end-Ordovician extinction are tied to global cooling and loss of shallow shelf habitat due to a drop in sea level, but recent work has also suggested significant bottom water anoxia occurred at the same time (Bartlett et al. 2018). The lack of impact on reef environments may be tied to drivers of extinction that did not necessarily impact reef-builders' ability to calcify, as suggested with later mass extinctions that featured a biased extinction of unbuffered calcifiers (Kiessling and Simpson 2011). Furthermore, some difference in Ordovician extinction levels could be due to the method of calculation. Proportional extinction at that stage boundary is based on genera with environmental affinity known from the brief Hirnantian stage—a time during which reefs are rare, and in which the end-Ordovician glaciation is actively underway. The elevated extinction in the stage transition prior may reflect actual extinction at the Ordovician-

Silurian boundary—a consequence of using last occurrences as markers for extinction when following stages are likely to be undersampled (Foote 2007). The broader research documenting a minimal impact upon reef ecology by the end-Ordovician extinction suggests the observed difference is not an artifact of the method.

3.6.3 Elevated extinction in non-crisis events—also linked to major turnover in reef-builders

High proportional extinction among reef-builders is visible at crisis and non-crisis intervals featuring turnover of dominant reef-building clades. Elevated extinction of reef-builders is observed at three non-crisis intervals: between the 2nd and 3rd Cambrian Series, between the Wuchiapingian and Changhsingian stages of the Permian, and at the end-Cretaceous, between the Maastrichtian Stage and the lowest Paleocene.

The elevated extinction of reefal taxa in the Middle Cambrian is linked to the loss of the archaeocyathid reef fauna, and a return to dominance of microbial reef-building (Wood 1999). Despite the drastic turnover of reef-building taxa, there was no significant drop in reef carbonate production that would be identified as a reef crisis *sensu* Flügel and Kiessling (2002).

Elevated proportional extinction of reefal taxa across the Wuchiapingian-Changhsingian stage boundary does not relate to an immediate change in reef-builders, but rather relates to turnover at the end of the following stage driven by to the end-Permian extinction. Due to the identification of extinction by the last occurrence, extinction here can reasonably be inferred to be an artefact of incomplete sampling during the brief Changhsingian Stage, followed by true extinction at the end-Permian (Foote 2007).

Finally, the high proportional extinction of reefal taxa at the Cretaceous-Paleogene boundary marks a transition in the reef system to one in which scleractinian corals are the dominant reef-builders (Kiessling and Baron-Szabo 2004). Although not a reef crisis as determined by Flügel and

Kiessling (2002), it is a period of marked turnover in the reef-building fauna, much like the Cambrian interval discussed above.

Despite the lack of status as reef crises, these intervals show greater similarity to other mass-extinction related crises than they do to other crisis- and non-crisis intervals. With respect to extinction of reefal taxa, the reef crises defined here are not a cohesive group. The processes governing extinction are not necessarily tied to what controls reef carbonate production, but rather reef crises may amplify extinction when coincident with significant turnover of major reef-building clades.

3.6.4 Extinction of reef-builders and reef-dwellers

The subdivision of reefal genera into reef-builders and reef-dwellers reduces sample sizes so that confidence intervals of proportional extinction are quite large, making it more difficult to identify significant differences between reef-builders and –dwellers in individual time bins. However, among the time intervals where a significant differences appear, no consistent bias exists for elevated proportional extinction of reef-builders above that of reef-dwellers, nor during reef crises above non-crisis, background intervals. The initial hypothesis predicting that extinction would be exacerbated among reef-builders during reef crises is not supported by the data. Such elevated extinction does exist in some crisis intervals, most notably the Pliensbachian-Toarcian, and Cenomanian-Turonian intervals. However, its absence during many other equally strong reef crises (measured by reef-rock volume) and mass extinctions (elevated extinction among many clades in many settings) means that the extinction risk of reef-building clades must be context dependent.

3.6.5 Persistence of reefal habitat preference

Persistence of reefal habitat preference highlights the incumbency of reefal taxa from stage to stage. Beyond whether reef crises impact extinction of reef-builders and reef-dwellers, this analysis allows for examination of how survivors contribute to the reef environment in recovery. Not returning to the reef environment could reflect competitive exclusion by new reefal taxa, and/or the adaptation to more nonreefal settings. The loss of reefal preference is expected considering reefs are known to predominantly export diversity off-reef (Kiessling et al 2010), but a difference in retained reefal preference between reef-builders and -dwellers would indicate variable strength of incumbency effects and perhaps a dissociation between reef-builders and –dwellers as a reef fauna.

Reefal preference among surviving genera varies dramatically from time bin to time bin, with some of the lowest values around reef crises, suggesting that previous incumbents are less likely to return to the reef environment after perturbation. However, just as with extinction data, there are exceptions among reef crises. For example, there is relatively high persistence of reefal preference across the Artinskian-Kungurian (~69%) boundary, over which ecologic turnover of reefal fauna has been observed to be very gradual (Weidlich 2002). Nevertheless, a low persistence of reefal preference is generally the case during reef crises observed here, suggesting a broad link between loss of reefal carbonate and reduced incumbency of reef taxa post-crisis.

More directly so than with extinction, turnover of major reef-builders should be reflected in a lack of reefal persistence among surviving reefal taxa. Thus, reef-crisis intervals that are associated with major turnover of dominant reef-builders, including the Frasnian-Famennian, Serpukhovian-Bashkurian, Changhsingian-Induan, Rhaetian-Hettangian, Pliensbachian-Toarcian, and the Cenomanian-Turonian intervals, reveal among the lowest sustained reefal preference of constituent taxa. Non-crisis intervals known for turnover of reef-building taxa, particularly the Floian-Dapingian interval of the Ordovician, follow suit, re-emphasizing that faunal turnover of reef-builders is more fundamental to persistence than the loss of reef habitat.

However, many time bins show similarly low reefal persistence, but unaccompanied by major, rapid turnover of reef-builders. These include the Visean-Serpukhovian, the Kungurian-Roadian, Roadian-Wordian and Wuchiapingian-Changhsingian intervals in the Paleozoic, and the Hettangian-Sinemurian and the Sinemurian-Pliensbachian intervals in the Mesozoic. The low reefal persistence here is driven by low reefal persistence of reef-dwellers, particularly in the Mesozoic, where reef-dwellers consistently leave the reef fauna both in reef crises and background intervals. Long-term instability of the reef system and perhaps increased competition in reefs during the Mesozoic Marine Revolution may have led to greater export of taxa off-reef than in the Paleozoic.

The drop in reef persistence across the Visean-Serpukhovian interval is problematic in that it was an interval of reef expansion and diversification of reef taxa, not contracting once more until late in the Serpukhovian (Webb 2002). Both reef-builders and reef-dwellers reveal low persistence of reefal preference (~22% and ~10%, respectively) during this interval. This low persistence may be due to a dramatic difference in sampling; the Visean reef fauna includes 124 genera, while the following two stages have only 22 qualifying reefal genera between them. Reef-building corals and bryozoans, in addition to reef-dwelling bivalves, bryozoans, crinoids and brachiopods, disappear from the identifiable reef fauna; beyond sampling effects, it is unclear what would cause this drop in reefal taxa.

3.6.6 Relationship to other potential reef crises

Perhaps the variability in extinction and persistence of reefal taxa during the crises identified here is indicative of too broad a threshold for identification of reef crises by Flügel and Kiessling (2002). Using the more restrained crisis identification of Kiessling (2011) removes reef crises with low proportional extinction (Serpukhovian-Bashkirian, Artinskian-Kungurian, and Berriasian-Valanginian), but adds two intervals with the same feature—the Floian-Dapingian, and Paleocene-Eocene boundaries. The first of these, in the Middle Ordovician (Floian-Dapingian), was driven by the loss of large microbe-dominated reefs and the slow shift to smaller reefs dominated by metazoans (such as sponges, bryozoans, and corals). The second potential reef crisis reflects the abrupt loss of skeletal reefs in the earliest Eocene, following the Paleocene-Eocene Thermal Maximum. The Floian-Dapingian crisis shows no significant difference in proportional extinction between reefal and nonreefal genera (Fig 2A), as well as between reef-builders and reef-dwellers (Fig 5A). The Paleocene-Eocene boundary has relatively low proportional extinction for both reefal (~7%) and nonreefal genera (~15%), with significant difference between them, and no significant difference between extinction of reef-builders and reef-dwellers (~4% and ~8%, respectively). In this manner, these two reef crises differ dramatically from other mass-extinction- linked reef crises.

In contrast, reefal preference over the Floian-Dapingian and Paleocene-Eocene boundaries reveals dynamics similar to all other reef crises identified by Kiessling (2011). No metazoan reef-builders from the Floian are found as reefal taxa in subsequent time bins, and the surviving reef-dwellers are no longer identified as reefal genera either; persistence of reef habit is thus nil in both groups. Similarly, reefal-genera maintain a very low preference for reefal habitats across the Paleocene-Eocene boundary, but in contrast, the pattern is primarily driven by the low incumbency of reef-dwellers. Reef-building genera, particularly corals, maintain their reef preference in subsequent stages, even though there is a documented gap in coral reef-building (Kiessling and Baron-Szabo 2004).

If either of these intervals were included in the grouping of reef crises, they would each be unique among reef crises, and would introduce similar inconsistencies in extinction pattern. The Floian-Dapingian transition is a challenge to interpret within this data set because the reef crisis is ultimately the loss of a global microbial reef-building, whereas this is an analysis of metazoan extinction associated with reef loss. Demosponges occur in conjunction with microbial reef-building within Floian reefs, but no other reef-building metazoans appear until the Dapingian and Darriwilian (Adachi et al 2011). The event features a dramatic turnover in the few reef-builder clades present –

particularly lithistid sponges -- and their extinction and incumbency habits are similar to those encountered during later major transitions in reef-builder composition, but the nature of that transition is fundamentally different from later intervals.

The Paleocene-Eocene boundary actually differs little from the other Cenozoic, non-crisis intervals. Reef-builders and reef-dwellers exhibit similar proportional extinctions from the beginning of the Cenozoic to the beginning of the Pliocene, and reef-builders retain similar reef preferences. The Paleocene-Eocene boundary interval may be an ocean acidification event (Honisch et al. 2012), but the community structures of reefs, and identities of major reef building groups (i.e. scleractinian corals), do not change over this interval.

Reef crises can have many different causes, and the response of constituent reef-builders and reef-dwellers may need to be examined on an individual basis. Nevertheless, the inclusion of these two potential crises makes no difference in the overall patterns observed with respect to extinction, but would further underscore the negative impact reef crises have upon the persistence of reefal habitat preference.

3.6.7 How cohesive are builders and dwellers as a 'reef fauna'?

Both reef-builders and –dwellers exhibit elevated proportional extinction at mass extinction-linked reef crises, suggesting similar susceptibility to the concatenation of stressors responsible for mass extinction, not necessarily the loss of reef habitat itself. However, they show consistently different levels of reef incumbency for reefs post-crisis. Reef-builders are more consistent in maintaining a reefal preference, suggesting an incumbency advantage; reef-dwellers are more likely to leave the reef environment, becoming nonreefal in preference and suggesting an inability to re-establish themselves in newly constituted post-crisis reefs. Moreover, where both exist in sufficient numbers, their proportional extinctions vary inconsistently: builders and dwellers fluctuate interval-to-interval as to which one exhibits the higher extinction rate. This inconsistency suggests that builders and dwellers are responding to different, time-specific conditions that affect one group more strongly than the other. Consequently, the two groups should probably be analyzed separately. Although there are broad similarities, as listed above, reef-dwellers do not consistently mirror the fate of reef-builders, and thus do not act as a cohesive reef fauna from stage to stage.

3.7 Conclusions

Reefal taxa exhibit low proportional extinction across the Phanerozoic, in comparison to nonreef taxa. This is likely linked to the relative eurytopy of reefal taxa. No consistent difference was observed in proportional extinction of reef-builders and –dwellers, but reef-builders and -dwellers do exhibit consistent difference in persistence of reefal preference. Reef-builders are strongly associated with the reef environment, and are more likely to return to the reef environment between time bins, including after reef crisis events. Reef-dwellers are more likely to leave the reef environment, although at no greater a proportion during reef crises than otherwise. As such, reef builders and dwellers respond in parallel to drivers of extinction but operate independently when it comes to incumbency, suggesting that builders and dwellers do not operate as a cohesive reef fauna. The distinct response of reef-builders and –dwellers can be informative in examining the nature of a reef crisis, and perhaps should be addressed more frequently in examining such intervals.

In some ways, proportional extinction and the persistence of reefal habitat preference align more consistently with intervals featuring major ecological turnover among dominant reef-builders than with episodes of reduced reefal carbonate production. Further work should better address the relationship of particular kinds of reef-builder turnover to reef crises, and to better distinguish the relationship between reef-dwellers and non-reefal carbonate taxa during these intervals. If reef-dwellers are passive occupiers of reefs, we might expect them to express dynamics closer to taxa that prefer nonreef carbonates.

Reef crises are heterogeneous in cause, and consequence. Nevertheless, with the exception of the Hirnantian-Rhuddanian, reef crises that are coincident with mass extinction events, or major turnovers of dominant reef-building clades, exhibit extinction and recovery dynamics that are coherent and distinctly different from other identified reef crises. When looking at reef crises, it would be worthwhile to examine these intervals separate from intervals that feature reduced carbonate production, synthesizing the rock-volume-based definition, and the ecologically grounded definition, of a 'reef crisis'.

Appendix A : Windley Key Fossil Reef Transects

Table A.1: 20m transect "A", with *in situ* framework elements, South Wall

Pleistocene Windley Key A				
Framework Start (m)	Framework End (m)	Height (m)	ID	Center (m)
0	0.27	0.31	O. annularis	0.135
0.82	0.89	0.44	O. annularis	0.855
1.42	1.5	0.4	O. annularis	1.46
1.77	1.88	0.46	O. annularis	1.825
2.17	2.39	0.12	P. asteroides	2.28
2.8	3.11	0.23	P. asteroides	2.955
3.21	3.28	0.15	P. asteroides	3.245
4.08	4.17	0.09	O. annularis	4.125
4.17	4.35	0.33	P. asteroides	4.26
4.64	4.81	0.5	P. asteroides	4.725
4.87	5.03	0.18	O. annularis	4.95
5.04	5.17	0.24	O. annularis	5.105
5.19	5.27	0.31	O. annularis	5.23
5.37	5.44	0.09	O. annularis	5.405
5.5	5.62	0.23	P. asteroides	5.56
5.72	5.88	0.26	P. asteroides	5.8
6.19	6.26	0.17	O. annularis	6.225
6.3	6.71	0.41	D. strigosa	6.505
8.04	8.37	0.98	D. strigosa	8.205
8.45	8.54	0.02	O. annularis	8.495
8.67	8.84	0.53	O. annularis	8.755
9.17	9.26	0.23	O. annularis	9.215
9.88	9.93	0.14	O. annularis	9.905
10.47	10.53	0.47	O. annularis	10.5
11.04	11.56	0.85	O. annularis	11.3
11.65	11.78	0.2	P. asteroides	11.715
11.89	12.05	0.11	O. annularis	11.97
12.7	12.83	0.32	O. annularis	12.765
12.91	12.94	0.1	O. annularis	12.925
13.07	13.24	0.28	O. annularis	13.155
13.44	13.58	0.2	P. asteroides	13.51

Table A.1, continued…

13.82	13.87	0.4	O. annularis	13.845
13.9	14.06	0.23	O. annularis	13.98
14.15	14.29	0.29	O. annularis	14.22
14.48	14.69	0.43	O. annularis	14.585
14.74	14.85	0.33	O. annularis	14.795
15.06	15.16	0.11	O. annularis	15.11
15.82	15.92	0.57	D. strigosa	15.87
16.05	16.19	0.2	D. strigosa	16.12
16.19	17.58	1.17	O. annularis	16.885
18.27	18.39	0.38	P. asteroides	18.33
18.45	18.56	0.59	O. annularis	18.505
19.02	19.15	0.95	O. annularis	19.085
19.45	19.65	0.16	O. annularis	19.55

Table A.2: 20m transect "B", with *in situ* framework elements. South Wall of quarry

Pleistocene Windley Key B				
Framework Start (m)	Framework End (m)	Height (m)	ID	Center (m)
0.15	0.19	0.16	O. annularis	0.17
0.24	0.28	0.2	O. annularis	0.26
0.39	0.49	0.29	O. annularis	0.44
0.61	0.81	0.29	O. annularis	0.71
0.84	1.83	0.72	D. labyrinthiformis	1.335
1.88	1.9	0.35	O. annularis	1.89
3.96	4.01	0.05	P. porites	3.985
4.29	4.36	0.15	O. annularis	4.325
4.55	4.74	0.19	O. annularis	4.645
5.02	5.08	0.06	O. annularis	5.05
5.15	5.27	0.12	O. annularis	5.21
6.31	6.42	0.3	P. asteroides	6.365
7.94	8.03	0.22	D. strigosa	7.985
8.08	8.24	0.41	P. asteroides	8.27
8.34	8.46	0.41	P. asteroides	8.27
8.83	8.97	1.57	O. annularis	8.9
10.07	10.24	0.18	O. annularis	10.155
10.75	10.78	0.06	P. asteroides	10.765

Table A.2, continued…

11.55	11.61	0.29	O. annularis	11.58
11.65	11.69	0.09	O. annularis	11.67
11.76	11.81	0.28	O. annularis	11.845
11.84	11.89	0.28	O. annularis	11.845
11.91	11.93	0.28	O. annularis	11.845
11.99	12.12	0.1	P. porites	12.055
12.36	12.48	0.24	O. annularis	12.42
13.18	13.28	0.23	P. asteroides	13.23
13.53	13.63	0.27	D. strigosa	13.58
14.09	14.2	0.13	P. asteroides	14.145
14.73	14.98	0.1	P. asteroides	14.855
15.35	15.58	0.12	P. asteroides	15.465
15.64	15.78	0.12	P. asteroides	15.71
16.41	16.64	1	O. annularis	16.525
16.64	16.95	0.31	O. annularis	16.795
18.56	18.64	0.05	D. strigosa	18.6
19.45	19.57	0.2	P. asteroides	19.51

Table A.3: 20m transect "C", with *in situ* framework elements, North wall

Pleistocene Windley Key C				
Framework Start (m)	Framework End (m)	Height (m)	ID	Center (m)
0.08	0.13	0.05	Orbicella annularis	0.105
0.48	0.53	0.03	O. annularis	0.505
0.55	0.58	0.02	O. annularis	0.565
1.28	1.34	0.19	O. annularis	1.31
1.99	2.05	0.01	Porites asteroides	2.02
2.13	2.18	0.03	P. asteroides	2.155
2.62	2.92	0.26	P. asteroides	2.77
3.05	3.08	0.25	Porites indet.	3.065
3.08	3.26	0.07	O. annularis	3.17
3.43	3.75	1.03	O. annularis	3.59
4.17	4.23	0.67	O. annularis	4.25
4.29	4.33	0.67	O. annularis	4.25
4.45	4.5	0.12	P. asteroides	4.475
4.66	4.71	0.32	O. annularis	4.685

Table A.3, continued…

4.89	5.08	0.26	O. annularis	4.985
5.35	5.5	0.07	O. annularis	5.425
5.81	5.83	0.02	O. annularis	5.82
6.36	6.49	0.21	O. annularis	6.425
6.63	6.83	0.5	O. annularis	6.73
7.32	7.47	0.1	O. annularis	7.395
7.54	7.64	0.24	O. annularis	7.59
7.67	7.8	0.18	O. annularis	7.735
7.88	7.93	0.34	O. annularis	7.905
8.04	8.11	0.09	O. annularis	8.075
8.75	8.8	0.03	Porites porites	8.775
8.85	8.89	0.03	P. porites	8.87
8.98	9.09	0.13	O. annularis	9.035
9.35	9.49	0.28	O. annularis	9.42
9.8	9.91	0.07	P. asteroides	9.855
10.74	10.93	0.64	O. annularis	10.835
11.75	12.08	0.32	P. asteroides	11.915
12.24	12.82	0.7	Diploria strigosa	12.53
13.44	13.54	0.54	O. annularis	13.49
13.91	13.94	0.11	P. asteroides	13.925
14.22	14.3	0.07	P. asteroides	14.26
14.97	15.02	0.09	O. annularis	14.995
15.45	15.5	0.06	P. asteroides	15.475
15.5	15.55	0.04	O. annularis	15.525
15.72	15.86	0.04	O. annularis	15.79
15.94	15.98	0.03	O. annularis	15.96
16.19	16.26	0.12	Colpophylla natans	16.225
16.46	16.52	0.6	O. annularis	16.49
17.05	17.47	0.4	D. strigosa	17.26
18.65	18.76	0.24	P. asteroides	18.705
19.35	19.5	0.13	O. annularis	19.425
19.53	19.8	0.12	O. annularis	19.665

Table A.4: 20m transect “D”, with *in situ* framework elements, North wall

Pleistocene Windley Key D				
Framework Start (m)	Framework End (m)	Height (m)	ID	Center (m)
0.19	0.36	0.26	Porites asteroides	0.275
0.52	0.59	0.25	Orbicella annularis	0.555
0.9	0.95	0.32	P. asteroides	0.925
0.96	1	0.25	O. annularis	0.98
3.1	3.97	0.83	Diploria strigosa	3.535
4.58	4.8	0.19	P. asteroides	4.69
4.82	4.94	0.13	O. annularis	4.88
5.26	5.5	0.1	P. asteroides	5.38
6.27	6.39	0.17	P. asteroides	6.33
7.21	7.58	0.34	D. strigosa	7.395
7.95	8.06	0.05	O. annularis	8.005
8.72	8.78	0.25	P. asteroides	8.75
9.45	9.49	0.23	O. annularis	9.47
9.64	10	0.31	O. annularis	9.82
10.09	10.13	0.03	O. annularis	10.11
10.24	10.55	0.65	Colpophylla natans	10.395
10.88	11.02	0.04	Porites porites	10.95
11.82	11.87	0.1	P. porites	11.845
11.93	11.97	0.09	O. annularis	11.95
12.36	12.54	0.37	O. annularis	12.45
12.55	12.6	0.06	O. annularis	12.575
12.73	12.89	0.35	O. annularis	12.81
14.35	14.38	0.08	O. annularis	14.365
15.84	15.95	0.08	O. annularis	15.895
17.32	17.41	0.05	C. natans	17.365
18.8	18.87	0.11	O. annularis	18.835
19.69	19.77	0.16	O. annularis	19.73

Table A.5: 20m transect "E", with *in situ* framework elements. North Wall

Pleistocene Windley Key E				
Framework Start (m)	Framework End (m)	Height (m)	ID	Center (m)
0.59	0.75	0.23	Porites asteroides	0.67
0.85	0.93	0.07	P. asteroides	0.89
0.99	1.04	0.09	Orbicella annularis	1.015
2.3	2.47	0.17	P. asteroides	2.385
2.53	2.67	0.2	P. asteroides	2.6
2.71	2.78	0.06	P. asteroides	2.745
3.39	3.42	0.25	O. annularis	3.405
3.56	3.61	0.16	O. annularis	3.585
3.64	3.74	0.04	O. annularis	3.69
3.94	4.01	0.25	O. annularis	3.975
4.07	4.34	0.22	O. annularis	4.205
5.11	5.18	0.04	O. annularis	5.145
5.59	5.66	0.1	O. annularis	5.625
5.74	5.77	0.06	O. annularis	5.755
5.9	5.93	0.08	O. annularis	5.915
6.45	6.51	0.78	Diploria strigosa	6.895
6.7	7.34	0.78	D. strigosa	6.895
11	11.08	0.39	P. asteroides	11.17
11.14	11.23	0.39	P. asteroides	11.17
11.25	11.34	0.39	P. asteroides	11.17
11.58	11.72	0.13	P. asteroides	11.65
12.24	12.38	0.14	P. asteroides	12.31
14.18	14.26	0.1	P. asteroides	14.22
14.45	14.68	0.18	P. asteroides	14.565
15.49	15.65	0.24	P. asteroides	15.57
16.91	16.96	0.09	P. asteroides	16.935
17.42	17.52	0.08	P. asteroides	17.47
17.71	17.78	0.19	P. asteroides	17.8
17.85	17.89	0.19	P. asteroides	17.8
17.94	17.98	0.09	P. asteroides	17.96
18.64	18.71	0.47	P. asteroides	18.675
18.82	18.93	0.47	P. asteroides	18.875
19.15	19.27	0.15	P. asteroides	19.21
19.66	19.73	0.12	P. asteroides	19.695

Table A.6: Summary of 10m SCI measurements on each of the five 20-meter transects. Transects A and B, on the southern wall, were more coral-dense, while Transect E exhibited few reef-builders, and subsequently, low SCI measurements. 10m measures were taken from half-meter shifts along a single tape transect, and thus represent the variation one would expect given arbitrary transect starting points.

	Transect A	Transect B	Transect C	Transect D	Transect E
Mean SCI	1.29	1.20	1.18	1.14	1.06
SD	0.06	0.05	0.07	0.03	0.03
Min SCI	1.23	1.13	1.09	1.07	1.02
Max SCI	1.43	1.31	1.30	1.24	1.10
Median SCI	1.27	1.19	1.15	1.14	1.06

Appendix B : Middle Paleozoic, Laurentian fossil reef data

Table B.1: Table of reef sites, builder morphotypes, facies, dimensions, relief, and references. Paleoreef database # relates to entries in PARED (https://www.paleo-reefs.pal.uni-erlangen.de), last accessed September 2018

PALEO-REEF DATABASE #	NAME	FORMATION	PERIOD	SERIES	DOMINANT BUILDER MORPHO-TYPE 0=Mud 1=Encrusting 2=Massive 3=Columnar 4=Tabular 5=Branching 6=multi	BUILDER MORPHOTYPE (2=dominant, 1=present, 0= not present)						TOTAL	LATERAL SIZE (m)	THICKNESS (m)	EST. RELIEF (N/L/M/H/H2/H3)	# OF ASSOCIATED FACIES	Citations
						0	**1**	**2**	**3**	**4**	**5**						
1355	Slave Field, AB	Slave Point	Devonian	Middle Devonian	6	0	0	2	0	2	1	3	2	25	H	4	Dunham et al, 1983
1487	Roberts Hill, Albany, NY	Onondaga	Devonian	Middle Devonian	5	0	1	1	1	0	2	4	230	15	H	5	Wolosz, 1992; personal observation
1501	Montague, NJ	Coeymans	Devonian	Lower Devonian	5	0	1	1	1	1	2	5	100	15	H	4	Precht, 1989
1593	Wyckoff Field, Jasper, Steuben Co., NY	Onondaga	Devonian	Middle Devonian										61	H	4	Friedman 1985
1467	Whitehorse, Jasper Basin, AB		Devonian	Upper Devonian	6	1	0	1	1	0	1	4	200	30	H2	4	Hedinger and Workum, 1989
1580	Rainbow Field, AB	Keg River	Devonian	Middle Devonian	6	0	0	2	1	0	2	3	3200	290	H3	14	Langton and Chin, 1968; Hriskevich, 1970
1356	Swan Hills Buildup, AB	Swan Hills	Devonian	Upper Devonian	6	0	1	2	0	2	2	4	10000	60	H3	12	Viau 1983; Harvard and Oldershaw, 1976; Wong and Oldershaw, 1980; Wendte and Stoakes, 1982
1504	Blue Fjord, Ellesmere Island	Blue Fjord	Devonian	Lower Devonian	6	0	1	1	1	1	1	5	10000	100	H3	10	Smith, 1989
1455	Cripple Creek, Fairholme, AB	Southesk	Devonian	Upper Devonian	6	1	0	1	0	1	1	4	100000	300	H3	7	Eliuk 1989
1498	Section-Slide Creeks, Miette, AB	Cairn	Devonian	Upper Devonian	6	0	1	1	0	1	1	4	15000	300	H3	6	Mountjoy, 1989

Table B.1, continued…

1523	Madeleine River, Gaspe, QC		Devonian	Lower Devonian	6	0	1	1	1	1	1	5	60	15	L	6	Bourque, 1972; Bourque et al, 1986
1459	Normandville, AB	Wabamun	Devonian	Upper Devonian	6	0	1	1	0	1	0	3	1500	10	L	4	Halin-Dehardja, 1989
1586	Columbus, IN		Devonian	Middle Devonian	4	0	1	0	1	2	0	3	25.9	2.74	L	3	Carozzi et al 1959
2443	Kelleys Island, OH	Lucas	Devonian	Middle Devonian	2	0	0	2	1	1	1	4	15	1.5	L	4	Bjerstedt and Feldmann, 1985
2441	Hudson River, E New York	Manlius	Devonian	Lower Devonian	2	0	1	2	1	1	0	4	NA	NA	L	1	Stock, 1991
2440	Hudson River, SE New York	Manlius	Devonian	Lower Devonian	2	0	1	2	1	1	0	4	NA	NA	L	1	Stock, 1991
1500	Cline River, Fairholme, AB		Devonian	Upper Devonian	2	0	0	2	0	0	0	1	30	1	L	1	Pratt, 1989
2212	Parsons Quarry, Tennessee	Rockhouse	Devonian	Lower Devonian	1	1	2	0	0	0	0	2	14	3	L	4	Gibson et al 1988
1485	Port Colburne, Ontario	Onondaga	Devonian	Middle Devonian	NA	NA	NA	NA	NA	NA	NA	NA	1500	20	M	8	Cassa and Kissling, 1982; Moore 1989
2550	Silica, Ohio		Devonian	Middle Devonian	5	0	0	0	0	0	2	1	30	4.6	M	NA	Stumm, 1969
1484	Leroy, Genesee County, New York	Onondaga	Devonian	Middle Devonian	5	0	1	1	1	1	2	5	46	6.1	M	7	Poore, 1969; Lindemann, 1989; personal observation
1502	Knoxboro, Central New York State	Coeymans	Devonian	Lower Devonian	5	0	1	1	0	1	2	4	NA	7	M	5	Isaacson and Curran, 1981; personal observation
3630	Lenox reef, Central New York State	Coeymans	Devonian	Lower Devonian	4	0	0	0	0	2	1	2	30.5	6.1	M	NA	Oliver, 1960; personal observation
1499	Formosa, Ontario	Amherstburg	Devonian	Lower Devonian	4	0	1	1	0	2	1	4	900	15	M	4	Fagerstrom 1961, Pratt 1989; personal observation
2197	Mt. Tom, New York	Onondaga	Devonian	Middle Devonian	4	0	0	1	0	2	1	3	185	14.6	M	2	Wolosz and Paquette, 1988; personal observation
1880	Alpena, Michigan		Devonian	Middle Devonian	2	0	1	2	0	0	1	3	“several hundred”	10.7	M	3	Grabau, 1903
1456	Mercy Bay, Banks Island, N.W.T.		Devonian	Upper Devonian	6	0	0	1	0	1	0	2	500	60	NA	NA	Embry and Klovan 1971; Embry 1989
1468	Boule Range, Jasper Basin, Alberta		Devonian	Upper Devonian	NA	NA	NA	NA	NA	NA	NA	NA	200	30	NA	NA	Mountjoy, 1965; Hedinger and Workum, 1989

Table B.1, continued…

1466	Rocky Pass, Jasper Basin, Alberta	Southesk	Devonian	Upper Devonian	NA	NA	NA	NA	NA	NA	NA	NA	200	30	NA	NA	Hedinger and Workum, 1989
1529	Carnwath River, N.W.T.		Devonian	Middle Devonian	NA	NA	NA	NA	NA	NA	NA	NA	14	9	NA	NA	MacKenzie, 1969; Mountjoy and MacKenzie, 1972
1532	Keg River Barrier Reef, Pine Point	Pine Point	Devonian	Middle Devonian	6	0	0	1	0	1	1	3	NA	215	NA	8	Skall, 1975
1470	Rosevear Field, Alberta	Swan Hills	Devonian	Upper Devonian	6	0	0	1	0	1	1	3	>100000	65	NA	8	Kaufman and Meyers 1989
1458	Golden Field, Alberta		Devonian	Middle Devonian	6	0	1	1	0	1	1	4	20000	40	NA	7	Gosselin et al 1989
1507	Gift Lake Slave Point Field, Alberta		Devonian	Middle Devonian	6	0	0	1	0	1	1	3	2000	24	NA	7	Tooth and Davies, 1989
1457	Evi Field, Alberta	Slave Point	Devonian	Middle Devonian	6	0	1	1	0	1	0	3	15000	10	NA	4	Gosselin et al 1989
1460	Allstones Creek, Alberta		Devonian	Upper Devonian	6	0	1	1	1	0	1	4	500	30	NA	3	Hedinger, 1989
1461	Hummingbird and Whiterabbit, Alberta	Fairholme	Devonian	Upper Devonian	NA	NA	NA	NA	NA	NA	NA	NA	10000	300	NA	2	Hedinger and Workum, 1989
1357	Nisku, Brazeau, Alberta		Devonian	Upper Devonian	5	2	1	0	0	1	2	4	1500	100	NA	NA	Machel, 1983
1594	Cyclone Field, McKean Co., Pennsylvania		Devonian	Middle Devonian										55	NA	4	Friedman, 1985
1452	Squaw Mountain, Ogilvie Mts, Alaska	Ogilvie	Devonian	Lower Devonian	2	0	1	2	0	1	0	3	2000	40		6	Clough and Blodgett, 1985; Clough and Blodgett 1989
1883	Lime Hills, Holitna Basin, Sleetmute, Alaska		Devonian	Lower Devonian	1	0	2	0	0	0	1	2	”100s of kms”	500		5	Clough and Blodgett, 1985
1449	White Man Gap, Canmore, Alberta	Cairn	Devonian	Upper Devonian	0	2	0	1	0	0	1	3					Bloy et al 1989
1509	Southesk Cairn, Alberta	Flume	Devonian	Upper Devonian									66000	325		9	Weissenberger and McIlreath, 1989
1353	Ancient Wall, Alberta		Devonian	Upper Devonian										300			Geldsetzer, 1989

Table B.1, continued…

3821	Swan Hills Buildup, Alberta	Swan Hills	Devonian	Upper Devonian										60			Viau, 1983
1354	Ancient Wall II, AB	Southesk + Mt. Hawk	Devonian	Upper Devonian													Geldsetzer, 1989
1454	Sierra, BC		Devonian	Middle Devonian													Collins and Lake, 1989
1486	Syracuse, NY	Onondaga	Devonian	Middle Devonian													Lindemann 1989
1881	Williamsville and Buffalo, NY	Onondaga	Devonian	Middle Devonian													Oliver 1952 (Thesis, Cornell)
1854	Crown Point, Elk River, TN	Carters Limestone	Ordovician	Upper Ordovician	1	0	2	1	0	0	1	3	381	18	H	6	Alberstadt et al 1974; Zurawski 1973 (Thesis, Vanderbildt), pers obs
1411 B	Salmon River, W Anticosti Isl.	Ellis Bay	Ordovician	Upper Ordovician	1	0	2	1	0	1	0	3	105	8	H	5	Copper, 1989
1393	S Mackenzie Mts. II, N.W.T.		Ordovician	Lower Ordovician	1	0	2	1	0	0	0	2		123	H	4	Pratt, 1989
2463	Deane Quarry + Alcoa Highway, Knoxville, TN	Holston	Ordovician	Upper Ordovician	1	1	2	0	0	0	1	3		100	H	5	Walker and Ferrigno, 1973
1392	S Mackenzie Mts., N.W.T.	Broken Skull	Ordovician	Lower Ordovician									50000	123	H	3	Pratt, 1989
2400 B	Bell Peninsula, Southampton Island, N.W.T.	Red Head Rapids	Ordovician	Upper Ordovician	1	0	2	0	0	0	0	1	1600	22	H2	2	Heywood and Sanford, 1976
2366	Meiklejohn Peak, southern NV	Lower Antelope Valley	Ordovician	Middle Ordovician	0	2	0	0	0	0	0	1	300	76	H2		Ross et al, 1975; Krause 2001; pers obs
1383	Mingan Islands II, QC Ile Nue de Mingan	Mingan	Ordovician	Middle Ordovician	6	0	1	1	1	1	1	5	30	6	L	4	Desrocheres and James, 1989
1382	Mingan Islands, QC Ile St. Charles	Mingan	Ordovician	Middle Ordovician	6	0	1	1	1	1	1	5	30	6	L	4	Desrocheres and James, 1989
1389	Port-au-Choix, NF	Table Point	Ordovician	Middle Ordovician	6	0	1	1	1	1	0	4	6	1	L	3	James and Klappa, 1989; pers obs
1390	Table Point, NF	Table Point	Ordovician	Middle Ordovician	6	0	1	1	1	1	0	4	6	1	L	3	James and Klappa, 1989;
1809	St. John Island, NF		Ordovician	Middle Ordovician	6	0	1	1	1	1	0	4	6	1	L	3	Klappa and James, 1980
2468	Fourth Chute, Ottawa Valley, Ontario		Ordovician	Upper Ordovician	5	0	1	0	0	0	2	2	1	0.15	L	1	Steele-Petrovich, 1988
1412	Vaureal River, E-Anticosti Isl., Quebec	Ellis Bay	Ordovician	Upper Ordovician	4	0	1	0	1	2	0	3	18	NA	L	5	Copper, 1989

Table B.1, continued…

2183	L'Original, Ottwa Valley, Ontario	Pamelia	Ordovician	Upper Ordovician	3	0	1	0	2	0	0	2	5	0.5	L	2	Steele-Petrovich and Bolton, 1998
2185	Braeside, Ottwa Valley, Ontario	Lowville	Ordovician	Upper Ordovician	3	0	1		2	0	0	2	0.4	1	L		Steele-Petrovich and Bolton, 1998
1898	Pine Pass, British Columbia	Beaverfoot	Ordovician	Upper Ordovician	2	0	0	2	1	0	0	2	NA	2.5	L	NA	Jansa, 1970; Cecile, 1989
1384	Long Point, Port au Port, Newfoundland	Lourdes	Ordovician	Upper Ordovician	2	0	1	2	0	1	1	4	12	3	L	4	James and Cuffey, 1989; pers obs
1391	Chicoutimi, Quebec	Chicoutimi limestone	Ordovician	Upper Ordovician	2	0	1	2	0	0	0	2	6	0.4	L	2	Harland et al, 1987; pers obs
2700	Kirkfield, Brich Island, Ontario	Bobcaygeon	Ordovician	Upper Ordovician	2	0	0	2	0	0	0	1	0.5	0.15	L	2	Kobluk and Noor, 1990
1812	Wool Point, New York	Day Point	Ordovician	Middle Ordovician	2	0	1	2	0	0	0	2	3		L	2	Pitcher, 1964, pers obs
1413	N-Anticosti Isl., Quebec	Vaureal	Ordovician	Upper Ordovician	2	0	0	2	0	0	0	1	3	1	L	NA	Copper 1989
1897	Ware, British Columbia	Skoki	Ordovician	Middle Ordovician	1	0	2	0	0	0	0	1	1	1	L	NA	Cecile and Norford, 1979; Cecile, 1989
1814 B	Lake Champlain region, Vermont	Crown Point	Ordovician	Middle Ordovician	1	0	2	1	1	0	0	3	90	7.6	L	3	Pitcher, 1964, pers obs
3519	La Grosse Romaine Island, Quebec	Romaine	Ordovician	Lower Ordovician	1	0	2	0	1	0	0	2	1	NA	L	2	Rigby and Desrocheres, 1995
2633	Hebron, Virginia	Chepultepec/ Stonehenge	Ordovician	Lower Ordovician	1	0	2	0	0	0	0	2	50	10	L	2	Bova and Read, 1987
1814	Lake Champlain region, Vermont	Crown Point	Ordovician	Middle Ordovician	1	0	2	1	0	0	0	2	13.1	7.6	L	2	Pitcher, 1964, pers obs
3468	Lake Champlain region, Vermont	Valcour	Ordovician	Middle Ordovician	1	0	2	1	1	0	0	3	10	1	L	2	Kapp and Stearn, 1975, pers obs
2665	Mohawk Valley, New York	Tribes Hill	Ordovician	Lower Ordovician	1	0	2	0	0	0	0	1	1	0.7	L	2	Friedman 1996
2713	New York Route 67, Amsterdam, New York	Tribes Hill	Ordovician	Lower Ordovician	1	0	2	0	0	0	0	1			L	2	Landing et al 1996

Table B.1, continued…

1811	Valcour and Garden Islands, New York	Day Point	Ordovician	Middle Ordovician	1	0	2	0	0	0	0	1	2	2	L	1	Pitcher, 1964, pers obs
1899	Kingston, Ontario	Gull River	Ordovician	Upper Ordovician	1	0	2	0	0	0	0	1	2.3	0.9	L	1	Greggs and Sargent, 1971
2701	North-central Kentucky	Grant Lake	Ordovician	Upper Ordovician	1	0	2	1	0	0	0	2	3	0.3	L	1	Cuffey, 1998
1865	Cedar Springs, Tennessee	Rockdell	Ordovician	Upper Ordovician	1	0	2	0	0	0	0	1	2		L		Ruppel and Walker, 1982
1397	Green Head, Newfoundland	Watts Bight	Ordovician	Lower Ordovician									80	12	L	3	Pratt and James, 1989; pers obs
1394	Mount Wilson, Alberta	Survey Peak	Ordovician	Lower Ordovician									15	2	L		Pratt, 1989
2714	Jeffersontown, Jefferson Co., Kentucky	Liberty	Ordovician	Upper Ordovician											L		Browne, 1964
3254	Pisgah Gap, Clinchport, Virginia	Bowen	Ordovician	Middle Ordovician											L		McKinney et al, 2001
1810	Birmingham, Alabama	Chickamauga	Ordovician	Upper Ordovician	6	0	1	1	0	1	1	4	6.1	5.3	M	3	Stock and Benson, 1982; Kolter and Vest, 1953; Gault and McKinney, 1980
2716	Montmorency river, Quebec City, Quebec	Deschambault	Ordovician	Upper Ordovician	5	0	0	0	0	0	2	1	5.8	1.2	M	1	Lavoie, 1995
1813	Isle La Motte, Vermont	Day Point	Ordovician	Middle Ordovician	1	0	2	1	1	0	0	3	90	6.1	M	2	Pitcher, 1964; pers obs
1404	Port au Port, Newfoundland	Catoche	Ordovician	Lower Ordovician	1	0	2	0	0	0	0	1	3	3	M	2	Pratt and James, 1989; pers obs
1857	Chickasaw, Arbuckle Mts., Oklahoma		Ordovician	Upper Ordovician	1	0	2	0	0	0	1	2		1	M	2	Cuffey and Cuffey, 1995; Wets et al 2001
2071	Ile Bizard, Montreal	Laval	Ordovician	Middle Ordovician	1	0	2	0	0	0	1	2	1	0.75	M	2	Kobluk, 1981; pers obs
2431	Bulleys Lump, Judge Daly Promot., Nunavut	Bulleys Lump	Ordovician	Lower Ordovician	1	0	2	0	1	0	1	3		5	M		de Freitas and Mayr, 1995
1411	W-Anticosti Isl., Quebec	Ellis Bay	Ordovician	Upper Ordovician									10	4	M		Copper, 1989
2968	Southern House Range, Utah	Fillmore	Ordovician	Lower Ordovician									30	1.5	M		Church, 1974
1901	Gore Bay, Manitoulin Island, Ontario	Georgian Bay	Ordovician	Upper Ordovician	2	0	1	2	0	0	0	3	NA	4	N	1	Copper and Grawbarger, 1978

Table B.1, continued…

1866	Gate City, Virginia	Rockdell?	Ordovician	Upper Ordovician									60000	60	N		Read, 1982
1868	Tazewell, Virginia	Rockdell?	Ordovician	Upper Ordovician									45000	35	N		Read, 1982
2458	Cow Head, Newfoundland		Ordovician	Lower-Middle Ordovician	1	0	2	0	1	1	0	3	NA	NA	NA	NA	Pohler and James, 1989; pers obs
2593	Cow Head, Newfoundland		Ordovician	Middle Ordovician	1	0	2	0	1	1	0	3	NA	NA	NA	NA	Pohler and James, 1989; pers obs
2571	Picadilly, Port au Port, Newfoundland	Table Point	Ordovician	Middle Ordovician	0	2	1	1	1	0	0	4	150	35	NA	NA	Stenzel and James, 1995; pers obs
2572	Burnt Island, Newfoundland	Table Point	Ordovician	Middle Ordovician	0	2	1	0	0	0	0	2	150	35	NA	NA	Stenzel and James, 1995
2184	Dunrobin, Ottwa Valley, Ontario	Pamelia	Ordovician	Upper Ordovician	3	0	1	0	2	0	0	2	1				Steele-Petrovich and Bolton, 1998
1815	Isle la Motte/Grand Isle, Vermont	Crown Point	Ordovician	Middle Ordovician	2	0	1	2	1	0	0	3				NA	Pitcher, 1964; pers obs
1405	Melville Peninsula, N.W.T.		Ordovician	Upper Ordovician	1	0	2	1	0	0	0	2	1500	30		4	Trettin 1975
2584	Hare Bay, Newfoundland	Catoche	Ordovician	Lower Ordovician	1	0	2	0	1	0	0	2		70			Stevens and James, 1976; Pratt and James, 1982
1816	St. Jean, Quebec	Crown Point	Ordovician	Middle Ordovician	1	0	2	0	0	0	0	1	40	2			Pitcher, 1964
1817	Terrebone, Quebec	Valcour	Ordovician	Middle Ordovician	1	0	2	0	0	0	1	2					Pitcher, 1964
1869	Porterfield, Virginia	Effna Limestone	Ordovician	Middle Ordovician	0	2	1						20000	250			Read, 1982
1870	Effna, Virginia	Effna Limestone	Ordovician	Middle Ordovician	0	2	1						65000	65			Read, 1982
1872	Murat, Virginia	Murat Limestone	Ordovician	Middle Ordovician	0	2	1						25000	65			Read, 1982
1873	Staunton, Virginia		Ordovician	Middle Ordovician	0	2	1						8000	55			Read, 1982; pers obs
1821	Lechuguilla, Southern Franklin Mts., Texas	McKelligon Canyon	Ordovician	Lower Ordovician									15	6			Toomey and Nitecki, 1979
3268	Monticello quarry, Jones Co., Iowa	Hopkinton Dolomite	Silurian	Llandovery	2	0	1	2	0	1	0	3		9	H	3	Philcox, 1970; Mikulic, 1981
3267	Elwood quarry, Clinton Co., Iowa	Hopkinton Dolomite	Silurian	Llandovery	2	0	1	2	0	1	0	3		9	H	3	Philcox 1970, Mikulic 1981
1882	Maumee, Ohio		Silurian	Upper Silurian	1	0	2	1	0	0	1	3	NA	21	H	3	Textoris and Carozzi, 1966

Table B.1, continued…

2022	Palisades Quarry, Linn Co., Iowa		Silurian	Wenlock	6	0	1	1	0	1	1	4	2500	30	H2	6	Philcox, 1972
2253	Attawapiskat River, Ontario	Attawapiskat	Silurian	Llandovery	4	0	1	0	1	2	1	4	700	8.7	H2	5	Chow and Stearn, 1989; Suchy and Stearn 1992
1419	Lock Haven, Pennsylvania	Mifflintown	Silurian	Wenlock	2	0	0	2	0	0	1	2	300	10	H2	4	Cuffey, 1989
3541	Lambton County Pinnacle reefs, Ontario	Guelph	Silurian	Middle Silurian	NA	NA	NA	NA	NA	NA	NA	NA	NA	140	H3	5	Coniglio et al, 2003
1863	Delphi, Indiana	Mississenawa and lower Liston Creek members, Wabash Fm	Silurian	Wenlock	6	0	0	1	1	1	1	4	NA	132	H3	5	Archer et al, 1980; Gaines, 1998 (MS, Cincinnati); Cumings and Shrock (1928), Sangree (1960), Textoris and Carozzi (1964), Shaver (1974a, 1976), and Droste and Shaver (1977)
1408	Gaspé Peninsula, Quebec		Silurian	Upper Silurian	6	0	1	1	0	1	1	4	400000	600	H3	7	Bourque and Amyot, 1989; University of Laval geosciences media
1431	Pipe Creek, Indiana		Silurian	Upper Silurian	1	0	2	1	1	0	1	4	1800	48	H3	4	Lehmann and Simo, 1989
812	Thornton, Illinois	Racine	Silurian	Wenlock	0	2	1	0	0	0	1	3	2000	90	H3	9	Ingels, 1963; Mikulic, 1999; pers obs
1890	Cabot Head, Bruce Peninsula, Ontario	Manitoulin	Silurian	Llandovery	6	0	1	0	0	1	1	3	2.5	1	L	3	Anastas and Coniglio, 1992
1418	Drummond Island II, Michigan	Manitoulin	Silurian	Llandovery	5	0	0	0	0	0	2	1	10	3	L	1	Cuffey, 1989
3257	Genesee Gorge, New York	Irondequoit Limestone	Silurian	Wenlock	1	1	2	1	0	0	1	4	4	2	L	2	Brett, 1999
816	Wiarton, Ontario	Guelph Dolomite	Silurian	Wenlock	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	M	NA	Lowenstam 1950
1427	Southhampton Island, N.W.T.	Severn River	Silurian	Lower Silurian	6	0	2	2	1	0	1	4	240	3	M	NA	Dewing and Copper, 1989
2972	Lake Timiskaming, Ontario		Silurian	Wenlock	6	0	1	1	1	0	0	3	4	2	M	NA	Copper and Armstong, 1999
1437	Wayne, West Virginia	McKenzie-Lockport	Silurian	Upper Silurian	6	0	0	2	0	1	2	3	NA	6.6	M	3	Smosna and Maxwell, 1989
1424	Altoona, Pennsylvania	Keyser Limestone	Silurian	Upper Silurian	6	0	0	1	0	1	1	3	10	3	M	3	Cuffey and Taylor, 1989
1885	Frontier Quarry, Lockport, New York	Lockport	Silurian	Wenlock	4	0	1	0	0	2	1	3	20	10	M	4	Crowley, 1973

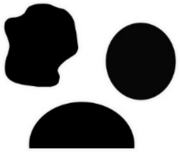
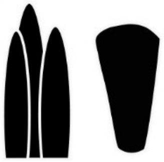
Table B.1, continued…

1886	Clarendon, New York	Lockport	Silurian	Wenlock	4	0	1	0	0	2	1	3	20	10	M	4	Crowley, 1973
1414	East Point, Anticosti Isl., Quebec	Jupiter (Now split into Menier Formation)	Silurian	Llandovery	2	0	1	2	0	1	1	5	80	10	M	6	Copper, 1989
2718	Reed North Quarry, Fairborn, Green Co., Ohio	Brassfield	Silurian	Llandovery	2	0	0	2	1	0	1	3	50	8	M	4	Schneider and Ausich, 1999
1430	Allenwood, Pennsylvania	Mifflintown	Silurian	Wenlock	2	0	0	2	1	0	0	2	5	2	M	2	Inners, 1989
1616	Mustoe, Highland Co., Virginia	Keyser	Silurian	Upper Silurian	2	0	0	2	0	1	1	3	100	8.8	M	NA	Smosna, 1984
1415	SW Point, Anticosti Isl., Quebec	Chicotte	Silurian	Llandovery	6	0	1	1	1	1	0	4	40	5	M	4	Copper, 1989
817	Cordova, Rock Island Co., Illinois	Gower	Silurian	Upper Silurian	NA	0	0	1	0	0	1	2			M		Lowenstam, 1950
2255	Comeault No. 1, Hudson Bay, Ontario		Silurian	Lower Silurian	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	Suchy and Stearn, 1992
2256	Kaskattama No. 1, Hudson Bay, Ontario		Silurian	Lower Silurian	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	Suchy and Stearn, 1992
1798	Lapel, Indiana		Silurian	Wenlock	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	Carozzi and Frost, 1966
813	Elmhurst, Illinois		Silurian	Wenlock	6	0	1	1	0	0	1	3	NA	NA	NA	NA	Lowenstam, 1950
1888	Temiscouta, Quebec	Lac Croche	Silurian	Upper Silurian	NA	NA	1	NA	NA	NA	NA	NA	30000	300	NA	NA	Bourque, 1989
1420	Alba, Michigan		Silurian	Wenlock	6	0	0	1	0	0	1	2	"several km"	60	NA	NA	Cuffey, 1989
1889	Pen Island No. 1, Hudson Bay, Ontario	Attawapiskat	Silurian	Lower Silurian	NA	NA	NA	NA	NA	NA	NA	NA	NA	12	NA	NA	Bourque, 1989
810	Wabash-Richvalley, Indiana		Silurian	Wenlock	NA	NA	NA	NA	NA	NA	NA	NA	75	12	NA	5	Carozzi and Zadnik, 1959
2407	Roberts Mountains, Nevada		Silurian	Middle-Upper Silurian	6	0	1	1	0	0	1	3	NA	750	NA	4	Winterer and Murphy, 1960
1851	Horlick Quarry, Racine, Wisconsin	Racine	Silurian	Wenlock	6	0	1	1	0	1	0	3	NA	NA	NA	2	Watkins, 1993
1796	Mitchell Quarry, Lisbon, Iowa		Silurian	Wenlock	4	0	0	1	0	2	0	2	400	55	NA	2	Hinman, 1968

Table B.1, continued…

1797	Hunt Quarry, Cedar Co., Iowa		Silurian	Wenlock	4	0	0	1	0	2	0	2	400	55	NA	2	Hinman, 1968
1852	Grafton, Wisconsin		Silurian	Wenlock	2	0	1	2	0	0	1	3	60	5	NA	1	Watkins, 1993
820	Wauwatosa, Milwaukee, Wisconsin	Racine	Silurian	Wenlock	1	0	2	1	0	0	0	2	140	19	NA	NA	Lowenstam, 1950; Schrock, 1939; Mikulic, 1999
2933	Lakeside Mountains, Utah		Silurian	Llandovery	1	0	2	0	0	0	0	1	NA	2.5	NA	NA	Sheehan, 2000
2929	Drake Island, Glacier Bay National Park, Alaska	Willoughby	Silurian	Ludlow	1	0	2	1	0	0	0	2	"several hundred"	100	NA	4	Soja et al, 2000
1423	Niagara Gorge, New York	Irondequoit	Silurian	Wenlock	1	0	2	1	0	0	1	2	4	2	NA	1	Cuffey and Hewitt, 1989
811	Georgetown, Indiana		Silurian	Wenlock	0	2	0	1	0	1	0	3	NA	NA	NA	NA	Lowenstam, 1950
3275	Rockford, Mecer Co., Ohio	Louisville Limestone Wabash, Fm	Silurian	Middle Silurian	0	2	0	0	1	1	1	4	NA	NA	NA	3	Shaver, 1974; Gaines, 1998 (MS, Cincinnati)
2400 B	Southampton Island, N.W.T.	Attawapiskat	Silurian	Llandovery /Wenlock	NA	NA	NA	NA	NA	NA	NA	NA		6			Heywood and Sanford, 1976
2400	Mansel Island, N.W.T.	Ekwan River	Silurian	Llandovery	NA	NA	NA	NA	NA	NA	NA	NA		3			Heywood and Sanford, 1976
1855	Cap River, Anticosti Isl., Quebec	Chicotte	Silurian	Llandovery	4	0	1	1	1	2	0	4	150	5		3	Brunton and Copper, 1994
1416	South Point, Anticosti Isl., Quebec	Jupiter	Silurian	Llandovery													Copper, 1989

Table B.2: Summary of morphotype adjectives synonymized

Builder Morphotypes	 **Encrusting**	 **Massive**	 **Columnar/Vaselike**	 **Tabular/Platelike**	 **Branching**	**Stromatactoid Mud**
Encountered Descriptive Terms	Encrusting Clotted Stromatolitic Thrombolitic (unspecified)	Massive Hemispherical Spheroidal Domal Nodular Globular Bulbous	Columnar Vase(-like) Digitate Horn-Shaped Rod Pillar(-like) Club(-like) Cone	Tabular Foliose/Foliase Lamellar Plate(-like)/Platiform Cup/Bowl	Branching Corymbose Dendroid Stick(-like) Dendroid	Stromatactoid-Mud
Context-Dependent Inclusion	Lamellar	Fasciculate	Stick(-like)		Digitate Fasciculate	

Appendix C : Chapter 3 data, code, and additional figures

Appendix C1: Analyses run with the conservative cutoff of ≥8 occurrences per stage

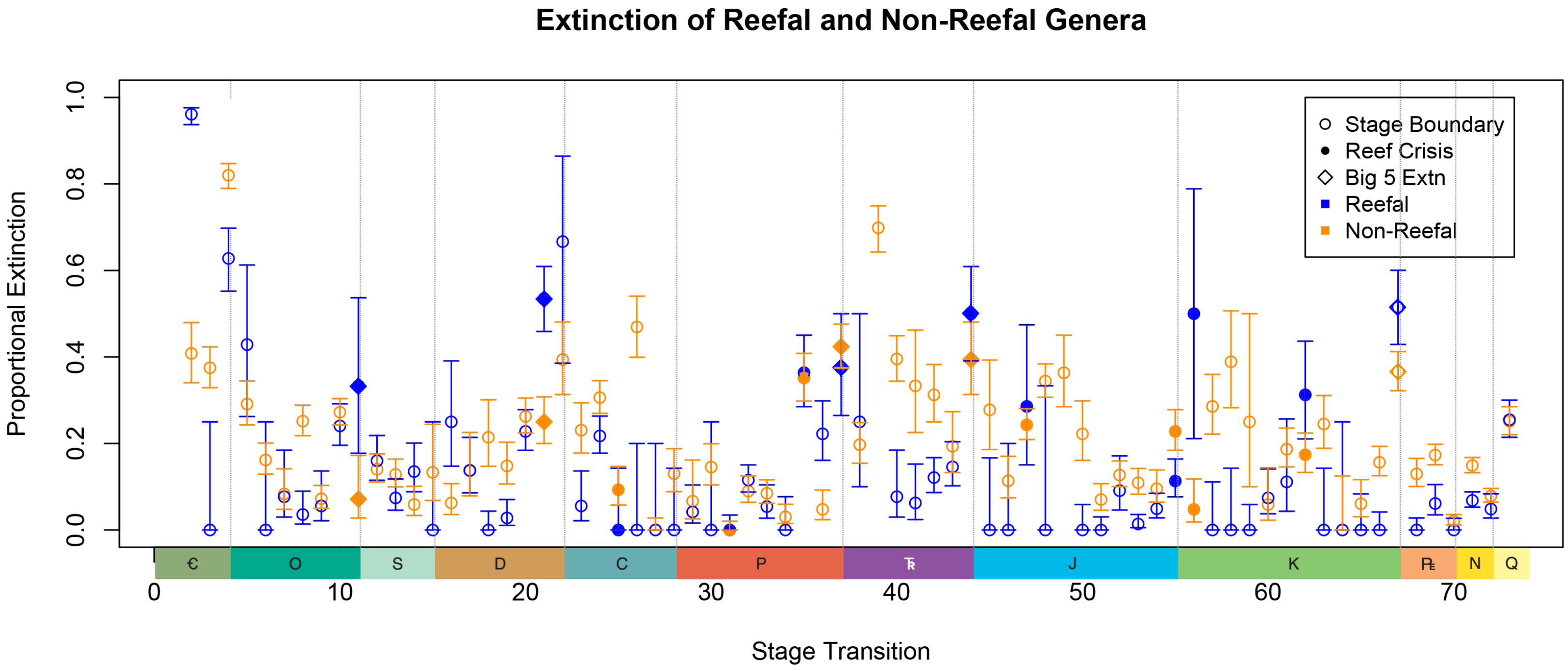


Figure C.1 Proportional extinction for reefal and nonreefal genera, filtered for genera with a minimum of 8 occurrences per time bin. Results similar to those presented with a 4-occurence cutoff, but lower sample sizes increases error in many Paleozoic and Mesozoic time-bins.

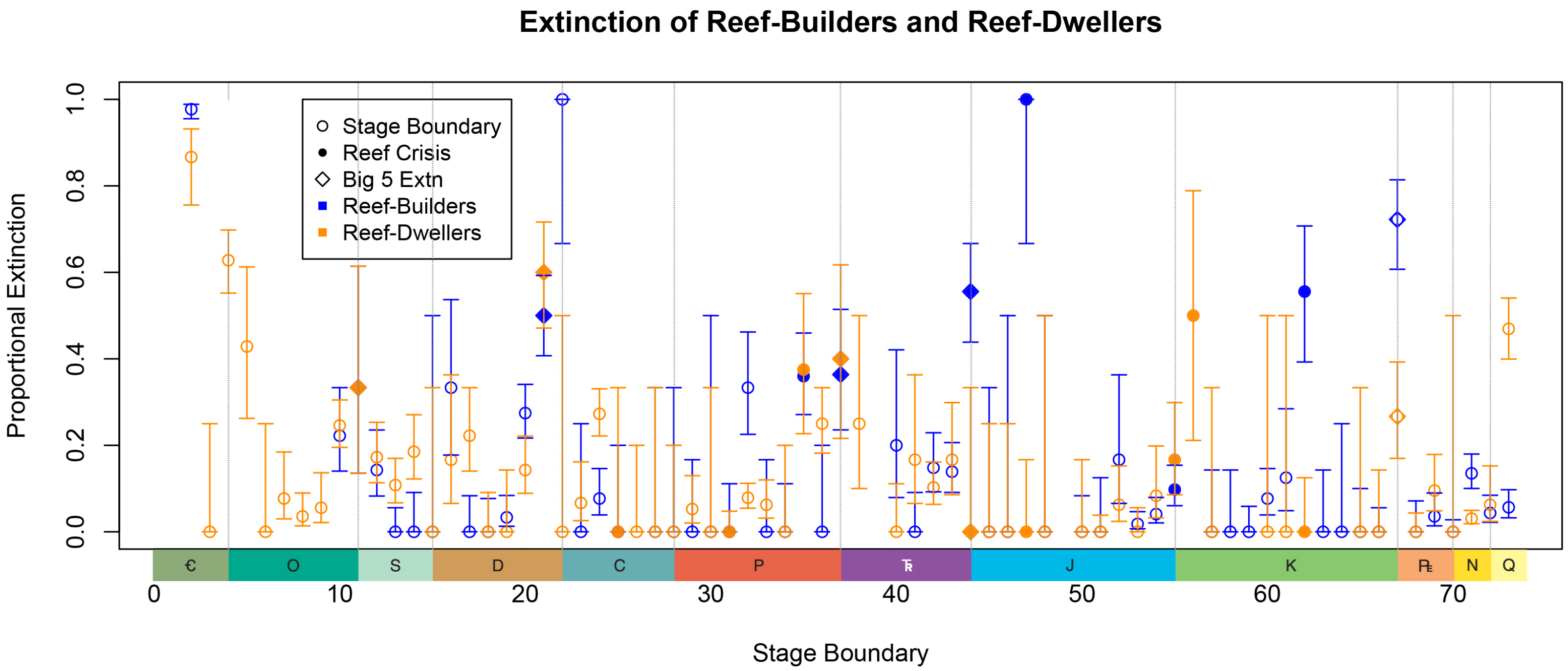


Figure C.2: Proportional extinction of reef-builders and reef-dwellers, limited to genera with 8 occurrences per time bin, features reduces statistical robustness. In addition, extinction becomes reduced as rarer or less widespread taxa get removed from the analysis.

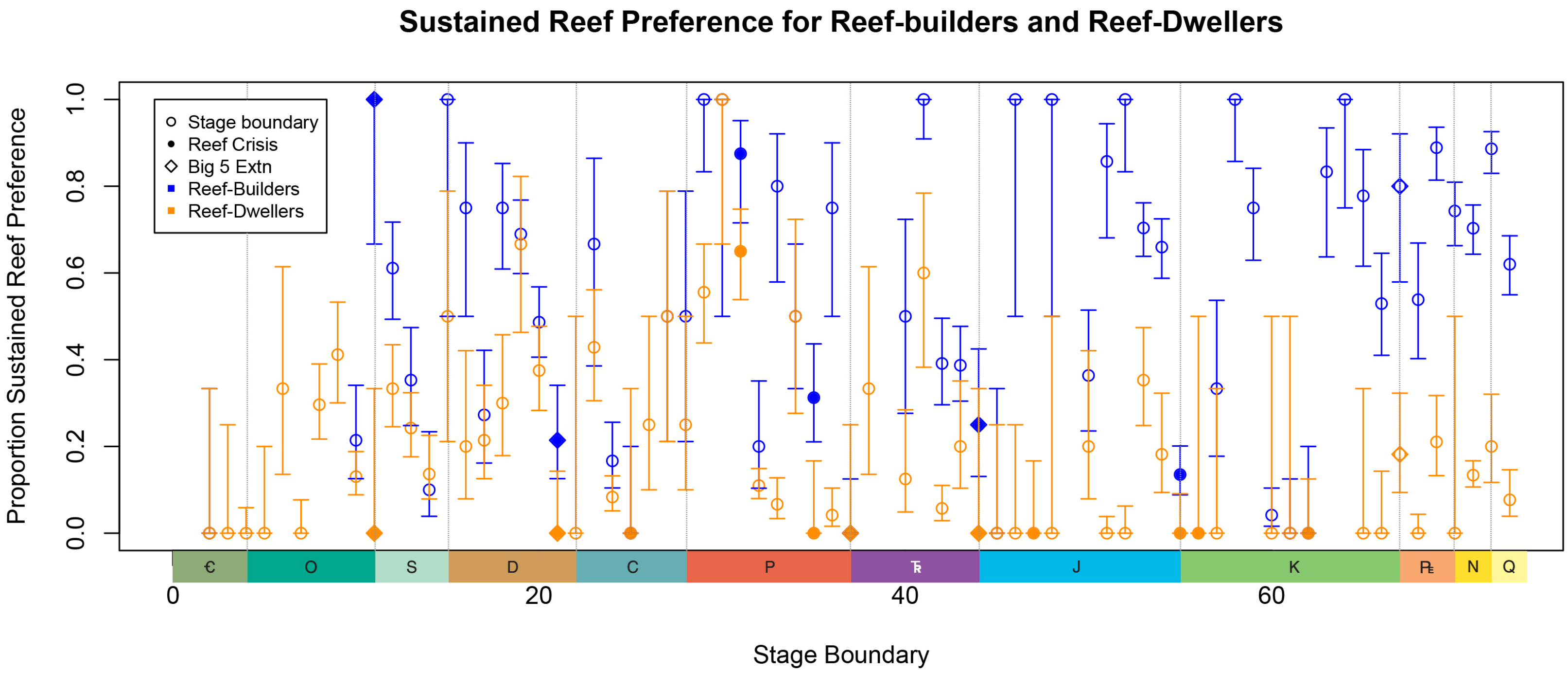


Figure C.3: Sustained preference for reef-builders and reef-dwellers, limited to genera with 8 or more occurrences in each time bin, dramatically reduces the robustness of the data, but the same pattern emerges. Reef-builders return to reefs at much higher numbers, although insignificantly so during reef crises

Appendix C2: List of designated reef-builder Orders and Suborders. Clades were selected due to prevalence as reef-builders, as noted in the literature, and is primarily inclusive of corals, sponges, and reef-building bivalves

Actinocerida
Actinostromatidae
Ajacicyathida
Agelasida
Amphidiscosa
Amphiporida
Archaeocyathida
Auloporida
Axinellida
Capsulocyathida
Chaetetida
Clavulina
Cystiphyllida
Favositida
Hadromerida
Hexactinosa
Hippuritoida
Labechiida
Lyssacinosa
Monocyathida
Orthocladina
Orthotetida
Scleractinia
Sphaerocoeliida
Spirosclerophorida
Stauriida
Stellospongiida
Stromatoporida
Syringostromatida
Tabuloconida
Vaceletida

SUPPLEMENTAL FILES:

1. Cleaned PBDB occurrence data for marine invertebrate genera of the Phanerozoic, April 2018., used for analyses in Chapter 3
2. Source code for analyses presented in Chapter 3

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