Integrating ecology and evolution in deep time: using Ecological Niche Modeling to study species’ evolutionary responses to climate from the Pliocene to the present-day biodiversity crisis

By

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Submitted to the graduate program in Geology and the Graduate Faculty of the University of Kansas in partial fulfillment of the requirements for the degree of Doctor of Philosophy

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Abstract

The aim of my dissertation was to elucidate how environmental changes have influenced evolutionary and distributional patterns in the near-shore molluscan fauna of the Atlantic Coastal Plain (southeastern U.S.) over the past three million years. Disentangling the long-term evolutionary responses of species to environmental change is important for understanding the mechanisms controlling evolutionary processes and for assessing how current and future climate changes will impact Earth’s biodiversity. My dissertation was comprised of three chapters that integrated both paleontological and neontological data to study the molluscan record of the Atlantic Coastal Plain. The first study in my dissertation focused on 14 extant marine mollusk species and their potential responses to future climate changes over the next ~100 years. Two hypotheses were tested: that suitable areas will shift northwards for these species, and that they will show varied responses to future climate change based on species-specific niche attributes. I found that species were not predicted to shift pole-ward, but rather showed varied responses to future warming. Many of the studied species will be hard hit by future climate changes, such that over 20% of their suitable area will disappear by the end of this century. The second study statistically analyzed whether the niches of mollusk species remained stable across three million years of profound environmental changes. Prior to this research, the long-term evolutionary dynamics of species’ niches to differing climatic regimes remained uncertain, even though the question is vital to understanding the fate of biodiversity in a rapidly changing world. I found that species’ tolerances were statistically similar from the Pliocene to the present-day, which suggest that species will respond to current and future warming by altering distributions to track suitable habitat, or, if the pace of change is too rapid, by going extinct. The last study tested whether niche breadth and/or geographic range size was a better predictor of extinction selectivity for mollusk species from the Pliocene. I hypothesized that species that went
extinct post Pliocene would have smaller geographic ranges and smaller niche breadths compared with those species that are still extant. I found that only realized niche breadth (i.e., the breadth of the environment actually occupied by a species) and geographic range size, rather than fundamental niche breadth, are inversely related to extinction probability. This finding has implications for assessing which species are more at risk as a consequence of current and future climate changes, and helps to sharpen our understanding of which macroevolutionary processes shape patterns of diversity over evolutionary time scales.

Together, these studies indicated that abiotic, environmental factors play a fundamental role in governing species’ distributions in deep time. More specifically, species did not seem to rapidly evolve in response to new environmental conditions, but tracked preferred habitat or faced extirpation if conditions exceeded their tolerance limits. These findings can be used to ensure that paleobiology does not become the biology of the future.
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difficult moments in graduate school. I will fondly remember our lunch outings and pasta parties.

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Introduction

My research interests are focused on gaining deeper insight into macroevolutionary patterns and processes preserved in the fossil record. The aim of my dissertation is to elucidate how environmental changes have influenced evolutionary and distributional patterns in the near-shore molluscan fauna of the Atlantic Coastal Plain (southeastern U.S.) over the past three million years. Disentangling the long-term evolutionary responses of species to environmental change is important for understanding the mechanisms controlling evolutionary processes (Ross & Allmon, 1990; Gould, 2002; Parmesan, 2006; Wiley & Lieberman, 2011) and for assessing how current and future climate changes (IPCC, 2007) will impact Earth’s biodiversity (Burrows et al., 1991; Araújo & Rahbek, 2006; Harley et al., 2006). Whereas modern biological inquiry can examine only a snapshot of a species’ lifetime, the paleontological record provides a ledger of species’ responses to constantly changing environments over millions of years (Roy et al., 1996; Patzkowsky & Holland, 2012).

Therefore, to fully understand the evolutionary and conservation implications of current climate changes, we must look to similar episodes of environmental change in the past using the entire duration of species’ lifetimes (Jablonski, 1991; McKinney, 1997; Dietl & Flessa, 2011). Here, I consider the Pliocene fossil record, which was the most recent period in Earth history when temperatures were sustained at levels expected at the end of this century (Robinson & Dowsett, 2008).

Study system

My dissertation is comprised of three chapters that integrate both paleontological and neontological data to study the molluscan record of the Atlantic Coastal Plain (Dietl & Flessa,
2011; Fritz et al., 2013). The past three million years of molluscan evolution in the Atlantic Coastal Plain provide an excellent record in which to study implications of climate change for two reasons. First, remains of fossil and recent mollusks are extremely abundant ((Allmon et al., 1993; Campbell, 1993; Hendricks, 2009) and present interesting diversity patterns (Todd et al., 2002; Vermeij, 2005). Overall diversity in the region has remained relatively unchanged since the Pliocene, despite ~70% extinction, indicating that extinctions were balanced by originations (Allmon et al., 1993).

Second, the Atlantic Coastal Plain experienced significant environmental disturbances, from the closing of the Isthmus of Panama about three million years ago to numerous Pleistocene glacial/interglacial cycles (Krantz, 1990; Toscano & York, 1992; Cronin & Dowsett, 1996). These environmental changes can be divided into three major intervals: (i) the early Pliocene, when sea surface temperatures were generally cooler than today; (ii) the ‘mid-Pliocene warm period’ (mPWP), ~3.3–3 Ma, when temperatures were generally warmer than today, reflecting closure of the Isthmus of Panama and reorientation of the Gulf Stream along the eastern coast of North America (Dowsett & Cronin, 1990); and (iii) a cooling period associated with the onset of Northern Hemisphere glaciations around 2.5–2.4 Ma and continuing to the present-day (Williams et al., 2009). Isotopic and biotic evidence suggests that there was reduced seasonality and warmer conditions along the eastern seaboard of the USA during the mPWP, with winter water conditions generally 3–5°C warmer than today in the Carolinas and Virginias (Dowsett & Wiggs, 1992; Knowles et al., 2009; Williams et al., 2009). These environmental changes provide the perfect backdrop to analyze how species are affected by abiotic changes over geological time scales.
<table>
<thead>
<tr>
<th>Species</th>
<th>Author</th>
<th>Details</th>
<th>Climatic Zone</th>
<th>Larval Strategy</th>
</tr>
</thead>
<tbody>
<tr>
<td>Anomia simplex</td>
<td>d’Orbigny, 1853</td>
<td>Referred to as the common jingle shell</td>
<td>Temperate—Tropical</td>
<td>Planktonic</td>
</tr>
<tr>
<td>Crassostrea virginica</td>
<td>Gmelin, 1791</td>
<td>The eastern oyster - of economic value.</td>
<td>Temperate—Tropical</td>
<td>Planktonic</td>
</tr>
<tr>
<td>Dinocardium robustum</td>
<td>Lightfoot, 1786</td>
<td>The Atlantic giant cockle – also used for food</td>
<td>Subtropical—Tropical</td>
<td>Planktonic</td>
</tr>
<tr>
<td>Lucina pensylvanica</td>
<td>Linnaeus, 1758</td>
<td>Also referred to as the Pennsylvania lucine</td>
<td>Tropical</td>
<td>Benthic</td>
</tr>
<tr>
<td>Mercenaria campechiensis</td>
<td>Gmelin, 1791</td>
<td>Referred to as the southern quahog. Commercially harvested.</td>
<td>Subtropical—Tropical</td>
<td>Planktonic</td>
</tr>
<tr>
<td>Bulla occidentialis</td>
<td>Adams, 1850</td>
<td>Referred to as buble snails or shells. Hermaphroditic.</td>
<td>Tropical</td>
<td>Planktonic</td>
</tr>
<tr>
<td>Crepidula fornicata</td>
<td>Linnaeus, 1758</td>
<td>Referred to as the common slipper shell. This species is considered invasive in Europe.</td>
<td>Temperate—Tropical</td>
<td>Planktonic</td>
</tr>
<tr>
<td>Neverita duplicata</td>
<td>Say, 1822</td>
<td>Commonly referred to as the 'shark eye' or moon snails. This is a predatory gastropod species.</td>
<td>Temperate—Tropical</td>
<td>Planktonic</td>
</tr>
<tr>
<td>Oliva sayana</td>
<td>Ravenel, 1834</td>
<td>Referred to as the lettered olive. This is a large predatory species.</td>
<td>Tropical</td>
<td>Planktonic</td>
</tr>
<tr>
<td>Terebra dislocata</td>
<td>Say, 1822</td>
<td>Referred to as the eastern auger.</td>
<td>Subtropical—Tropical</td>
<td>Benthic</td>
</tr>
</tbody>
</table>

Table 0.1 Ten core extant species that served as the link across all three chapters, some of which are economically important.
Research chapters

I used the above-described system to investigate over 100 bivalve and gastropod species that occur in the Neogene record of the Atlantic Coastal Plain. My goal was to uncover general patterns for how species respond to environmental change, and thus I utilized taxa that were both ecologically and phylogenetically distinct. Ten core extant species served as a link across all three chapters, some of which are economically important (Table 0.1); remaining species were classified within 50 bivalve and 16 gastropod genera. I personally vetted and compiled an extensive database of species’ occurrences spanning over three million years and covering the entirety of the Atlantic Coastal Plain. These data were derived from visits to several natural history collections and from detailed analyses of the literature. In order to ensure appropriate stratigraphic context and age controls for these occurrences, I assembled a stratigraphic database for all Pliocene–Recent geologic units of the Atlantic Coastal Plain (Appendix S2.2). Correlations and unit ages were determined by literature survey and use of various stratigraphic databases.

The first study in my dissertation focused on 14 extant marine mollusk species and their potential responses to future climate changes over the next ~100 years. Two hypotheses were tested: that suitable areas will shift northwards for these species, and that they will show varied responses to future climate change based on species-specific niche attributes (Saupe et al., 2014, in press). Ecological niche models (ENMs) were used to forecast potential distributions according to three scenarios of future change for three time slices using climate data from the Hadley Climate Centre (UK). Contrary to my hypothesis, I did not find a coherent pattern of areas with suitable environments expanding at high-latitude range boundaries, with simultaneous contraction at their low-latitude boundaries. These results contrast with previously-documented trends among terrestrial and other marine species, which are rapidly shifting their ranges to higher latitudes. Furthermore, although one might
expect that warming would benefit tropical species, I found that many of the studied species will lose significant portions of their suitable habitat and may even face extirpation by the end of this century. Alternatively, my second hypothesis was supported in that species were predicted to have differing responses to future warming, which depended upon the particulars of their niche characteristics. The species-specific nature of responses to climate change is consistent with those observed in the fossil record during past episodes of climate change.

The second study focused on ten fossil species and statistically analyzed whether their niches remained stable across three million years of profound environmental changes (Saupe et al., in review). Prior to this research, the long-term evolutionary dynamics of species’ niches to differing climatic regimes remained uncertain, even though the question is vital to understanding the fate of biodiversity in a rapidly changing world. I found that the environmental preferences of species remained stable across three million years. My results suggest that species will respond to current and future warming by altering distributions to track suitable habitat, or, if the pace of change is too rapid, by going extinct. My research also supports the use of methods that project species’ present-day environmental requirements to future climatic landscapes to assess conservation risks (e.g., Peterson et al., 2002; Thuiller et al., 2005; Saupe et al., 2014, in press). At the macroevolutionary scale, this research provides evidence that species’ distributions are structured by environmental factors.

The last study tested whether niche breadth and/or geographic range size were better predictors of extinction selectivity for mollusk species from the Pliocene. Small geographic range sizes have often been associated with increased risk of extinction in both neontological (Schwartz et al., 2006; Fritz et al., 2009; Boulangeat et al., 2012) and paleontological (Jablonski & Hunt, 2006; Payne & Finnegan, 2007; Harnik, 2011) studies, while theory suggests that specialist species should be at higher risk during times of environmental change (Eldredge, 1979; Vrba, 1980; McKinney, 1997; Devictor et al., 2008; Colles et al., 2009; Myers & Saupe, 2013). Using ENM and paleoclimatic data, I was able to quantify niche
breadth for Pliocene species that (i) have survived to the present-day and (ii) have since gone extinct. I hypothesized that species that went extinct post Pliocene would have smaller geographic ranges and smaller niche breadths compared with those species that are still extant. However, contrary to my hypothesis, I found that only realized niche breadth (i.e., the breadth of the environment actually occupied by a species) and geographic range size, rather than fundamental niche breadth, are inversely related to extinction probability. This finding has implications for assessing which species are more at risk as a consequence of current and future climate changes (Mace et al., 2008), and helps to sharpen our understanding of which macroevolutionary processes shape patterns of diversity over millions of years (Lieberman & Vrba, 1995; Myers & Saupe, 2013).

The results of these studies highlight the importance of integrating neontological and paleontological data to study macroevolutionary patterns through time. My research indicates that abiotic, environmental factors play a fundamental role in governing species’ distributions across millions of years. More specifically, species do not seem to rapidly evolve in response to new environmental conditions, but rather they track preferred habitat or face extirpation if conditions exceed tolerance limits. The lack of evolution in niche attributes potentially provides a mechanism explaining patterns of morphological stasis observed in the fossil record (Eldredge & Gould, 1972; Eldredge et al., 2005). I also discovered that the breadth of the fundamental niche (i.e., whether a species is an environmental specialist or generalist) is not a major factor controlling extinction probability. Indeed, the actual amount of niche space occupied by the species (i.e., the realized niche) and geographic range size seem to be the main factors impacting survivorship. The future models I constructed for these mollusks predict that they will be hard hit by climate changes, particularly since the pace of future change may exceed past rates. Thus, even though they survived conditions in the Pliocene similar to those predicted for the end of this century, the speed at which we approach these changes may be too rapid for species to keep pace.
At the heart of it, I am fascinated by Earth’s biodiversity, both past and present. As a child, I would marvel at the red-eyed tree frogs, pangolins, tarsiers, fennec foxes, and jumping spiders that would peer at me from the pages of nature magazines. I began a journey to study this biodiversity because I want to understand how and why it evolved, and ultimately by doing so, I hope to better protect it for generations to come. With respect to my dissertation, human-induced climate changes will have critical implications for biodiversity in general and for commercial mollusks, since near shore environments provide over $US14 trillion/year in ecosystem goods and services (Costanza et al., 1997). However, protecting diversity is not only vital for our economy and for maintaining our food and medicine reserves (Chapin et al., 2000; Parmesan and Yohe, 2003), but for preserving the sense of awe we receive from our flora and fauna—for ensuring that beauty remains in this world. I hope that my dissertation, with a look towards the past, can inform our future—let us not make paleobiology the biology of the future.

References


IUCN’s system for classifying threatened species. *Conservation Biology, 22*, 1424–1444.


Chapter 1. Climate change and marine mollusks of the western North Atlantic: future prospects and perils

Abstract

Numerous studies have examined potential responses of terrestrial biotas to future climate change, but fewer have considered marine realms. We forecast how marine molluscan faunas of the Atlantic Coastal Plain might respond to environmental change over the remainder of this century. We test the hypotheses that suitable areas will shift northwards for studied species, and that species will show varied responses to future climate change. We generated ecological niche models (in GARP and MAXENT) for 14 ecologically, economically and potentially medically important mollusk species, using present-day summaries and future forecasts of climate from the Hadley Centre and known species occurrence data from natural history collections. Niche models were used to forecast potential distributions according to three scenarios of future change for three time slices. Northern extremes of suitability are predicted to shift northwards for only three (GARP) or four (MAXENT) of the 14 species, whereas the southern edge of suitability is predicted to shift southwards for seven (GARP) and one (MAXENT) of the 14 species. When changes in the geographical centroids of suitability are considered, no significant poleward shifts are anticipated for individual species. Instead, half of the study species (many economically important) experience substantial (> 20%) loss of suitable environmental area, even under the lowest-emission future climate scenario. Furthermore, the direction and magnitude of the response to predicted climate change is species-specific. We do not find a coherent pattern of areas with suitable environments expanding at high-latitude range boundaries, with simultaneous contraction at their low-latitude boundaries. Tropical marine mollusks may thus show varied responses as average temperatures warm. These results contrast with trends among terrestrial and other marine species, which are rapidly shifting their ranges to higher latitudes. Conversely, the differing responses of these species to future warming are consistent with responses of species to past episodes of change, as observed in the fossil
Introduction

Predicting the impacts of future climate change on Earth’s biodiversity is critical to preserving biological resources and for understanding evolutionary processes (Thomas et al., 2004; Chen et al., 2011). The advent of ecological niche models (ENMs) has facilitated these types of predictions, being the standard framework used to project species’ abiotic requirements onto future climate landscapes, in order to assess likely changes in distributional potential. ENM analyses, however, have focused primarily on terrestrial species, leaving the predicted responses of marine taxa understudied to date. This imbalance reflects the difficulty of obtaining representative datasets for marine species’ occurrences and environmental parameters, and of studying marine processes (Richardson & Poloczanska, 2008; Dambach & Rödder, 2011; Robinson et al., 2011). Recently, however, new marine-orientated data resources have allowed for rapid developments in the study of marine species, from present-day patterns of suitability (e.g. Lima et al., 2007; Pauly et al., 2011; Reiss et al., 2011; Tyberghein et al., 2012; Yesson et al., 2012) to predicting species’ responses to changing climate (e.g. Clark et al., 2003; Cheung et al., 2009; Dambach & Rödder, 2011; Lenoir et al., 2011; Russell et al., 2012; Jones et al., 2013).

Here, we use novel present-day summaries and modeled future climates from the Met Office Hadley Centre (Jones et al., 2011) to study 14 abundant, well-sampled, ecologically and phylogenetically diverse marine mollusk species (Table 1.1) from the near-shore continental shelf of the western North Atlantic. Three of these species are commercially important: the Atlantic oyster, *Crassostrea virginica* (Gmelin, 1791); the southern hard-shell clam, *Mercenaria campechiensis* (Gmelin, 1791); and the giant Atlantic cockle, *Dinocardium robustum* (Lightfoot, 1786). We also include *Crepidula fornicata* (Linnaeus, 1758), an invasive species detrimental to aquaculture in Europe, and *Conus* spp., which have
biomedical potential (Alonso et al., 2003).

We test two hypotheses regarding the likely responses of these mollusks to future changes: (1) that they will respond to changing climate by shifting their distributions polewards, and (2) that they will respond to changing climate as a function of species-specific niche attributes, not congruently as an assemblage. Previous research supports the first hypothesis, because marine ectotherms tend to occupy the full extent of latitudes within their thermal limits (Pörtner & Knust, 2007; Tewksbury et al., 2008; Sunday et al., 2012). Consequently, ectotherms should shift northwards in response to warming, because temperatures outside their thermal envelopes decrease their capacity to perform aerobically, and detrimentally impact other physiological processes (Somero, 2002; Pörtner & Knust, 2007).

Poleward range shifts have formed the dominant observed (Jones et al., 2010; Sorte et al., 2010) and anticipated (Cheung et al., 2009; Albouy et al., 2013) response by marine species to climate change, but recent research indicates that this focus underestimates the impacts of climate change on species’ distributions. Evidence suggests that multidirectional distributional shifts are probably due to complexity of the species’ niches. VanDerWal et al. (2013) propose that multidirectional shifts might be more pronounced for tropical or subtropical species than for temperate species, but this hypothesis remains relatively untested because of the prevailing focus on temperate species. Thus, our study, which focuses on both temperate and tropical species, may shed light on these response dynamics (see Table S1.1 in Appendix S1.1).

We also test whether the focal species are likely to respond to changing climate independently and idiosyncratically, with differing distributional shifts. Based on species’ responses to longer-term climate oscillations (e.g. Foster et al., 1990) and previous studies (e.g. Edwards & Richardson, 2004; Pörtner & Knust, 2007; Peterson et al., 2008a; Drinkwater et al., 2010; VanDerWal et al., 2013), we anticipate diverse responses to
changing climate that are related to the unique climatic envelope of each species. If non-congruent responses were identified, assemblage composition and community structure could be affected (Harley et al., 2006; Worm et al., 2006).

Materials and Methods

Study area.

We trained models for each species in an area generated by buffering distributional data by 10.5° and dissolving buffered areas to create a continuous region. This buffered region represented a simple hypothesis of distributional potential for these species, tempered by sampling effort. We excluded areas that were not adequately sampled (e.g. South America), because the inclusion of undersampled areas may result in false absences during model calibration. Isolated occurrence points were also excluded from the training region for this reason, and because we deemed them potentially unreliable. In effect, we sought to focus on the union of the area sampled by researchers and that most likely accessible to the species sensu Phillips et al. (2009), VanDerWal et al. (2009) and Peterson et al. (2011). Models were calibrated on these circumscribed areas (Barve et al., 2011) and projected to the entire study region, which comprised the eastern seaboard of North America, the Gulf Coast, the Caribbean and part of South America, from 28° S to 56° N and from 110° W to 33° W. All spatial analyses were conducted within these bounds (Fig. 1.1).
**Figure 1.1** Distributional data for all 14 marine mollusk species within the western North Atlantic. For individual maps, see Figs S1.1.1–1.1.4 in Appendix S1.1.

**Distributional data.**

Presence-only distributional data were obtained from the Florida Museum of Natural History (FLMNH), the Academy of Natural Sciences of Drexel University, the University of Michigan Museum of Zoology, the Natuurhistorisch Museum Rotterdam and the U.S.
National Museum of Natural History (Fig. 1.1, Table 1.1, Figs S1.1.1–S1.1.4 in Appendix S1.1). The data obtained were representative of the known distributions of these species (Table S1.1.1), the majority of which occupy depths from c. 0 to 70 m, and are subtropical to tropical (see Table S1.1.1 for details). Only adult forms (benthic) were considered in this study; as such, potential variation in the environmental preferences of larval stages was not captured [most species considered here have planktotrophic larvae, except Conus anabathrum Crosse, 1865, Melongena corona (Gmelin, 1791), Terebra dislocata (Say, 1822) and Lucina pensylvanica (Linnaeus, 1758)]. Although assessing heterogeneity in environmental preferences through ontogeny was of interest, it would have been difficult to implement for marine species whose planktonic or free-swimming larval forms lack distributional records (Hiddink, 2003; Robinson et al., 2011).

We georeferenced distributional data following the point-radius method (Wieczorek et al., 2004) using either GOOGLE EARTH 6.0 combined with the MANIS GEOREFERENCING CALCULATOR (Wieczorek et al., 2001) or BIOGEOMANCER (Guralnick et al., 2006). The exact protocols depended upon the particular locality string and followed standard georeferencing guidelines (Chapman & Wieczorek, 2006). Only distributional data with spatial uncertainty less than 6.5 km were retained, totalling 1334 records across the 14 species (Table 1.1). These minor levels of uncertainty in the data should not influence model performance (Graham et al., 2008), given that they were finer than the spatial resolution of our environmental data (1° × 1°). We subsampled the occurrence data to leave one record per environmental pixel, to account for sampling biases (Royle et al., 2012; Yackulic et al., 2013).
Table 1.1 Model evaluation results for 14 mollusk species from the western North Atlantic. The second column indicates number of spatially unique points used to calibrate each model. The following columns report $P$-values and area under the curve ratios from the partial receiver operating characteristic analyses (partial ROC), designed to assess model significance. A similar number of external occurrence points were used in partial ROC analyses. The ‘% pts omitted’ column specifies the proportion of external testing points omitted by binary present-day models at a 5% omission threshold.

<table>
<thead>
<tr>
<th>Species</th>
<th>No. of spatially unique training points</th>
<th>MAXENT</th>
<th>GARP</th>
</tr>
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<tr>
<td></td>
<td>$P$</td>
<td>AUC ratio</td>
<td>% pts omitted</td>
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<td>Gastropoda</td>
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<tr>
<td><em>Strombus alatus</em></td>
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<td>1.64</td>
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<tr>
<td><em>Terebra dislocata</em></td>
<td>18</td>
<td>0.0002</td>
<td>1.61</td>
</tr>
</tbody>
</table>

Environmental data.

Niche models for present-day distributions were constructed using eight surface-level environmental variables from the Ocean Cycle model (Diat-HadOCC) component of the Hadley Centre Global Environmental Model version 2 with Earth System components (HadGEM2-ES; Moss et al., 2010; Collins et al., 2011; Martin et al., 2011) and a world bathymetry layer (Amante & Eakins, 2009). The eight Diat-HadOCC variables represented modeled averages for 1991–2010 at 1° × 1° resolution: dissolved inorganic carbon (DIC); diatom phytoplankton concentration; non-diatom phytoplankton concentration; zooplankton; sea-surface temperature (SST); sea-surface salinity (SSS); total alkalinity; and nitrogen concentration. The bathymetry grid was resampled from 2′ resolution to 1° using the natural-neighbour interpolation function in ArcGIS 10 (Sibson, 1981). These data provided a rich environmental characterization with which to assess how species may respond to...
environmental change. Although temperature and salinity have been reported to constrain the distributions of other marine invertebrates (e.g. Jones et al., 2009; Tunnell et al., 2010; Russell et al., 2012), the additional parameters were potentially important in determining the suitability of environments for marine mollusks (Talmage & Gobler, 2009).

Future environmental parameters were derived from HadGEM2-ES under the new Intergovernmental Panel on Climate Change (IPCC) 5th Assessment Report Representative Concentration Pathways (RCP) 2.6, 4.5 and 8.5 emission scenarios (Moss et al., 2010), representing least to greatest estimated greenhouse gas emissions, respectively; these scenarios allowed us to understand and assess variation among possible future climates. We evaluated RCP scenarios for 2021–2040, 2041–2060 and 2081–2100. Future projections for depth changes in the ocean were not available, so present-day bathymetry was used. Keeping bathymetry at present-day conditions should not affect our analyses, given the resolution of our study and the fact that sea level is predicted to rise only c. 20–65 cm over this interval (IPCC, 2007).

**Modeling algorithms.**

GARP (Genetic Algorithm for Rule-Set Prediction) provides an evolutionary computing algorithm for building ENMs based on non-random associations between known occurrence points for a species and sets of environmental coverages (Stockwell & Peters, 1999). We used DESKTOPGARP 1.1.3 (available at: http://www.lifemapper.org/desktopgarp/) with an internal testing feature (i.e. a random 50% of input data held back to evaluate model quality), resulting in 100 models for each species, with a 0.01 convergence limit and maximum of 1000 iterations. The ‘best subsets’ procedure was implemented (Anderson et al., 2003), wherein the ten best models were summed in ARCGIS 10 (ESRI, Redlands, CA, USA) to create a map of model agreement, with pixel values ranging from 0 to 10. We changed the values of two peripheral pixels from each environmental layer, because
DESKTOPGARP rescales predictor variable values to the range 0–254. This ensured that the lowest and highest values from projection regions and time slices were also present in calibration regions, producing consistent projections in GARP.

MAXENT (version 3.1.1) minimizes the relative entropy between two probability densities (one from the distributional data and one from the background or study area) defined in covariate space (Elith et al., 2011). We used the default parameters, including logistic output, random test percentage 0, regularization multiplier 1, and 10,000 background points. Linear, quadratic, product, threshold and hinge feature types were enabled, and we removed duplicate presences. We also ran MAXENT with extrapolation disabled, which truncates the model response curves outside values found in the calibration region and elicits a response curve closer to that of GARP (Owens et al., 2013).

Model analysis and verification.

Post-processing of ENMs.
Maps of projected ENMs were initially converted into integer grids, retaining three significant digits, and reclassified as either 0 (unsuitable area) or 1 (suitable area) for ease of comparison (Liu et al., 2005) using threshold values that allowed a maximum of 5% omission error based on the calibration data. A certain percentage of occurrence data was accepted as omission error in model predictions, because error may exist in the dataset (Peterson et al., 2011). Although the choice of threshold may affect analyses (Nenzen & Araújo, 2011; Jones et al., 2013), the raw model results exhibited patterns similar to those obtained using thresholds. Calculations of the area predicted to be suitable within the study region were performed by projecting grids onto a global cylindrical equal-area projection, and summing the areas in ARCMAP. Once the maps were reclassified, we calculated the potential cumulative area lost and gained from the present to the three future time slices sensu Cheung et al. (2009) and Thuiller et al. (2005). These maps were not representative of distribution sensu stricto, but rather areas of predicted environmental suitability. The
assumption was that species would track and fill suitable areas. Hence, the cumulative environmental suitability maps potentially misrepresented diversity in the present (i.e. subject to assumptions regarding which areas were accessible to the species; Barve et al., 2011) and for the future (Aranda & Lobo, 2011). Our analysis, however, aimed to characterize potential new area gained and lost across species. To visualize cumulative suitable area lost/gained as a function of latitude, we tabulated the distributions of values across particular latitudes in R 2.15.0 (R Core Team, 2012), and standardized based on numbers of pixels available (Fig. 1.2).

Latitudinal range shifts through time were calculated using gCentroid in the RGEOS package in R 2.15.0 (Bivand & Rundel, 2011). First, present-day and future binary suitability maps were converted to polygons in ArcGIS 10. These (often non-contiguous) polygons were then imported into R to find the ‘centre of mass’ or true centroid of areas presenting suitable conditions for each time slice.

Model quality metrics.
We assessed present-day model quality using three approaches (Table 1.1, Table S1.1.1). The first two analyses relied on external testing data (50% of occurrence points) set aside for each species (i.e. not used in model calibration). First, we calculated omission error rates, with false negatives defined as distributional data points falling at sites identified (wrongly) as unsuitable by the models (Anderson et al., 2003). Second, we tested model predictions via partial receiver operating characteristic analyses (partial ROC; Peterson et al., 2008b). We used a Visual Basic routine developed by N. Barve (University of Kansas, Lawrence, KS; http://hdl.handle.net/1808/10059), using an expected error rate of $E = 5\%$ (Peterson et al., 2008b). We performed 1000 bootstrap iterations by resampling 50% of test points with replacement. Third, we compared our models qualitatively with previously published distributions (see Table S1.1.1 for references). We found few map-based depictions of these species distributions in the literature, so we compared our models to
textual descriptions of species’ ranges. We assessed the correspondence of our models with published distributional summaries, with regard to omission error rather than commission error, because species may often be absent from suitable regions owing to biological or historical constraints, or may not be sampled (Peterson et al., 2011).

Model extrapolation.

When transferring models to different situations, conditions outside the range of values of environmental variables in the calibration region may be encountered, leading to extrapolation. MAXENT identifies areas of potential strict extrapolation via clamping and multivariate environmental similarity surfaces (MESS; Elith et al., 2011). We used Mobility Oriented Parity (MOP), a modification of MESS, to (1) assess where strict extrapolation may occur, and to (2) calculate environmental similarity from a given pixel in a transfer time/region to those within the calibration region (Owens et al., 2013). We compared environmental similarity using the closest 10% of pixels in the environmental space of the study area to a given pixel, in both the present-day projection and the RCP 8.5 2081–2100 time slice within R (Owens et al., 2013). We chose the RCP 8.5 2081–2100 time slice for visualization of extrapolation because these environmental parameters deviated most from present-day parameters.

The above approach focused on ranges of values for environmental variables independently, but novel combinations of values for these predictors should also be considered (combinational extrapolation). Zurrell et al. (2012) extended the MESS concept to identify parts of environmental space within sampled ranges of individual univariate predictors, but representing new multivariate combinations of variables (combinational extrapolation). These new combinations could pose the same extrapolation problems to a model. We ran the R script of Zurrell et al. (2012) to detect such areas, creating environmental overlap masks for present-day projections and the RCP 2.6 2081–2100 and RCP 8.5 2081–2100 time slices.
Sensitivity tests on predictor data.

We performed sensitivity tests to assess how the inclusion of environmental predictors might affect our modeling results. First, we excluded bathymetry from analyses, because it may provide only indirect information on a species’ physiology, and indirect variables should be avoided when transferring models in space and time (Peterson et al., 2011). Similarly, we assessed whether numbers of variables and correlations among them (tested using ‘cor’ in R 2.15.0; see Fig. 1.2.1 in Appendix S1.2) artificially induced declines in suitable areas anticipated under future climate-change scenarios. That is, we repeated the exercise using a less-correlated subset of predictor variables (i.e. only bathymetry, diatom phytoplankton concentration, nitrogen concentration, SST and SSS). Because results of these exercises were closely similar and we had no reason to exclude particular variables, we present only those results derived from the full analysis (Table S1.2.1 in Appendix S1.2).

To ascertain which variables drove the predicted broad-scale future changes, we reprojected future models holding each temporally varying variable constant (i.e. using the present-day value for that variable and future values for all other variables), totalling eight iterations per species. These jackknifed simulations were compared to the original projected future distributions to assess how changes in a particular variable influenced future projections, thereby identifying the variable(s) that cause the changes. We performed the reverse analysis to assess congruence between the approaches, wherein we held variables at present-day conditions except for one variable set to future values. This process was repeated for all variables for each species, but rather than being compared to original future projections, the latter simulations were compared to present-day models. The above analyses were undertaken using MAXENT for the 2081–2100 time slice of the RCP 2.6 and RCP 8.5 scenarios to illustrate generalities of the system’s behaviour (see Tables S1.2.2 & S1.2.3 in Appendix S1.2).
Results

We present the lowest scenario for greenhouse gas emissions (RCP 2.6) – that is, the best-case scenario – unless otherwise noted (the more extreme scenarios are documented in Appendix S1.1, with results mirroring those from the conservative scenario, albeit with greater reductions in suitable area predicted for all species). Results for MAXENT represent those under the default settings, which produced fewer overall changes in suitability, unless otherwise noted.

Model analysis and verification.

Model quality metrics.

Model evaluation exercises suggest satisfactory model performance, with the possible exceptions of Lucina pensylvanica and Mercenaria campechiensis. Omission error rates are generally low: 78% of models have < 15% omission error (Table 1.1). Partial ROC tests are statistically significant, except for the GARP models for L. pensylvanica and M. campechiensis (Table 1.1). Finally, our models accord well with published distributions (Table S1.1.1 and Figs S1.1.5–S1.1.8 in Appendix S1.1): only one (M. campechiensis) omits large regions known to be inhabited. Errors occur along the northern extreme of the species’ range, where records document M. campechiensis in waters off New Jersey, but models predict suitable areas only as far north as Georgia and South Carolina. Less severe omission errors occur in MAXENT models for Oliva sayana Ravenel, 1834 and Strombus alatus Gmelin, 1791, where small suitable areas are again missing from northern reaches of these species’ ranges.

Model extrapolation.

Novel environments occur in areas that do not intersect with model predictions for either the present-day or the RCP 8.5 2081–2100 projection (Fig. S1.3.1 and Table S1.3.1 in Appendix S1.3). Environmental overlap masks indicate that the present-day projections are largely unaffected by novel combinations of environmental parameters, except for regions off'
the coast of Brazil. Conversely, future time slices show large numbers of pixels presenting novel environmental combinations (Fig. S1.3.2 in Appendix S1.3).
**Figure 1.2** Cumulative suitable area lost/gained for all 14 marine mollusk species in the western North Atlantic for Representative Concentration Pathways (RCP) 2.6 emission scenario, tabulated across latitudes and standardized for the available area per latitude.
**Future suitability patterns.**

*Poleward range shifts.*
Northern and southern extremes of suitability for most species are predicted to remain relatively constant through the remainder of this century, even when allowing for model extrapolation. Northern extremes of suitability are predicted to shift northward for only three (GARP; *Bulla occidentalis* Adams, 1850, *Crassostrea virginica* and *Crepidula fornicata*) or four (MAXENT; plus *Conus spurius* Gmelin, 1791) of the 14 species, whereas the southern edge of suitability is predicted to shift southwards for seven (GARP; *Conus anabathrum*, *Conus spurius*, *Crassostrea virginica*, *Melongena corona*, *Mercenaria campechiensis*, *Lucina pensylvanica* and *Terebra dislocata*) and one (MAXENT; *Melongena corona*) of the 14 species (Fig. 1.3). When changes in the geographical centroid of suitability are considered, no significant poleward shifts in suitable conditions are observed for individual species (Fig. 1.3). Across all species, the average change in centroid position from now to the end of century is only 1.4° (MAXENT) or 5.1° (GARP), but this shift occurs towards the equator, not polewards (see Table 1.2 and Figs S1.1.10 & S1.1.11 in Appendix S1.1 for other RCP scenarios). The centroid of suitable conditions shifts northwards for some species (e.g. *Crepidula fornicata* and *Crassostrea virginica*) and southwards for others (e.g. *Mercenaria campechiensis* and *Terebra dislocata*).

**Table 1.2** Average change in centroid position across all 14 marine mollusk species from the present to 2081–2100 for each IPCC Representative Concentration Pathways (RCP) emission scenario, expressed in degrees latitude.

<table>
<thead>
<tr>
<th>RCP scenario</th>
<th>MAXENT</th>
<th>GARP</th>
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<tbody>
<tr>
<td>2.6</td>
<td>−1.43</td>
<td>−5.14</td>
</tr>
<tr>
<td>4.5</td>
<td>−3.46</td>
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<tr>
<td>8.5</td>
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</tr>
<tr>
<td>Mean</td>
<td>−3.09</td>
<td>−4.33</td>
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</table>
Species-specific versus assemblage responses. Most species are predicted to exhibit declines in available suitable area. Ten (MAXENT) or 12 (GARP) of the 14 species show a contraction of suitable area (Figs 1.4 & 1.5), including the medically or economically important species Conus anabathrum, Dinocardium robustum and Mercenaria campechiensis. Even so, the amount of decline and regions affected vary among species considered, as the centroid analyses indicate (Fig. 1.3).

Half of species show reductions in suitable area of more than 20% by 2080 (Anomia simplex d’Orbigny, 1853, Conus anabathrum, Dinocardium robustum, Mercenaria campechiensis, Oliva sayana, Strombus alatus and Terebra dislocata). GARP estimates reductions in suitable conditions of around 60% for four of these taxa (Conus anabathrum, Dinocardium robustum, Mercenaria campechiensis and Terebra dislocata), whereas MAXENT predicts less dramatic, but still substantial (25–47%), losses for the same species. Running MAXENT without extrapolation suggests declines in suitable area similar to those under default settings for most species. Even closely related taxa are predicted to respond to warming differently: Conus spurius gains area (MAXENT) or has minor retractions (GARP and non-extrapolation version of MAXENT), unlike C. anabathrum, which is anticipated to undergo dramatic reductions in suitable area.
Figure 1.3 Latitudinal extent (light shading) and change in centroid of suitable conditions (dark line) for each of the 14 marine mollusk species in the western North Atlantic from the present (P) to each time slice (2021–2040, 2041–2060 and 2081–2100) for IPCC Representative Concentration Pathways (RCP) 2.6 emission scenario. Note that both the absolute extent and centroid of suitable conditions remains fairly stable through time. Some species (e.g. *Crassostrea virginica* and *Crepidula fornicata*) have extents and centroids that shift slightly north, while others have extents and centroids that shift slightly south (e.g. *Mercenaria campechiensis* and *Terebra dislocata*). This variability highlights the species-specific nature of the predicted responses to future climate change.
Figure 1.4 Histograms depicting the number of marine mollusk species that gained or lost suitable area in the western North Atlantic per time slice, algorithm and RCP emission scenario compared to present-day models. Darker colours indicate gains in suitable area, whereas lighter colours indicate loss of suitable area.

Across the full set of species, the loss of suitable conditions generally increases with time. Declines in suitable conditions are common across the study area, particularly at latitudes 10–15° N (Fig. 1.2). Some regions may become unsuitable for many of the species considered: e.g. the Lesser Antilles, Bay of Campeche, the Atlantic seaboard south of South Carolina, and the Bahamas (Figs S1.1.9, S1.1.12 & S1.1.13 in Appendix S1.1).

Few species are predicted to see newly suitable area or an overall expansion in distributional potential. For instance, *Bulla occidentalis* and *Crassostrea virginica* are the only species that see distributional potential increasing under both modeling algorithms.
MAXENT models anticipate relative stasis or increases in available area for *Conus spurius* and *Lucina pensylvanica*. Under the non-extrapolative version of MAXENT, however, only *L. pensylvanica* gains suitable area. Although the loss of distributional area outpaces any absolute gains, predictions for newly suitable areas tend to be concentrated near the equator (Fig. 1.2, Figs S1.1.9, S1.1.12 & S1.1.13). Despite expected reductions in distributional potential under future climate scenarios, all species are predicted to retain some continuously suitable areas through time (Table 1.3). The average area reconstructed as stable and suitable in all time slices across all species is 61.8% (MAXENT) and 49.0% (GARP), expressed as a percentage of the present-day suitable area.
Figure 1.5 Percentage change in suitable area in the western North Atlantic for each of the 14 marine mollusk species from the present day to three future time slices (2021–2040, 2041–2060 and 2081–2100) for all (RCP) emission scenarios. See Table 1.1 for full species names.
Table 1.3 Percentage of area predicted to remain suitable for 14 marine mollusk species within the study region according to RCP 2.6, 4.5 and 8.5 emission scenarios. The ‘Present’ column designates the percentage of present-day suitable area for particular species within the study region. The ‘All suitable’ column indicates the amount of area that remained continuously suitable geographically throughout all time slices, expressed as a percentage of the present-day suitable area.

<table>
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Variables responsible for future trends.

Based on jackknife manipulation, changes in single variables do not seem to drive model predictions for most species, although the suitable area typically decreases or remains stable when individual variables are held constant. In fact, the only individual variables that suggest a potential increase in suitable area for several species are non-diatom phytoplankton and SST (Table S1.2.2). Decreases, increases and stasis in suitable area for single species depend on the variable held constant, which is perhaps to be expected given the complexity of the model parameters and abiotic environmental preferences of species. Reverse analyses, with focal variables set to future values and all other variables held at present-day values, produce similar results (Table S1.2.2).

Discussion

Poleward range shifts.

Our initial hypothesis that suitable environmental conditions for species will expand at poleward range boundaries, with simultaneous contraction at low-latitude boundaries, is not broadly supported. Species did not present consistent patterns of poleward expansion, and although suitable area is lost near the equator, it is also lost across the entire study area. In fact, newly suitable environmental areas are predicted to become available at low latitudes. These results match aspects of the predictions of Burrows *et al.* (1991) and VanDerWal *et al.* (2013), but differ from other analyses of marine taxa (Cheung *et al*., 2009; Jones *et al*., 2010; Sorte *et al*., 2010; Sunday *et al*., 2012), which suggest that marine species will shift their distributions polewards in response to warming climates. These opposing responses may derive, as suggested by VanDerWal *et al.* (2013), from having a primary focus on tropical rather than temperate species, with the narrower climatic tolerances of tropical species producing unpredictable distributional shifts under changing climate. Interestingly, however, the temperate-zone species considered here exhibit the same multidirectional distributional
shifts as the entirely subtropical and tropical assemblages.

We suspect that northern waters will remain too cold for tropical and subtropical species to shift northwards, while substantial environmental perturbations in present-day distributional areas will cause the predicted reductions in suitable area for most of our species. Evidence for this hypothesis is twofold. First, temperature is implicated in causing declines in suitable area, and future values for this variable at species’ northern range margins appear to remain outside the environmental tolerance limits determined from species’ niche models. Tropical species are particularly sensitive to temperature changes, because their upper lethal thermal limits are closer to the maximum habitat temperature than those of temperate species (Compton et al., 2007; Tewksbury et al., 2008; Sunday et al., 2012; Araújo et al., 2013). Second, environmental overlap analyses suggest that there will be significant environmental perturbation, with virtually all regions having novel environmental combinations in the future. Temperature, however, is not the sole driver of losses in suitable area, because future temperature values in present-day distributional areas remain largely within absolute thermal tolerance limits for these species as determined from niche modeling. Consequently, other variables, such as changes in primary productivity, may work in combination with temperature changes to restrict future predicted species’ distributions.

**Species-specific responses.**

We also find idiosyncratic and species-specific responses to changing climate. The amount and direction of the predicted responses depends upon the niche characteristics of each species (Foster et al., 1990; Peterson et al., 2008a; VanDerWal et al., 2013), with the areas lost and gained varying between taxa. No consistent response is observed when solely tropical, or subtropical or temperate species are considered. Nevertheless, although the predicted responses are species-specific, the dominant signal for the 21st century is one of severe (>20%) distributional reductions for most of our study species, and this aspect of our study matches the patterns documented for terrestrial species (Thuiller et al., 2005; Pereira et
al., 2010; Visconti et al., 2011) and some marine species (e.g. Albouy et al., 2013).

**Modeling constraints.**

The results from any predictive study that employs modeling must be treated with some caution. For instance, the assumptions inherent in transferring ENMs among time periods have been discussed in detail elsewhere (Pearman et al., 2008; Peterson et al., 2011), including those associated with the supposition that niches remain stable in the face of environmental change (Peterson, 2011). Other limitations include applying a global Earth System model to the continental shelf (see Holt et al., 2009; Collins et al., 2011), where predictor variables are difficult to validate at the spatial scale considered, and in coastal environments. At the moment, however, these environmental data are the best available, particularly for future projections of both biogeochemical and physical parameters. Ideally, as with other recent studies (Fordham et al., 2012a), we would explore the implications of multiple such models, but that was impossible given the current availability of data.

Our environmental data warrant further consideration with respect to their efficacy in characterizing the niches of marine mollusks. For example, some concern exists regarding whether ocean surface data accurately simulate benthic conditions for these taxa. Although potentially problematic, surface data have previously been employed to characterize the distributions of benthic species that live in shallow waters on the continental shelf (e.g. Bentlage et al., 2013), particularly since surface conditions track benthic conditions to some degree at times of the year when mixing occurs (see Noble, 2001; Korty et al., 2008). Additional caveats include the inability to account for substrate type, a factor that affects fine-scale distributional patterns in benthic mollusks. Inclusion of this variable, however, would be impossible at the coarse spatial resolution of our study.

Aside from these abiotic constraints, our application of ENM does not account for dispersal or population dynamics (Anderson et al., 2009; Fordham et al., 2012b, 2013). These finer-scale processes, however, may play second fiddle to environmental gradients at
broad spatial scales, which have been shown to limit the latitudinal ranges of marine ectotherms (Gaines et al., 2007; Tomašových & Kidwell, 2009; Robinson et al., 2011; Buckley et al., 2012; Sunday et al., 2012).

Another issue worth noting is that we considered commercially-harvested species: *Crassostrea virginica*, *Dinocardium robustum* and *Mercenaria campechiensis*. These species will become increasingly vulnerable to overfishing with changing climate, which could precipitate population declines not visible to most modeling applications. These species may also prove more difficult to model, since present-day and historical harvest pressures affect perceptions of a species’ niche via non-detection in abiotically suitable areas (Mellin et al., 2012; Russell et al., 2012). The inclusion of harvest pressure is likely to indicate a more dire (and perhaps more realistic) future for those species.

If our results are generally applicable, though, they suggest far-reaching effects of climate change on marine mollusks, an essential component of marine ecosystems. Our models not only anticipate extensive degradation of conditions for these species, but also some range shifts that will change the composition of local assemblages. Notably, invasion and community re-organization can also precipitate extinction (Harley, 2011; Urban et al., 2012), such that community-level analyses that consider interspecific interactions would help clarify the fate of these mollusks (Davis et al., 1998; Araújo & Guisan, 2006). As with changing interspecific interactions, pollution and overharvesting pose similar severe threats to the survival of species (Harley, 2011; Russell et al., 2012). Thus, the already-substantial amount of 21st-century marine biotic degradation predicted by our models is almost surely an underestimate.

**References**


Physical and Engineering Sciences, 367, 939–951.


Chapter 2. Macroevolutionary consequences of profound climate change on niche evolution in marine mollusks over the past 3 million years
Abstract

In order to predict the fate of biodiversity in a rapidly changing world, we must first understand how species adapt to new environmental conditions. The long-term evolutionary dynamics of species’ physiological tolerances to differing climatic regimes remains obscure. Here, we unite paleontological and neontological data to analyze whether species’ physiological tolerances remain stable across three million years of profound environmental changes using ten phylogenetically, ecologically, and developmentally diverse mollusk species from the Atlantic Coastal Plain, USA. We additionally investigate whether these species’ upper and lower thermal tolerances are constrained across this interval. We find that these species’ environmental preferences are stable across the duration of their lifetimes, even when faced with significant environmental perturbations. Our results suggest that species will respond to current and future warming by altering distributions to track suitable habitat, or, if the pace of change is too rapid, by going extinct. Our findings support methods that project species’ present-day environmental requirements to future climatic landscapes to assess conservation risks. At the macroevolutionary scale, we provide evidence that species’ distributions are structured by environmental factors.
Introduction

Earth’s climate is rapidly changing, altering all facets of our planet at an unprecedented rate, from the biosphere, to the hydrosphere, to the atmosphere (IPCC, 2013). Given these changes, debate exists as to whether species can adapt their physiological tolerances to altered environmental conditions (Pearman et al., 2008; Lavergne et al., 2010; Hoffmann & Sgrò, 2011). Determining whether species’ climatic preferences (niches) evolve or remain stable in the face of environmental change over the long term is important for implementing proper conservation measures and mitigating threats posed to biodiversity (Pereira et al., 2010; Dawson et al., 2011; Moritz & Agudo, 2013), and for shedding light on macroevolutionary dynamics (Eldredge et al., 2005; Roy et al., 2009; Valentine et al., 2012; Jablonski et al., 2013; Romdal et al., 2013).

Here, we unite paleontological and neontological data (Dietl & Flessa, 2011; Fritz et al., 2013) to test niche stability across three million years of environmental changes using ten phylogenetically, ecologically, and developmentally diverse bivalve and gastropod species from the Atlantic Coastal Plain, USA (Table S2.1.1 in Appendix S2.1). Species’ niches were quantified using ecological niche modeling (ENM) (Peterson et al., 2011) for three time periods within the Pliocene—recent molluscan record of the Atlantic Coastal Plain: mid-Pliocene Warm Period (mPWP; 3.264–3.025 Ma), Eemian Last Interglacial Period (LIG; 130 Ka), and present-day interval (PI). Our null hypothesis is that niches remained stable across this interval. We additionally investigate whether these species’ upper and lower thermal tolerances are constrained across millions of years. Recent research suggests that tolerances to heat are largely conserved within terrestrial species, but that tolerances to cold are more variable (Araújo et al., 2013). This asymmetry is thought to diminish in the marine realm, where ectotherms are limited by both cold and warm conditions due to decreased aerobic capacity (Somero, 2002; Pörtner & Knust, 2007; Sunday et al., 2011). This study is the first
to incorporate both modern and fossil data across millions of years to understand ecological and evolutionary responses of species to changes in their environment, though see (Malizia & Stigall, 2011; Stigall, 2012) for analyses in deep time. Although characterizing the entirety of a species’ fundamental niche (FN) is often difficult (Araújo et al., 2013), we study close approximations here, given that recent biophysical approaches have determined that FNs can be represented by limited sets of parameters like temperature (Kearney et al., 2010; Kearney et al., 2013). This is particularly true for marine ectotherms, which have been shown to closely match range limits within their thermal tolerances (Sunday et al., 2011).

Theoretical (Kawecki, 1995; Holt, 1996) and empirical studies both support (Martínez-Meyer et al., 2004; Martínez-Meyer & Peterson, 2006; Strubble et al., 2013) and reject niche stability (Broennimann et al., 2007; Rödder & Lötters, 2009; Malizia & Stigall, 2011; Stigall, 2012). The debate has even continued at the genetic level, where recent research indicates that genetic reshuffling in *Drosophila* species can occur in response to climate change (Umina et al., 2005; Balanyá et al., 2006); however, it is still unknown if these genetic changes translate into evolution of actual physiological tolerances. The context in which niche evolution is considered is important with respect to whether change occurred in actual physiological tolerances (i.e., the FN), or whether it occurred because of differences in resource utilization or underlying environmental structure (i.e., changes in the realized niche; RN). Characterizing the entirety of the FN is difficult (Peterson et al., 2011), and studies may incorrectly indicate niche evolution if environmental availability is not considered (Peterson, 2011; Araújo & Peterson, 2012; Broennimann et al., 2012). The aforementioned studies have contributed much to our understanding of how species’ physiological tolerances evolve; however, questions remain as to the dominance of niche evolution *versus* stability, particularly since most studies lacked a temporal component that would allow for analysis of change across the entire duration of a species’ lifetime (i.e., Mys; Eldredge et al., 2005).
The Atlantic Coastal Plain record is ideal for elucidating the coevolution of species’ niches and the environment. Not only has the region experienced profound environmental changes from the closure of the Central American Seaway beginning in the Pliocene (Allmon, 2001) to glacial/interglacial cycles (Cronin, 1988; Haug & Tiedemann, 1998), but these environmental changes have been associated with patterns of extinction, species turnover, and ecological change (Allmon et al., 1993; Todd et al., 2002; Vermeij, 2005; Klaus et al., 2011). The mid-Pliocene Warm Period (~3.1 Mys), included in this study, is considered a climatic analog for conditions expected at the end of this century, and can contribute to how target species may fare under future climate scenarios (Dowsett et al., 2009). Results are vital for proper mitigation of the risks posed by current and future climate changes to Earth’s biodiversity (Moritz & Agudo, 2013; Warren et al., 2013).

Materials and Methods

Study area.
All models were calibrated within a region bounded by the Americas and 34°W longitude, and 48°N and 44°S latitude (Fig. 2.1). We sought the union of the area sampled by researchers and that was most likely accessible to the species across spatial and temporal dimensions (Phillips et al., 2009; VanDerWal et al., 2009; Peterson et al., 2011). With the exception of L. pensylvanica and T. dislocata, which have benthic larvae, target species are capable of dispersing long distances as planktonic larvae on ocean currents.

Taxa.
We selected ten species that occur in both the modern and fossil (from ~3.1 Ma to recent) records of the Atlantic Coastal Plain, USA. These species were chosen because they have diverse phylogenetic positions, varied ecological habits and developmental modes, and abundant distributional data available from fossil and modern localities (Table S2.1.1 in Appendix S2.1). We used morphological criteria to identify target species. Each taxon is
readily diagnosable, and the unique combinations of apomorphies that these species possess are present in their fossil representatives. All evidence suggests that these lineages represent species that have distinct evolutionary trajectories, a supposition supported by the fact that most invertebrate species have durations of >3 million years (Eldredge et al., 2005).

**Distributional data.**

*Present-day.*

Presence-only distributional data were downloaded from five institutions, including the Florida Museum of Natural History (FLMNH), Academy of Natural Sciences of Drexel University, University of Michigan Museum of Zoology, Natuurhistorisch Museum Rotterdam, and U.S. National Museum of Natural History; records are representative of the known, modern-day distributions of these species (Table S2.1.1 and Figs. S2.1.3-S2.1.5 in Appendix S2.1) (Saupe et al., In Press). We assigned latitude and longitude coordinates to distributional data following standard georeferencing protocols (Chapman & Wieczorek, 2006). Only records with spatial uncertainty <15 km were retained, ensuring that they were matched correctly with corresponding environmental data of a coarser spatial resolution (i.e., 1.25 x 1.25°) (Graham et al., 2008). We subsampled distributional data to leave one record per environmental pixel to account for sampling biases, which reduced records from 1,522 to 324 across the ten species (Table S2.1.1 in Appendix S2.1). This process did not affect the resultant overall distribution of the species, but rather prevented certain localities with multiple records from being unduly weighted in the analyses (Royle et al., 2012; Yackulic et al., 2013).

*Fossil.*

We considered fossil distributional data from Pliocene (~3.264–3.025 Ma) and Last Interglacial (~130 Ka) strata of the Atlantic Coastal Plain, USA. To ensure distributional data were derived from geologic units of similar ages to our periods of interest, we generated a stratigraphic database for all Pliocene–recent geologic units of the Atlantic Coastal Plain
Correlations and unit ages were determined by extensive literature survey and use of various stratigraphic databases, resulting in 10 viable formations for the Pliocene and 16 for the LIG (see Appendix S2.2). We note that these formations are not exactly 3.1 Ma and 130 Ka, respectively, but closely approximate the environmental data currently available.

Distributional records were obtained from onsite investigations of collections to ensure proper species identification, including the Florida Museum of Natural History, Paleontological Research Institution, Virginia Museum of Natural History, Academy of Natural Sciences of Drexel University, and Yale Peabody Museum. As with present-day distributional data, we subsampled fossil distributional data to leave one record per environmental pixel, such that Pliocene records were reduced from 1,140 to 104 records across the ten species, and LIG records were reduced from 442 to 110 records (Table S2.1.1 in Appendix S2.1). At least six spatially-explicit distributional records were used for model calibration for any given species/time period; studies have shown this number to be statistically robust for extant species (Hernandez et al., 2006; Pearson et al., 2007).

Environmental data.

Environmental data were derived from the coupled atmosphere-ocean HadCM3 global climate model (GCM) (Gordon et al., 2000; Pope et al., 2000) for three time slices: mid-Pliocene Warm Period (mPWP; 3.264–3.025 Ma), Eemian Last Interglacial Period (LIG; 130 Ka), and pre-industrial (PI; ~1850–1890). Ideally, we would use an ensemble-modeling approach that considered multiple GCMs (Fordham et al., 2012); however, model output from the LIG was available to us only from HadCM3. This GCM has been successfully used within a large range of Quaternary and pre-Quaternary modeling studies. Pre-industrial output was chosen for present-day modeling to match the spread of collecting dates for distributional data, which included museum records from the early to mid 1900’s. Boundary conditions for the mPWP GCM used the alternate PRISM3D PlioMIP dataset described in
(Haywood et al., 2011). LIG boundary conditions were from (Singarayer & Valdes, 2010) and (Singarayer et al., 2011). Here, atmospheric gas concentrations were derived from ice core records (Petit et al., 1999; Spahni et al., 2005; Loulergue et al., 2008), and orbital parameters were derived from (Berger & Loutre, 1991). The pre-industrial experiment was equivalent to (Braconnot et al., 2007). All experiments were run for 500 model years, and environmental parameters were derived from the final 30 years of each experiment at 1.25 x 1.25° resolution (~140 x 140 km at the equator). Where ocean data were unavailable (i.e., sites presenting macrofossil data, but where the GCM indicated land), we used an inverse-distance weighted algorithm to extrapolate model data.

Monthly salinity and temperature outputs were converted to maximum, minimum and average yearly coverages for both surface and bottom conditions using ArcGIS. From these coverages, we eliminated variables that significantly co-varied (assessed using the ‘cor’ function in R.15.2; R Core Team, 2012). Ultimately, two bottom variables: yearly average salinity and temperature, and four surface variables: maximum and minimum salinity, and maximum and minimum temperature, were retained. Both maximum and minimum temperature were preserved, since these variables possessed some degree of independent scatter and were deemed biologically important for marine ectotherms (Tomašových & Kidwell, 2009; Buckley et al., 2012; Sunday et al., 2012).

To avoid inaccurate niche representations due to truncated model response curves (Owens et al., 2013), we assessed peripherality of distributional data with respect to the environment of the calibration region using histograms produced in R.15.2. Results indicated peripherality of data is not a problem, with the potential exception of bottom salinity and temperature variables.

**Modeling algorithm.**

Ecological niche models (ENMs) were generated using Maxent v. 3.3.3 (Phillips et al., 2006), a widely employed and popular modeling algorithm (Fig. 2.1 and Figs. S2.1.1-S2.1.2
in Appendix S2.1). Maxent minimizes the relative entropy between two probability densities — one from the distributional data and one from the background or study area — defined in covariate space (Elith et al., 2011). We enabled only quadratic features to simulate realistic bell-shaped response curves that are known from physiological experiments of plants and animals (Austin, 1985; Austin et al., 1994; Hooper et al., 2008; Angilletta, 2009). However, to test model sensitivity, we also enabled all features (i.e., linear, quadratic, product, threshold, and hinge), which produced models similar to those with only quadratic features. We calibrated models using all spatially-explicit data points for each species/time slice, running 100 bootstrap replicates with a ten percent random test percentage. We took the median of the 100 replicates and converted to integer grids, retaining three decimals, in ArcMap v.10.1. The mean value for these grids was used to threshold to binary predictions (Liu et al., 2005; Freeman & Moisen, 2008). This method is particularly suitable when prevalence data varies among models, as with past and present time slices (Freeman & Moisen, 2008).

To correct for biases in fossil distributional data, we implemented a bias file within Maxent for past modeling. The bias file describes the probability that an area was sampled; thus, regions with rock outcrop (i.e., areas where species may actually be detected or sampled) were weighted twice as heavily as regions without rock outcrop. Maxent will then factor out this bias during the modeling process (see (Dudík et al., 2005) for details). This method essentially accounts for incomplete knowledge of a species distribution sensu (Svenning et al., 2011).

Model verification.

Two model validation methods were used, depending on the prevalence of distributional records (Table S2.1.2 in Appendix S2.1). For species/time slices with <25 points, we assessed statistical significance using a jackknife procedure under a least training presence threshold (Pearson et al., 2007). This method, however, may produce over-
optimistic estimates of predictive power for sample sizes >25, and thus these species/time slices were tested via partial Receiver Operating Characteristic analyses (“partial ROC”) (Peterson et al., 2008). Distributional records were divided into five random replicates of 75% training and 25% testing points. Maxent models were re-calibrated using these training sets, performing 1000 bootstrap iterations with random test percentage equal to 20. The median model from these replicates was assessed for statistical significance using testing sets within a Visual Basic routine developed by N. Barve (U. Kansas; http://hdl.handle.net/1808/10059). The error rate was set to $E = 1\%$ (Peterson et al., 2008), and we performed 1,000 bootstrap iterations by resampling 50% of test points with replacement.

**Niche comparisons.**

*Geographic projections.*

We used ENMTools v1.3 (Warren et al., 2008; Warren et al., 2010) to quantify similarity of ENMs within each lineage through time (Table 2.1 and Appendix S2.3). ENMTools uses randomization tests to compare observed similarity to that expected under a null hypothesis. The null is rejected if models are more (or less) similar than expected by chance, based on the environment within the geographical regions of interest (Warren et al., 2010). Similarity is quantified using Schoener’s $D$ (Schoener, 1968), with values ranging from 0 to 1, or more to less similar, respectively.

For each of the ten species, we compared observed niches across three different time periods: mPWP, LIG, and PI. Comparisons were made in two directions *sensu* (Warren et al., 2008; Warren et al., 2010; Broennimann et al., 2012); i.e., the model of time A was compared to the model of time B projected to time A and *vice versa*. This was done because it is possible for two niches to be more similar than expected based on the environment available for one time slice, but less similar than expected based on the environment available for the other (or some combination thereof). To ensure accurate response curves
when projecting, we disabled clamping and enabled extrapolation within Maxent (Owens et al., 2013). Null distributions consisted of 100 random models generated within Maxent, with model parameters drawn from the study system. Statistical significance was assessed by creating histograms in R: if the observed value fell outside the null distribution to the high end, niches were more similar than expected by chance, whereas if the observed value fell outside the null distribution to the lower end, niches were more different than expected by chance. Observed values that fell within the null distribution did not allow for discrimination of similarity or differences based on the environment available to the entities in question. Note that because the present analysis was aimed at demonstrating the absence of change (null hypothesis), rather than being a ‘fishing expedition’ looking for any evidence of change, it was not necessary to apply the Bonferroni adjustment for the geographic or environmental comparisons (Perneger, 1998).

Environmental comparisons. The quantitative framework provided by (Warren et al., 2008; Warren et al., 2010) has proven a powerful tool for assessing niche similarity; however, this method makes comparisons using the geographical projections of niches, which can introduce error when analyzing niches through time and in different environments (Williams & Jackson, 2007; Williams et al., 2007). Consequently, we also calculated metrics of niche overlap in gridded environmental space using the methodology of (Broennimann et al., 2012). Here, ordination techniques (Thuiller et al., 2005; Hof et al., 2010) allow for direct comparison of species-environment relationships in environmental space, and corrects observed distributional densities for each region in light of the availability of environmental space using kernel density functions (Table 2.1 and Appendix S2.3). Niche overlap is measured along gradients of a multivariate analysis, and statistical significance is assessed using the same framework employed in ENMTools. Tests of niche equivalency and niche similarity were performed, but
we focused on niche similarity, since niches will rarely, if ever, be absolutely identical (Warren et al., 2008).

We tested for similarity using a principal component analysis (PCA) applied to all six environmental parameters. We also tested for similarity by reducing niche dimensionality to three variables, including surface coverages for maximum salinity, maximum temperature, and minimum temperature. These variables were retained because they explained the most variance in the data and were deemed biologically important (Tewksbury et al., 2008; Jones et al., 2009; Tunnell et al., 2010; Sunday et al., 2012). Analyses performed with this reduced set of variables are potentially more informative, since over-parameterization can constrict niche estimates and lead to approximations closer to the RN, not the FN. Moreover, these additional variables may be uninformative with regards to species’ niche attributes, which would add noise to comparisons and contribute to type II errors. PCA analyses were calibrated on both environments (project=false). We used both the PCA-occ and PCA-env functions; the former calibrates the PCA based only on the distributional data, whereas the latter uses data from the entire environmental space of the two study systems; results were equivalent, and thus we present only those from PCA-env. A bin size of 100 was used to characterize the environment, running 1000 replicates for similarity tests. Since prevalence of distributional data varies through time, i.e., past time slices typically contained fewer data points, we generated input data from ENMs, subsampling one point per pixel in binary predictions so that comparisons were unbiased with regard to the amount of input data. This also ensured that comparisons were being made using approximations closer to the FN, rather than the RN.

We also tested similarity in raw variables (Table 2.2 and Appendix S2.3). We used the script of (Broennimann et al., 2012) to analyze each of the six variables individually, and we modified the script to compare raw variables in two dimensions, while still accounting for differences in availability of environments in a given time period. We were interested in
testing for evolution in overall temperature parameters, and thus we assessed similarity using average bottom temperature and maximum surface temperature. Significance was evaluated by generating histograms in R to determine where observed D values fell in relation to the null distributions.
Table 2.1 P-values for multi-dimensional niche comparison tests (1) using a PCA applied to all six environmental variables (Broennimann et al., 2012); (2) using a PCA applied to the three most important environmental variables; (3) using raw average bottom temperature and maximum surface temperature with a modified script of Broennimann et al. (2012); and (4) using ENMTools (Warren et al., 2008, 2010) on projections of ecological niche models. Bold values indicate non-significant results. All significant results (P<0.05) indicate niches are statistically more similar than expected given the environmental background of the time slices, except for the result with the asterisk, which indicates a niche comparison that was statistically dissimilar. Note that it is possible for two niches to be more similar than expected based on the environment available for one time slice, but less similar than expected based on the environment available for the other. See Appendix S2.3 for graphical depictions of

<table>
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<th>PI—LIG</th>
<th>LIG—PI</th>
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<th>PI—mPWP</th>
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Results

Model verification exercises suggest that ENMs are statistically significant for each time period and species ($P < 0.05$, see Table S2.1.2 in Appendix S2.1); model depictions are presented in Fig. 2.1 and Figs. S2.1.1-S2.1.2 in Appendix S2.1. Together, the suite of niche comparisons (360 in total) indicates these species’ niches are stable across millions of years. Of the ten ecologically diverse species, nine show niche similarity for the majority of the comparisons. Probabilistically, this result would be obtained only 1% of the time assuming equal likelihood for evolution versus stability. *Bulla occidentalis* is the only species with non-significant results across the comparisons, such that its niche dynamics cannot be adequately assessed. We obtain evidence of niche similarity for tests on both principle component analyses (PCAs) and raw variables. Moreover, minimum and maximum temperature tolerances are generally conserved through time.
**Figure 2.1** Representative ecological niche models for the present, LIG, and mPWP time slices for two species: *Anomia simplex* and *Oliva sayana*. Binary and continuous predictions are presented, with binary predictions thresholded using the mean suitability value from the continuous output. For the binary predictions, yellow=suitable and dark blue=unsuitable, whereas for the continuous predictions, darker grays indicate higher suitability. All analyses were conducted within the geographic extent shown. See Fig. S2.1.1-S2.1.2 in Appendix S2.1 for remaining species analyzed.
Environmental comparisons.
Comparisons on multi-dimensional niches indicate overwhelming signals of niche stability across time slices. Three analyses were performed to this effect: (1) comparisons on the first two axes of a PCA applied to all six environmental variables, (2) comparisons on the first two axes of a PCA applied to the three most important variables (i.e., maximum and minimum surface temperature, and maximum surface salinity), and (3) two-dimensional comparisons of maximum surface temperature and average bottom temperature (see Appendix S2.3). Of these 180 comparisons, 149 indicate significant similarity, and no comparison finds evidence of niche evolution.

Comparisons considering all six environmental variables indicate niches are statistically similar for virtually all species and time slices (46 of 60 comparisons) (Table 2.1). When niche dimensionality was reduced to the most important variables, nine species show statistically similar niches for all comparisons, with the exception of one or two inconclusive tests for *C. fornicata*, *D. robustum*, *L. pensylvanica*, and *N. duplicata* (49 of 60 comparisons; Fig. 2.2 and Table 2.1). *Bulla occidentalis* is the only species with non-significant tests across the time slices. Niches also show stability when raw variables are considered. Seven of the ten species have statistically similar niches across all time comparisons (42 of 60 comparisons; Table 2.1). Two other species, *O. sayana* and *C. virginica*, have statistically similar niches with the exception of one or two inconclusive tests, respectively. Quantifying niche similarity for *B. occidentalis* proves more difficult, as three of six niche comparisons are non-significant.
Figure 2.2 Representative results from the analyses using a PCA on the three most important environmental variables (maximum and minimum surface temperature, and maximum surface salinity) for *Anomia simplex* and *Oliva sayana*. Comparisons are shown for the Last Interglacial (LIG, ~130 Ka), mid-Pliocene Warm Period (mPWP, ~3.1 Ma), and present-day (PI). The histograms show the null distribution of similarity values (D), with the observed value in red. All comparisons indicate that niches are statistically more similar than expected given the environmental backgrounds. For other comparisons, see Appendix S2.3 and Table 2.1.
We also tested whether species conserved their upper and lower thermal tolerance limits, an important consideration for marine ectotherms as temperatures warm (Sunday et al., 2011; Araújo et al., 2013). To this effect, we tested whether species exhibited similarity in their maximum and minimum surface temperature preferences across three million years, resulting in 120 comparisons (see Appendix S2.3). Species seem to conserve their upper thermal tolerance limits; however, results are less conclusive for minimum temperature tolerances (Table 2.2). Across the suite of species, the majority of comparisons are statistically more similar with regard to maximum surface temperature, although five species have one or two comparisons that are inconclusive (B. occidentalis, D. robustum, L. pensylvanica, N. duplicata, O. sayana, and T. dislocata). There is no apparent pattern as to which tests are inconclusive (Table 2.2). Comparisons are also statistically similar with regard to minimum temperature tolerances. However, the structure of this variable changes significantly through time, making it difficult to quantify similarities or differences. Consequently, many comparisons are statistically insignificant (Table 2.2). For example, all mPWP—LIG comparisons are inconclusive with the exception of N. duplicata, and half of the comparisons for B. occidentalis and L. pensylvanica are also inconclusive.

**Geographic comparisons.**

We also tested for similarity and differences using the geographic projections of niches, rather than comparing niches entirely in environmental space. Results from these analyses mirror those from the environmental comparisons. Niches are statistically similar for seven of the ten species across all comparisons (42 of 60 comparisons; Table 2.1 and Appendix 2.3). *Crassostrea virginica* and *L. pensylvanica* have one comparison that is inconclusive (LIG—mPWP and PI—mPWP, respectively), while the niche of *B. occidentalis* is significantly dissimilar for the LIG—mPWP comparison and non-significant for the PI—mPWP comparison.
Table 2.2  P-values for comparison tests on (1) maximum surface temperature tolerances; and (2) minimum surface temperature tolerances. Comparisons were performed using the framework of (Broennimann et al. (2012)). Bold values indicate non-significant results. All other comparisons are statistically more similar than expected given the environmental background of the variable in question. See Appendix S2.3 for graphical depictions of similarity tests.

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<tr>
<th>Species/Comparison</th>
<th>mPWP—LIG</th>
<th>LIG—mPWP</th>
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Discussion

Our statistical tests find no support for niche evolution. Instead, we observe niche stability across three million years of considerable environmental changes, from extreme warmth during the mPWP to glacial cycles during the Pleistocene (Cronin, 1988; Haug & Tiedemann, 1998; Dowsett et al., 2009). These species were either shifting their niche preferences in response to changing conditions at scales too rapid to be detected by our analyses, which seems unlikely, or their preferences remained stable across this temporal interval. Taking our results at face value, niche stability has profound implications for understanding conservation priorities and for elucidating macroevolutionary dynamics.
Implications for survival of taxa during times of change.

These results impact our understanding of how species respond to climate change on both long and short time scales. As climate continues to change, species that are unable to adapt to new conditions face two futures: extinction or shifting distributions to follow suitable areas. Already, both responses have been documented or predicted as a result of current climate changes. Marine and terrestrial species are forecast to experience climate-driven extinctions into the 22nd century (Sinervo et al., 2010; Maclean & Wilson, 2011; Bijma et al., 2013). Indeed, the niche stability we have documented may doom many marine species to extinction over the next 100+ years, particularly if they live at their thermal tolerance limits (Tewksbury et al., 2008; Sunday et al., 2012) and are unable to alter upper thresholds. The target species considered here are predicted to experience severe distributional reductions by the end of this century when variables other than temperature and salinity are considered (Saupe et al., In Press), but wholesale extinction is unlikely. This prediction is supported by their survival in the Pliocene, albeit in geographically-reduced areas as determined from occurrence data, when conditions were purportedly similar to those expected at the end of this century (Robinson & Dowsett, 2008). These small areas of suitability – or micro-refugia – are thought to have played an important role in species’ survival during past episodes of climate change (Cheddadi et al., 2006; Graham et al., 2006; Willis & MacDonald, 2011).

If species are able to keep pace with the changing environment, distributional shifts, rather than extinctions, are expected (Warren et al., 2013). Under this scenario, dispersal ability becomes an important parameter predicting species’ responses to climate change (Trakhtenbrot et al., 2005). Present-day elevational, latitudinal, and bathymetric shifts (Hickling et al., 2006; Sorte et al., 2010; Chen et al., 2011) have already been observed in response to current warming patterns, and, indeed, the fossil record provides abundant evidence for habitat tracking during rapid Pleistocene climate cycles (Roy et al., 1996; Hof et
In support of the inadaptability of niches, species followed their climate envelopes over great distances during the Pleistocene, often creating non-analog community assemblages (Williams & Jackson, 2007).

The stability of niches also affords some confidence to the methods used to assess extinction vulnerability and distributional shifts (e.g., ENM or species distribution modeling; SDM) (Peterson et al., 2011). Consequently, concerns over inaccurate forecasts owing to niche adaptation are somewhat alleviated (Pearman et al., 2008; Hoffmann & Sgrò, 2011). Nevertheless, ENM or SDM methods typically do not account for dispersal limitations or altered biotic interactions (Davis et al., 1998), though see (Fordham et al., 2013), nor do they consider that species can alter their behavior or microhabitat preferences to buffer against environmental changes (Kearney et al., 2009; Lavergne et al., 2010).

**Macroevolutionary implications of stable niches.**

We show that species’ distributions are structured by environmental changes, and thus species themselves are largely controlled by external, abiotic factors (Valentine & Moores, 1970; Vrba, 1985; van Dam et al., 2006; Roy et al., 2009; Jablonski et al., 2013). Although species may modify their behavior or resource utilization, large-scale parameters of their niches do not change. The FN places constraints on species’ interactions with the environment, which potentially governs speciation and extinction processes over long time scales (Jablonski et al., 2013; Myers & Saupe, 2013). Some researchers have suggested that niche stability may promote allopatric speciation (Vrba, 1985; Peterson et al., 1999; Wiens & Graham, 2005; Kozak & Wiens, 2006); that is, environmental perturbations may separate two populations, with these populations prevented from merging back together because of FN constraints, eventually leading to diversification.

Niche stability also provides a potential mechanism for the morphological stasis observed within species over millions of years (Eldredge et al., 2005). More specifically, niche stability requires species to track preferred habitats as the environment changes,
thereby continuously joining and separating populations on scales < 10,000 years. In this framework, any localized phenotypic adaptation is unlikely to be fixed across an entire species, such that no overall net changes are observed for the species as a whole, since localized changes may cancel one another out (Eldredge et al., 2005).

**Potential caveats.**

Although our analyses are quantitatively robust, our study is not without limitations. First, our models may approximate the potential niche (PN), rather than the FN (Jackson & Overpeck, 2000; Soberón & Nakamura, 2009), given that FNs are often difficult to characterize without detailed physiological studies (Peterson et al., 2011; Araújo et al., 2013). However, niche estimates were calculated from time-averaged environmental preferences (Kidwell & Holland, 2002), which will closely approximate real physiological tolerance limits, particularly since marine ectotherms tend to occupy the full extent of latitudes within their thermal limits (Tewksbury et al., 2008; Sunday et al., 2012). Second, and related to accurately characterizing the FN, estimates of present-day and past niches may not be equivalent and thus not comparable. This, of course, is of lesser concern here since we documented niche stability rather than niche evolution. Third, we acknowledge that recognition of ‘species’—especially in the fossil record—is sometimes contentious, and while these species are diagnosably distinct throughout their duration, they may not constitute single evolutionary lineages. Nonetheless, if they represent closely-related species (i.e., species complexes), the fact that we still obtained niche conservatism suggests this pattern is robust even across speciation events. Fourth, we analyzed data from warm time periods, as distributional data do not exist for glacial periods (e.g., the last glacial maximum, ~21 Ka). Therefore, our analyses may have missed rapid niche evolution that occurred in response to these colder conditions. Although possible, the scenario is unlikely because of the rate at which niche evolution would have had to occur, and because of the paucity of evidence for physiological adaptations both in the fossil record (Foster et al., 1990; Roy et al., 2005).
1996; Hof et al., 2011) and in experimental studies (Araújo et al., 2013). Moreover, environmental conditions at the mPWP, LIG, and PI differ to a significant degree, such that we were still able to discern whether species adapted to new conditions or tracked stable climate envelopes. Finally, and related to this issue, because paleoclimate models were only available for certain key temporal intervals, we could not capture the entire temporal history of these species in the context of an ENM framework.

Conclusions

Here, niche evolution is analyzed over millions of years in a synthetic context uniting both modern and paleontological marine data and paleoclimatic models. We find that niches remain stable across the duration of species’ lifetimes, even within a context of significant environmental perturbations. Given their responses to past environmental changes, our results indicate that species will respond to current and future warming by altering distributions to track suitable habitat, or, if the pace of change is too rapid, by going extinct. We urge continued examination of the threats that climate change poses to biodiversity to ensure proper implementation of conservation measures, and we stress the value of integrating paleontological and neontological data to explore these issues.

References


Chapter 3. Estimating extinction risk as a function of niche breadth and geographic range size: a case study using Pliocene—recent Atlantic Coastal Plain mollusks
Abstract

Determining which species are more prone to extinction is vital for conserving Earth’s biodiversity and for providing insight into macroevolutionary processes over time. Here, we utilized the exceptional record of Pliocene—recent Atlantic Coastal Plain mollusks to test the relative effects of geographic range size and niche breadth on survivorship of species from the Pliocene to the present-day. We assessed the vulnerability of 93 bivalve and gastropod species to extinction as a function of both fundamental and realized niche breadths, and geographic range size. We additionally examined whether extinct species lost more suitable habitat during the Last Glacial Maximum (~21 Ka) than still-extant species. Contrary to our expectations, extant species did not have larger fundamental niche breadths than extinct species. By contrast, the realized niche emerged as a key predictor of extinction risk. Our results reiterate the well-supported idea that geographic range size is a key predictor of extinction risk. Similarly, the degree of suitable area lost during the Last Glacial Maximum predicted survivorship for studied mollusks. A potentially intriguing aspect of these results is that fundamental niche breadth appears to be decoupled from geographic range size with regard to extinction risk. In essence, this suggests that occupied environmental breadth (i.e., the realized niche) provides a greater buffer against extinction than potential tolerance limits (i.e., the fundamental niche), and the degree to which species are able to fill their fundamental niches provides the measure of extinction risk. This information can be used not only to implement proper conservation policies as we face current extinctions, but also to understand the properties promoting or inhibiting extinction—and perhaps speciation—across evolutionary time.
**Introduction**

Determining which species are more prone to extinction is vital for conserving Earth’s biodiversity (McKinney, 1997; Thuiller et al., 2005; Schwartz et al., 2006; Barnosky et al., 2011; Harnik, 2011; Lee & Jetz, 2011; Barnosky et al., 2012) and for providing insight into macroevolutionary processes over evolutionary time scales (Eldredge, 1979; Vrba, 1987; Kiessling & Aberhan, 2007; Payne & Finnegan, 2007; Jablonski, 2008). Although several traits have been identified as correlating with extinction risk (McKinney, 1997; Mace et al., 2008; Fritz et al., 2009), one of the most robust is geographic range size, with both neontological (Purvis et al., 2000; Thomas et al., 2004; Schwartz et al., 2006; Harris & Pimm, 2008) and paleontological (Jablonski & Roy, 2003; Jablonski & Hunt, 2006; Kiessling & Aberhan, 2007; Liow, 2007; Payne & Finnegan, 2007; Foote et al., 2008; Stigall, 2010; Harnik, 2011; Harnik et al., 2012) studies finding that large geographic range size increases species’ survivorship (although see Stanley [1986b], Norris [1992], Vermeij [1993], and Myers et al. [2012] for notable exceptions). Fewer studies, however, have focused on species’ environmental niche breadths, and the impact this variable has on extinction risk.

Here, we utilize the exceptional record of Pliocene—recent Atlantic Coastal Plain mollusks to test the relative effects of geographic range size and niche breadth on survivorship of species from the Pliocene to the present-day. We assess the vulnerability of 93 diverse bivalve and gastropod species to extinction as a function of both fundamental (FN) and realized (RN) niche breadth, as well as geographic range size. We additionally examine whether extinct species lost more suitable habitat during the Last Glacial Maximum (LGM; ~21 Ka) than still-extant species. We hypothesize that FN breadth determines survivorship to a greater degree than RN breadth and geographic range size, but that extant species have larger values for all of these traits.

The FN is defined as the set of all combinations of abiotic environmental variables in which a species can survive (Soberón & Nakamura, 2009; Peterson et al., 2011), and has
been posited to be a species-level trait that is stable within and across lineages (Martínez-Meyer & Peterson, 2006; Myers & Saupe, 2013; Strubble et al., 2013; Saupe et al., in review). As climate changes, we suggest that this suite of tolerances (i.e., the FN) contributes to a species’ ability to survive environmental changes. In contrast, the RN is a subset of the FN that a species occupies at a given time, and which can be constrained for reasons relating to resource use, biotic factors such as competition, and/or dispersal barriers (Pearman et al., 2008; Peterson et al., 2011; Araújo & Peterson, 2012).

The Neogene Atlantic Coastal Plain molluscan record provides a well-characterized system in which to analyze the dynamics of niche breadth and geographic range over time for several reasons. Molluscan remains are abundant and particularly well studied with respect to patterns of extinction, species turnover, and ecological change across this interval (Allmon et al., 1993; Todd et al., 2002; Vermeij, 2005; Klaus et al., 2011). Moreover, both bivalves and gastropods have proven excellent study systems for analyzing diversity dynamics through time (Jablonski & Hunt, 2006; Crampton et al., 2010; Nürnberg & Aberhan, 2013). Climatic changes from the Pliocene to the recent have also been well characterized using global climate models (Haywood et al., 2011).

Potential difficulties arise in testing the relative effect of niche breadth and geographic range size on diversity dynamics because their relationship is complex and often not monotonic (Gaston, 2003; Peterson et al., 2011; Myers & Saupe, 2013). In particular, they frequently co-vary, such that the effects of geographic range are not easily decoupled from those of niche breadth. With that said, species with large geographic range sizes can have small niche breadth if the underlying environment is homogeneous, whereas species with broad niche breadths can have small geographic ranges if they are limited by dispersal, biotic or other geographic barriers (Eldredge, 1979; Gaston, 2003; Araújo & Peterson, 2012; Myers & Saupe, 2013).

Niche breadth is often considered an inverse measure of ecological specialization
(Smith, 1982). Indeed, specialist species (stenotopes) have long been thought to be more prone to extinction than generalist species (eurytopes), especially during times of environmental change (Simpson, 1944; Eldredge, 1979; Vrba, 1987; Brown et al., 1995; McKinney, 1997; Fernandez & Vrba, 2005). To date, both paleontological (Kammer et al., 1997; Keller et al., 1997; Heim & Peters, 2011; Harnik et al., 2012; Nürnberg & Aberhan, 2013) and neontological (Thuiller et al., 2005; Broennimann et al., 2006; Colles et al., 2009; Devictor et al., 2010; Boulangeat et al., 2012) studies have examined the influence of RN breadths on extinction probability, with the general conclusion that broader niche breadths increase species’ longevity. Here, we use ecological niche modeling (ENM) to compare both FNs and RNs. We acknowledge that accurately estimating FNs without mechanistic studies is difficult (Kearney & Porter, 2009), and our results may approximate the existing FN (also known as the potential niche), or some version of >RN (Jackson & Overpeck, 2000; Peterson et al., 2011). Recent biophysical approaches, however, have suggested that FNs can be represented by limited sets of parameters like temperature (Kearney et al., 2010; Kearney et al., 2013), and we additionally use model parameters that match known physiological response curves of species (Austin, 1985; Austin et al., 1994; Hooper et al., 2008; Angilletta, 2009). Thus, obtained estimates may at least be congruent with species’ potential suitable area.

Ultimately, identification of the traits that promote or inhibit extinction provides insight into the causal mechanisms generating patterns of diversity over evolutionary time scales (Eldredge, 1989; Stanley, 1990; Kammer et al., 1997; Jablonski, 2008). The fossil record provides a ledger of such evolutionary winners and losers, which can be used to generate a list of threat factors leading to species’ extinctions. These rule sets are important, because of the time-intensive nature of estimating extinction risk for individual species and populations, and because of the rising concerns over the future of marine ecosystems and biodiversity (Worm et al., 2006; Hendriks et al., 2010; Russell et al., 2012; Jones et al.,
Material and Methods

Study extent.
All analyses were conducted within the Atlantic Coastal Plain. Models were calibrated within a region bounded by the Americas and 34°W longitude, and 48°N and 44°S latitude. We sought the union of the area sampled by researchers and which was most likely accessible to the species during the Pliocene (Phillips et al., 2009; VanDerWal et al., 2009; Peterson et al., 2011).

Taxa.
We selected target taxa from 30 genera of gastropods classified within eight families (Bursidae, Conidae, Fasciolariidae, Muricidae, Personidae, Ranellidae, Strombidae, and Tonnidae) and 71 genera of bivalves classified within six families (Arcidae, Cariidae, Carditidae, Lucinidae, Tellinidae, and Veneridae) in the Digital Atlas of Neogene Life (Hendricks et al., 2013). We utilized all species having Pliocene presences in the Digital Atlas, with the exception of those with poor sampling, extreme micro-endemism, or poor model quality, detailed below. We eliminated species with very restricted distributions to account for potential artifacts that might arise from sampling bias by using a two-step process: we retained species with ≥ four spatially unique occurrence points at 2.5 arc-minute (~4.5 km) resolution; and we also excluded species with only one spatially unique occurrence point at 1.25° resolution (i.e., the scale of the environmental data). This procedure ensured that poorly sampled species were removed from niche estimations. A total of 47 extinct (of 80) and 46 extant (of 65) species remained after eliminating poorly sampled species as well as those with non-significant niche models (see niche modeling sections below for details), resulting in a total of 16 gastropod genera and 50 bivalve genera. Many extant species have fossil records that extend into the Pliocene (~3.1 Ma), as most marine invertebrates have durations > 3 million years (Stanley, 1979; Eldredge et al., 2005; Patzkowsky & Holland, 2013; Saupe et al., 2014).
Pliocene records for these extant species were verified by examination of museum collections and literature survey.

**Distributional data.**

We considered fossil distributional data from Pliocene (~3.264–3.025 Ma) strata of the Atlantic Coastal Plain, USA. Distributional records were primarily obtained from the Florida Museum of Natural History (FLMNH), with additional records from the Academy of Natural Sciences of Drexel University, Paleontological Research Institution, Yale Peabody Museum, and Virginia Museum of Natural History, for ten viable stratigraphic units identified using the database of Saupe *et al.* (in review) (Table 3.2). The holdings of the FLMNH represent the largest collection of Neogene Atlantic Coastal Plain mollusks, with extensive distributional coverage for hundreds of species across the eastern seaboard (Fig. 3.1). For each species, we subsampled distributional data to leave one record per environmental pixel (Tables 3.1.1 and 3.1.2). This was done to prevent certain localities with multiple records from being unduly weighted in niche modeling analyses (Royle *et al.*, 2012; Yackulic *et al.*, 2013), and did not affect the resultant overall distribution of the species. The spatial resolution of the environmental data (1.25 x 1.25°, described below) limited the number of spatially unique occurrence points available per species. We retained species with ≥ two spatially unique occurrence points at 1.25° resolution whose models were significant and congruent with those constructed using more occurrence data (Tables 3.1.1 and 3.1.2). Moreover, all species possessed at least four spatially unique occurrence points at 2.5 arc-minute resolution, a number shown to be statistically robust for modern species (Hernandez *et al.*, 2006; Pearson *et al.*, 2007). The frequency distribution of occurrences per species retained in the analyses was right-skewed on a normal plot (Fig. 3.2), a pattern found for many other extant terrestrial and marine taxa (Gaston, 1998; Gaston & He, 2002). This indicates our data are commensurate with neontological data, which are presumably unbiased.
with regard to sampling. Additional corrections for potential sampling biases are described in ecological niche modeling protocols.
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<td>cribaria</td>
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<td>discus</td>
<td>Reeve, 1850</td>
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<td>grus</td>
<td>Holmes, 1858</td>
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<td>13</td>
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<td>&lt;0.001</td>
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Table 3.1.2 Studied gastropod species, including their extinction status, number of spatially unique occurrence points at 2.5 arc-minutes and 1.25°, and significance level of the niche model under the jackknife test of Pearson et al. (2006). This test was not possible for species with two points, and in these cases, models were deemed significant when they did not omit either point after thresholding.

<table>
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<tr>
<th>Family</th>
<th>Genus</th>
<th>Species</th>
<th>Author</th>
<th>Extinction status</th>
<th># of pts 2.5 arc-minute</th>
<th># of pts 1.25°</th>
<th>P-value</th>
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<td>Sowerby ii, 1850</td>
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<td>doucus</td>
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</table>

Environmental data.

Environmental data were derived from the coupled atmosphere-ocean HadCM3 global climate model (GCM) (Gordon et al., 2000; Pope et al., 2000) for the mid-Pliocene Warm Period (mPWP; 3.264–3.025 Ma). Model results were also projected to the Last Glacial Maximum (LGM; ~ 21 Ka). Boundary conditions for the mPWP GCM used the alternate PRISM3D PlioMIP dataset described in Haywood et al. (2011), and boundary
conditions for the LGM GCM used those in Singarayer & Valdes (2010) and Singarayer et al. (2011). All experiments were run for 500 model years, and environmental parameters were derived from the final 30 years of each experiment at 1.25 x 1.25° resolution (~140 x 140 km at the equator). Where ocean data were unavailable (i.e., sites presenting macrofossil data but where the GCM indicated land), we used an inverse-distance weighted algorithm to extrapolate model data.

We converted the monthly salinity and temperature outputs from the GCMs to maximum, minimum, and average yearly coverages for both surface and bottom conditions using ArcGIS 10.1. We centered and standardized data in each of these 12 coverages, performing a principal components analysis (PCA) on the correlation matrix using the PCARaster function in the ENMGadgets package in R (Barve & Barve, 2014). Data were transformed in order to create new axes that summarized variation in fewer, independent dimensions, and to reduce co-linearity among variables. We retained the first four principle components, which explained cumulatively ≥ 97% of the variance in the dataset, for model calibration. The PCA structure for the Pliocene was enforced for the LGM using the PCAProjections function in the ENMGadgets package in R (Barve & Barve, 2014).

Ideally, we would use an ensemble-modeling approach that considered multiple GCMs (Fordham et al., 2012). However, model output was available to us only from HadCM3, with this GCM having been successfully used within a large range of Quaternary and pre-Quaternary modeling studies.

Table 3.2 Potential mPWP formations (~3.1 Ma) for species’ occurrence data used in analyses.
Ecological niche modeling.
ENMs were generated using a maximum entropy algorithm, Maxent v. 3.3.3 (Phillips et al., 2006). Maxent estimates environmental suitability for a species when the null expectation is equivalent to uniform (Elith et al., 2011), with results often similar to those under general linear models (Fithian & Hastie, 2012; Renner & Warton, 2013). We enabled only the linear and quadratic features in Maxent to produce realistic response curves that match those known from physiological experiments of plants and animals (Austin, 1985; Austin et al., 1994; Hooper et al., 2008; Angilletta, 2009). To correct for biases in fossil distributional data, we implemented a ‘bias file’ within Maxent. The bias file describes the probability that an area was sampled; thus, regions with rock outcrop (i.e., areas where species may actually be detected or sampled) were weighted twice as heavily as regions without rock outcrop. Maxent will then factor out this bias during the modeling process (Dudík et al., 2005). This method essentially accounts for incomplete knowledge of a species distribution (Svenning et al., 2011). Pliocene models were projected to LGM conditions to determine if extinct species retained suitable area during glacial times. To avoid inaccurate projections as a result of novel environmental conditions, we deactivated clamping and allowed for extrapolation following Owens et al. (2013).

Potential niche characterizations.
The modeling process produces continuous suitability surfaces, which require interpretation to determine limits of suitability for a species. This process is usually done via

<table>
<thead>
<tr>
<th>mPWP (~3.1 Ma) Formations</th>
</tr>
</thead>
<tbody>
<tr>
<td>Duplin</td>
</tr>
<tr>
<td>Goose Greek</td>
</tr>
<tr>
<td>Guaiiguaza</td>
</tr>
<tr>
<td>Hopegate</td>
</tr>
<tr>
<td>Intracoastal</td>
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</tbody>
</table>
thresholding, wherein models are converted to binary output (i.e., 1=suitable; 0=unsuitable). We used the mean model suitability score as the threshold, given this method provides greater independence from input occurrence data and performs well with low and varying prevalence data (Liu et al., 2005; Freeman & Moisen, 2008). We recognize that choice of threshold can affect model results (Liu et al., 2005; Jiménez-Valverde & Lobo, 2007); however, the threshold method we employed does not constrict suitability as severely as traditional methods like least training presence (LTP) or MaxSSS (Pearson et al., 2007; Liu et al., 2013), which often produce approximations closer to the realized niche (RN), rather than the potential niche (PN) or the fundamental niche (FN) (Peterson et al., 2011).

**Niche breadth calculations.**

We consider niche breadth in the classic Grinnellian sense (Grinnell, 1917) of abiotic environmental variables, defined by Hutchinson (1957) as a hyper-volume in multi-dimensional space, within which a species can maintain viable populations. Niche breadths were calculated using NicheA (Qiao et al., 2012). From thresholded niche models, we quantified niche volumes from the first three principle component axes within environmental space, which explained > 89% of the variance in the dataset (Fig. 3.3). To increase the potential resilience of our results, we used two different methods to calculate niche volumes: minimum volume complex polyhedrons (CPH) around suitable area in three-dimensional environmental space (Cornwell et al., 2006; Monahan & Tingley, 2012), and minimum volume ellipsoids (MVE) around suitable area in three-dimensional environmental space (Van Aelst & Rousseeuw, 2009). To our knowledge, this represents one of the first times niches have been quantified in three dimensions, although see Cornwell et al. (2006) and Blonder et al. (2014).

**Geographic area calculations.**

Again, to increase the potential resilience of our results, geographic area occupied by a species was calculated in two ways: summing the number of suitable pixels from projected
niche models, and creating minimum convex polygons around the unfiltered (all) occurrence
data for each species. To calculate the latter, we used the minimum bounding geometry
function in ArcGIS 10.1 and calculated polygon areas using the USA Contiguous Albers
Equal Area Conic map projection (Gaston & Fuller, 2009) (Fig 3.1). We also calculated
amount of area projected to remain suitable for these species during the LGM (~21 Ka) by
counting suitable pixels in model projections.

**Realized niche characterizations.**

To examine whether the breadth of environment occupied by species (a species’ RN)
impacts extinction selectivity, we calculated CPH and MVE niche breadth volumes for
species’ occurrence data in environmental space. Moreover, we tested the sensitivity of these
calculations to potential sampling biases by degrading the available fossil record to the same
number of occurrence points (lowest number) for all species exceeding this two-point
occurrence prevalence. We calculated niche breadth as the environmental distance between
the two points on the first principle component layer, which explained ~ 39% of the variance
in the dataset, following approaches similar to those employed by Colwell & Futuyma (1971)
and Essl et al. (2009). We used the median value from the 100 replicates as the niche breadth
for a species. Niche breadths for species with only two occurrence points were calculated in
the same fashion, without bootstrap replication. This process is similar to rarefaction, which
is commonly utilized for paleontological data, and attempts to correct for differing abundance
values (Miller & Foote, 1996; Barnosky et al., 2005; Kiessling & Aberhan, 2007). Finally,
we thresholded obtained niche models using the LTP method (Pearson et al., 2007), which
constrains estimates of suitability to the lowest value associated with an occurrence point.
Essentially, the process only predicts suitable environments that a species has occupied (i.e.,
estimates closer to the RN). In this study, the mean number of pixels predicted suitable across
all species decreased over 200% using a LTP threshold compared to a mean threshold.
**Niche model significance testing.**
For the majority of species, we assessed statistical significance of the niche models using a jackknife procedure of Pearson *et al.* (2007) (Tables 3.1.1 and 3.1.2). For those species with only two spatially explicit occurrence points, models that correctly predicted both occurrence points were deemed significant (note that both points will always be correctly predicted under a LTP threshold). Species were eliminated if models were not significant using either of these approaches.

**Statistical tests.**
We performed binary logistic regressions using both geographic range and niche breadths to determine if variables are correlated with respect to survival or extinction. No significant results were obtained using these multivariate tests. Consequently, we performed univariate analyses. Since area and volume calculations were not normally distributed, we log transformed all variables and used one-way nonparametric Mann-Whitney U tests for analyses (Table 3.3). We tested four hypotheses: (i) whether extant species had greater niche breadths than extinct species, (ii) whether extant species had larger geographic ranges than extinct species, (iii) whether extant species occupied broader realized environmental space than extinct species, and (iv) whether extant species had more suitable area remaining during the LGM than extinct species. We performed ten Mann-Whitney U tests, because we calculated FN breadth in two ways, RN breadth in five ways, and geographic area in two ways, in order to test the resiliency of our results to differing estimation methods (see Table 3.3).
Figure 3.1 Distributional data (blue dots), area polygons (pink), and thresholded niche model projections for FN (light green) and RN (dark green) estimates for two representative bivalve species: Laciolina magna and Merisca aequistriata in the mPWP. Note that because of differences in distributional range for each species, the maps are not shown to the same scale.
Results

Contrary to our original hypothesis, extant species did not have significantly larger niche breadths than extinct species, although values are close to alpha (α) level of 0.05 ($P = 0.071$ and $P = 0.088$ for CPH and MVE calculations, respectively) (Table 3.3). Extant species, however, did have significantly larger geographic ranges than extinct species, both when considering suitable area predicted by the model ($P = 0.030$) and area calculated from polygons ($P = 0.002$). Consequently, there does not seem to be a one-to-one correspondence between niche breadth predicted by the models and amount of suitable area available geographically (Table 3.3).

Figure 3.2 Histogram of number of occurrences per species at 1.25° resolution in the mPWP. Note the right-skewed nature of the frequency distribution, which mirrors that for many extant taxa (Gaston, 1998; Gaston & He, 2002).
The RN, however, does seem to be a significant predictor of extinction (Table 3.3). Extant species occupy significantly larger volumes of environmental space than extinct species, using estimates based on both the occurrence data ($P = 0.006$ and $P = 0.009$ for CPH and MVE calculations, respectively) and the LTP niche models ($P = 0.011$ and $P = 0.018$ for CPH and MVE calculations, respectively). Moreover, these results are robust to the bootstrap resampling tests ($P = 0.044$).

When niche models are projected to glacial conditions (LGM; ~21 Ka), extinct species lose more suitable area than extant species ($P = 0.022$) (Table 3.3). This result holds when change (percent decrease) in suitable area from the Pliocene to the LGM is calculated; in other words, extinct species lose more suitable area, on average, than extant species ($P < 0.01$).

We tested four hypotheses with respect to the FN, RN, geographic range size, and amount of area lost during the LGM. Given that hypotheses were tested a priori, correction for multiple comparisons is not required. However, conservatively, all previously-significant tests remained significant for the lowest p-value for each estimation method applying a Holm–Bonferroni correction (Holm, 1979; Ludbrook, 1998), which performs well while still controlling the family-wise type 1 error rate. Furthermore, although we were interested in using a one-tailed test to assess whether extant species had greater values for niche breadths and geographic range size, a more stringent two-tailed test still provides significant results for all analyses, with the exception of the rarefaction RN breadth method and geographic area under the mean niche model (see “Two-tailed test” results in Table 3.3). We further stress tested our results by running all analyses using species with $\geq 3$ spatially unique points at 1.25° resolution. Again, we obtained the same patterns of significance, with the exception of the MVE and rarefaction calculations for RN breadth and geographic area under the mean niche model (see “$\geq 3$ points” results in Table 3.3).
Table 3.3 Results from Mann-Whitney U tests. Tests assessed: (i) whether extant species had greater niche breadths than extinct species, (ii) whether extant species occupied broader realized environmental space than extinct species, (iii) whether extant species had larger geographic ranges than extinct species, and (iv) whether extant species had more suitable area remaining during the LGM than extinct species. Results from both the one-tailed and more conservative two-tailed tests are provided, as well as those from one-tailed tests using only species with ≥ 3 spatially unique points at 1.25° resolution.

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<th>Two-tailed test</th>
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<td></td>
<td></td>
<td>W</td>
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<td></td>
<td></td>
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<tr>
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<td></td>
</tr>
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<td>Distance</td>
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<td>0.044</td>
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<tr>
<td>Amount of suitable area</td>
<td>Pixel count</td>
<td>1343.5</td>
<td>0.022</td>
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Figure 3.3 Representations of niche volumes in three-dimensional principle component space for the same two representative species, *Laciolina magna* and *Merisca aequistriata*. The left column depicts the minimum volume complex polyhedrons (CPH) for both thresholded mean niche models (FN; light pink) and LTP niche models (RN; dark pink). The right column depicts the minimum volume ellipsoids (MVE) for thresholded mean niche models (FN; light pink) and LTP niche models (RN; dark pink).

Discussion

Our initial hypothesis that extant species have greater FN breadths than extinct species was not supported. Indeed, FN breadth appears to be decoupled from geographic range size, with only the latter a significant predictor of extinction risk. By contrast, along
with geographic range size, the RN emerged as a key predictor of extinction risk, as did the
degree of suitable area lost during the LGM. These results suggest that occupied
environmental breadth (i.e., RN) provides a greater buffer against extinction than potential
tolerance limits (i.e., the FN). In a way, this makes intuitive sense, although the pattern is
counter to our original predictions. That is, the degree to which species are able to fill their
FNs is what provides a measure of extinction risk.

Our results are congruent with previous studies that find evidence for a positive
relationship between niche breadth and species’ longevity (Kammer et al., 1997; Keller et al.,
1997; Nürnberg & Aberhan, 2013). Namely, most studies have analyzed RN dynamics using
estimates derived from areas occupied by a species or genus. Taken together, these findings
necessitate a reformulation of the argument that specialist species are more prone to
extinction: being a generalist or specialist sensu stricto appears secondary to the unique
historical, dispersal, and biotic constraints that dictate species’ occupation of suitable
environments at a particular time. Note that this argument, in and of itself, assumes species
are often in disequilibrium with the environment (Araújo & Pearson, 2005; Varela et al.,
2009). Species’ population dynamics and dispersal ability have been stressed previously as
important to estimating extinction risk (Pulliam, 2000; Kotiaho et al., 2005; Anderson et al.,
2009; Fordham et al., 2012; Fordham et al., 2013), as has the importance of biotic constraints
(Davis et al., 1998; Araújo & Luoto, 2007; Van der Putten et al., 2010).

Large geographic ranges have long been considered a factor promoting species’
longevity, and our results provide additional support for this relationship (Jablonski & Roy,
2003; Jablonski & Hunt, 2006; Kiessling & Aberhan, 2007; Liow, 2007; Payne & Finnegan,
2007; Foote et al., 2008; Stigall, 2010; Harnik, 2011; Harnik et al., 2012). Geographic range
is usually considered a buffer against extinction for three reasons. First, species with large
geographic ranges are unlikely to experience environmental perturbations across their entire
distributional area, and consequently will survive such disturbances, irrespective of their
tolerances. This argument is primarily geographic in nature. Conversely, a second argument equates large geographic range size with large environmental tolerances. The assumption is that generalist species will have enhanced survival, since environmental changes are unlikely to exceed their broad tolerance limits. This explanation, however, blurs the distinction between geographic area and environmental tolerance as the primary controller of extinction selectivity. Finally, species with larger geographic ranges are frequently assumed to be more abundant (Lawton et al., 1994). Since extinction ultimately occurs when a species’ population size is reduced to zero, abundance is often considered important in gauging extinction risk (Stanley, 1986b; Johnson, 1998; Purvis et al., 2000; Mace et al., 2008).

However, geographic range size and abundance are not always positively related: rare species can be widespread and vice versa (Lavergne et al., 2004). Studies attempting to decouple abundance from geographic range size have found that local abundance has little effect on extinction risk, whereas geographic range size does (Kiessling & Aberhan, 2007; Harnik et al., 2012; although see Stanley [1986b] and Powell [2007] for exceptions).

Certainly, species’ geographic ranges are controlled by their RNs and, ultimately, by their FNs. Indeed, disentangling the effect of these variables is challenging (Barve et al., 2011; Harnik, 2011; Peterson et al., 2011; Nürnberg & Aberhan, 2013). Still, the fact that we recovered a signal for RN breadth and geographic range size, and not for FN breadth, indicates there is some independence in these measures.

**Study considerations.**

We focused on the impact of niche breadth and geographic range size on extinction patterns in Pliocene—recent Atlantic Coastal Plain mollusks. Nutrient declines, however, have often been implicated in biotic turnover in the region during this time, with the relative role of temperature and nutrient levels in producing extinction much debated (Stanley, 1986a; Vermeij, 1989; Allmon et al., 1993; Jackson et al., 1999; Roopnarine & Beussink, 1999;
Allmon, 2001). Many have argued that declining nutrients disrupted species’ habitat, which subsequently enhanced speciation and extinction post-mPWP. The formation of the Central American Isthmus around ~3.5 Ma was thought to precipitate these nutrient declines by changing oceanic circulation across the western Atlantic (Allmon, 2001). Although we found that both RN breadth and geographic range size are predictors of extinction risk, our results do not exclude nutrient decline as a significant factor in observed biotic turnover.

Mechanistically, our results warrant consideration in other respects. For instance, as with any paleontological or modern ENM analysis, sampling biases may lead to incorrect geographic range and niche breadth estimates. Our results, however, hold when more stringent rules for species’ prevalence are enforced. Sampling biases may also skew the taxa included in our analysis. In other words, species with genuinely small FNs may not be detectable in the fossil record, potentially explaining why the FN was not recovered as a significant predictor of extinction risk. This argument is not particularly compelling here, though, given that we analyzed species with very small to very large geographic range sizes (644 to 691,023 km$^2$) and niche volumes (40.6 to 560 and 14.7 to 192 for MVE and CPH calculations, respectively). Moreover, the frequency distribution for species’ prevalence data is similar to those for extant taxa (Gaston, 1998; Gaston & He, 2002), indicating our data are commensurate with neontological data, which are presumably biologically valid data sources (Fig. 3.2).

Age-area effects may plague analyses that consider geographic range size dynamics through time (Gaston, 1998; Myers et al., 2012; Jablonski et al., 2013), such that newer species have yet to achieve full distributional extent, and older species have artificially shrunken distributions. Neither of these scenarios, however, appears to bias analyses herein. First, origination times did not vary dramatically between species that are still extant and those that are now extinct. In other words, studied species originated anywhere from the Miocene to the Pliocene, irrespective of whether they are now extinct or still extant. Second,
species that went extinct primarily survived past the late Pliocene and early Pleistocene, indicating they were not ‘already on their way out’ during the mPWP.

In conclusion, our results provide a mechanism for assessing extinction risk, and highlight the importance of both RN breadth and geographic range size as extinction predictors. This information will be vital as we attempt to stem massive biodiversity losses predicted in the coming decades (Thomas et al., 2004; Tewksbury et al., 2008; Barnosky et al., 2011; Barnosky et al., 2012). Macroevolutionarily, the argument that specialist species have higher extinction (and origination) rates still holds (Vrba, 1987; Eldredge, 1989; McKinney, 1997; Nürnberg & Aberhan, 2013), but must be tempered by additional factors, such as ease of dispersal to suitable environmental areas and biotic factors such as competition. We show that the FN does not impact extinction probabilities, which leads to additional consideration of the arguments presented by Myers and Saupe (2013). Relationships between the FN, RN, and geographic range size are complex, and a variety of data inputs, including ecological parameters pertaining to competition and dispersal abilities, may be required to produce a truly synthetic view of the factors driving macroevolutionary patterns. Of course, the results presented here come from a particular set of taxa and a particular geographic region during a climatically distinctive interval of geologic time, and additional data are required from other taxa and study systems to determine whether our results can be extrapolated more broadly.

References


Barve, N. & Barve, V. (2014) ENMGadgets: tools for pre and post processing in ENM workflow. *R package version 0.0.5*.


Appendix S1.1

Appendix S1.1 (a) Maps of distributional data for each of 14 species of marine mollusks in the western Atlantic Ocean (Fig. S1.1.1–S1.1.4). (b) Results from RCP 2.6 (conservative) scenario of future change, including suitability maps (Figs S1.1.5–1.1.8), comparison of models to previously published distributional descriptions (Table S1.1.1), and cumulative potential suitable area lost and gained (Fig. S1.1.9). (c) Results from RCP 4.5 & 8.5 scenarios, with figures depicting latitudinal extent changes (Figs S1.1.10 & S1.1.11), and cumulative potential suitable area lost and gained for these scenarios (Figs S1.1.12 & S1.1.13). (d) Nomenclatural note on C. anabathrum.
Appendix S1.1a. Species distributional data

Figure S1.1.1 Distributional data for *Anomia simplex*, *Bulla occidentalis*, *Conus anabathrum* and *Conus spurius*.
Figure S1.1.2 Distributional data for *Crassostrea virginica*, *Crepidula fornicata*, *Dinocardium robustum* and *Lucina pensylvanica*.
Figure S1.1.3 Distributional data for *Melongena corona, Mercenaria campechiensis, Neverita duplicata* and *Oliva sayana*. 
Figure S1.1.4 Distributional data for *Strombus alatus* and *Terebra dislocata*. 
Appendix S1.1b. Niche modeling results for RCP 2.6

**Figure S1.1.5** Niche modeling results for *A. simplex*, *B. occidentalis*, *C. anabathrum* and *C. spurius*. Four time slices are shown: present day (1991–2010) and three future projections (2021–2040, 2041–2060 and 2081–2100) from the most conservative scenario of future change (RCP 2.6). A threshold has been applied, allowing for a maximum of 5% omission error based on presence data.
Figure S1.1.6 Niche modeling results for *C. virginica*, *C. fornicata*, *D. robustum* and *L. pensylvanica*. Four time slices are shown: present day (1991–2010) and three future projections (2021–2040, 2041–2060 and 2081–2100) from the most conservative scenario of future change (RCP 2.6). A threshold has been applied, allowing for a maximum of 5% omission error based on presence data.
Figure S1.1.7 Niche modeling results for *M. corona*, *M. campechiensis*, *N. duplicata* and *O. sayana*. Four time slices are shown: present day (1991–2010) and three future projections (2021–2040, 2041–2060 and 2081–2100) from the most conservative scenario of future change (RCP 2.6). A threshold has been applied, allowing for a maximum of 5% omission error based on presence data.
Figure S1.1.8 Niche modeling results for *S. alatus* and *T. dislocata*. Four time slices are shown: present day (1991–2010) and three future projections (2021–2040, 2041–2060 and 2081–2100) from the most conservative scenario of future change (RCP 2.6). A threshold has been applied, allowing for a maximum of 5% omission error based on presence data.
Table S1.1.1 Comparison of models to previously published distributional descriptions. We included multiple descriptions only if they conflicted. Models are congruent if all areas occupied by a species are predicted as suitable. We were less concerned about areas predicted suitable but not thought to be occupied by species, as these regions may be habitable, but the species is prevented from occupying them due to biological or dispersal limitations.
| Species               | Refs | Previously published distribution* | Depth (m) | Zone                  | MAXENT                                                | GAR |Congruence                                                      |
|-----------------------|------|-----------------------------------|-----------|-----------------------|-------------------------------------------------------|--    |                                                               |
| **Bivalvia**          |      |                                   |           |                       |                                                       |     |                                                               |
| *Anomia simplex*      | [1]  | 30.3° N to 20° N; 90.5° W to 80° W; USA: Florida: East Florida, West Florida, Florida Keys; Mexico: Campeche State, Yucatán State, Quintana Roo | 0–80; live 1–11 | Temperate to tropical | Congruent with 2nd & 3rd references – may be missing suitability in Venezuela and Colombia, but references do not mention such areas |     | Congruent                                                      |
|                       | [2]  | Eastern Canada to Florida, Bermuda, Bahamas, West Indies, Gulf of Mexico, Caribbean Central America, South America (to Argentina) |           |                       |                                                       |     |                                                               |
|                       | [3]  | Massachusetts to Florida, Texas; Brazil; Bermuda |           |                       |                                                       |     |                                                               |
| **Crassostrea virginica** | [1–5] | 49° N to 18° N; 88.11° W to 65° W; naturally occurs in the Gulf of St Lawrence, Canada, along the Atlantic coast of the United States to the Gulf of Mexico to the Yucatán Peninsula, Mexico, and to the West Indies and the coast of Brazil | 0–79; live 0.3–9 | Temperate to tropical | Congruent | Congruent | Congruent                                                      |
| **Dinocardium robustum** | [1,3] | 37° N to 20° N; 94° W to 77° W; Virginia to Florida, Texas; Mexico | 0–18; live 11 | Subtropical to tropical | General congruence – may be missing suitable area in VA and/or MD |     | General congruence – potentially missing suitable area in VA and/or MD |
|                       | [2]  | Maryland to Florida, West Indies, Gulf of Mexico, Caribbean Central America |           |                       |                                                       |     |                                                               |
| **Lucina pensylvanica** | [1]  | 35° N to 9° N; 91° W to 67° W; USA: North Carolina, Florida: East Florida, West Florida, Florida Keys; Mexico: Alacran Reef, Quintana Roo; Honduras: Swan Island; Cuba: Holguín | 0–3 | Tropical | Congruent with 1st ref. – may be missing suitable area in Carolinas |     | Congruent                                                      |
Table S1.1.1: Part 2

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<th>MAXENT</th>
<th>GARF</th>
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<td>[4]</td>
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<tr>
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<td>48° N to 25° N; 97.2° W to 25° W; Canada to Florida, Texas and Louisiana</td>
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<td>Congruent, but no mention of a Brazilian distribution</td>
<td>Congruent, but no mention of a Brazilian distribution</td>
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<tr>
<td><em>Melongena corona</em></td>
<td>[1,4,8]</td>
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<td>0–2; live 0–1.2</td>
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<td>42.5° N to 16° N; 97.2° W to 70° W; Cape Ann, MA, to Florida to Texas</td>
<td>0–58; live 0–26</td>
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<td>Tropical</td>
<td>Not congruent – model does not predict as far north as actual distribution (FL vs. NC)</td>
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Table S1.1.1: Part 4

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<td>USA: North Carolina, South Carolina, Florida: East Florida, West Florida; USA: Louisiana, Texas; Mexico: Campeche State, Cayo Arcas, Campeche, Yucatán State, Campeche Bank, Alacran Reef, Quintana Roo</td>
<td>live 0–46</td>
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<td>USA: Maryland, Virginia, North Carolina, South Carolina, Georgia, Florida: East Florida, West Florida; USA: Louisiana, Texas; Mexico: Campeche State, Yucatán State, Quintana Roo; Costa Rica, Colombia, Venezuela: Sucre, Isla Margarita; Jamaica, Puerto Rico, Brazil: Para, Rio Grande do Norte</td>
<td>live 0–22</td>
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</table>

*Note that small islands cited as within a species’ distribution may not be accounted for in our models because of the large pixel size (1° × 1°).

REFERENCES
4 Smithsonian Marine Station (2011) Field guide to Indian River Lagoon. Smithsonian Marine Station at Fort Pierce, FA. Available at: http://www.sms.si.edu/IRLFieldGuide/index.htm
Figure S1.1.9 Cumulative potential suitable area loss and gain over three time slices (2021–2040, 2041–2060 and 2081–2100) for the lowest-emission scenario of future change (RCP 2.6). Darker reds indicate higher potential suitable area loss or gain. Results are derived from binary model output and have been normalized based on present-day suitability.
Appendix S1.1c. Results from RCP 4.5 and 8.5 scenarios

Poleward range shifts.

Even under the higher-emission scenarios (RCP 4.5 & 8.5), there appear to be few genuine poleward range shifts (Figs S1.1.10 & S1.1.11). For those species whose centroids are predicted to shift polewards (e.g. *Conus anabathrum* and *Dinocardium robustum* for RCP 4.5 or *Anomia simplex*, *C. anabathrum*, *Crassostrea virginica* and *D. robustum* for RCP 8.5), the shifts primarily occur due to overall reductions in suitable area – the reductions still transpire within the former absolute extent of suitability for the species. The average change in centroid position is 3.46 (MAXENT) and 4.14 (GARP) for RCP 4.5, and 4.37 (MAXENT) and 3.7 (GARP) for RCP 8.5 in an equatorward direction (Table 1.2). As with the RCP 2.6 scenario, predictions for species vary as to how the absolute extent and centroid position change, which emphasizes the idiosyncratic nature of predicted responses.

Species-specific versus assemblage responses.

Declines in suitable area are predicted to be more severe under the RCP 4.5 and 8.5 scenarios than under RCP 2.6. Thus, even though the particulars of species’ responses differ, and some species are predicted to retain or even gain suitable area under RCP 4.5 and 8.5, the dominant signal is one of declining available suitable environmental conditions for marine mollusks. In RCP 4.5, 11 (MAXENT) or 14 (GARP) of the 14 species are predicted to undergo some degree of range contraction by the end of the century, whereas in RCP 8.5, 12 (MAXENT) and 14 (GARP) of the species are predicted to experience reductions in suitable area by the end of the century (Figs 1.4 & 1.5). When MAXENT without extrapolation is considered, all species experience declines by 2081–2100 under both RCP 4.5 and 8.5. Of the species predicted to lose suitable area, average decline in 2081–2100 is 46.4% (MAXENT) and 64.5% (GARP) for RCP 4.5, and 61.0% (MAXENT) and 88.7% (GARP) for RCP 8.5. GARP predicts 99–100% declines in suitable area for half of the species considered (*A. simplex*, *Conus anabathrum*, *Conus spurius*, *Dinocardium robustum*, *Lucina pensylvanica*,...
*Mercenaria campechiensis* and *Strombus alatus*) in 2081–2100 for RCP 8.5; MAXENT predicts similarly high losses for these species (> 45%), with the exception of *C. spurius*. The latter species, however, also loses significant suitable regions under the non-extrapolation iteration of MAXENT. Furthermore, when MAXENT extrapolation is deactivated, suitability in the RCP 8.5 2081–2100 projections resembles that predicted for the GARP models across all species. The two MAXENT iterations differ dramatically because we restricted the ability of MAXENT to extrapolate to conditions outside those in the training region and, potentially, to novel combinations of climate. As indicated by our environmental overlap analyses (see ‘Environmental overlap’ section of Appendix S1.3), RCP 8.5 2081–2100 projections contain pixels with almost entirely novel environmental combinations.

When patterns across all species are considered, losses of suitable conditions are expected across the entirety of the study region, but are concentrated from 20° N to 4° S (Figs S1.1.12 & S1.1.13). The Yucatán Peninsula and the east coast of Florida exhibit the greatest change in suitable conditions through time. Local (to species-wide) extinctions in the RCP 4.5 and 8.5 scenarios are predicted to intensify through time (Figs S1.1.12 & S1.1.13).

The only species predicted to gain, or at least not lose, suitable conditions through all time slices in RCP 4.5 are *Bulla occidentalis*, *Crassostrea virginica* and *Conus spurius* with MAXENT (Figs 1.4 & 1.5). In RCP 8.5, only *B. occidentalis* and *C. virginica* retain suitable area with MAXENT (Figs 1.4 & 1.5). GARP predicts increases in suitable area in the first time slice for *C. virginica* under both RCP 4.5 and RCP 8.5, but suitable area for this species decreases in the remaining time slices. As discussed above, when re-running MAXENT models with extrapolation deactivated, the disparity between the MAXENT and GARP models diminishes, with MAXENT predicting declines in suitable area for all of the above species by the end of this century under both RCP 4.5 and RCP 8.5.

Gains in suitable area remain relatively constant (Figs S1.1.12 & S1.1.13), regardless of the RCP scenario or time slice. Interestingly, these gains drop off in the 2081–2100 time
slice under GARP because of the dramatic declines in suitable area predicted for all species. Unlike the RCP 2.6 scenario, relatively little area is predicted to remain continuously suitable for the majority of species under RCP 4.5 and 8.5 scenarios. The average geographical area predicted as continuously suitable in all time slices is 52.3% (MAXENT) and 22.0% (GARP) for RCP 4.5, and 34.2% (MAXENT) and 8.0% (GARP) for RCP 8.5 (Table 1.3). The values are expressed as percentages of present-day suitable area.
Figure S1.1.10 Latitudinal extent (light shading) and change in centroid of suitable conditions (dark line) from the present (P) to each time slice (2021–2040, 2041–2060 and 2081–2100) for the RCP 4.5 scenario. Note that few species are predicted to undergo significant shifts in the centroid of their suitable conditions, with the absolute extent of suitable conditions fairly constant. Those species with centroids that are predicted to shift polewards (e.g. *D. robustum*) did so because of an overall reduction in suitable area, but the reduction occurs within the former absolute extent of suitability for the species.
Figure S1.1.11 Latitudinal extent (light shading) and change in centroid of suitable conditions (dark line) from the present (P) to each time slice (2021–2040, 2041–2060 and 2081–2100) for the RCP 8.5 scenario. There is more change in centroid position in this scenario, but the change occurs, for the most part, within the absolute bounds of suitability for these species. Note that, for species like *D. robustum*, the absolute range and centroid of suitable conditions are predicted to shift slightly northwards, whereas for species like *T. dislocata*, the absolute range and centroid of suitable conditions are predicted to shift slightly southwards. This variability highlights the idiosyncratic nature of predicted responses of these species to changing environment.
Figure S1.1.12 Cumulative potential suitable area loss and gain for the moderate-emission scenario of change (RCP 4.5). Darker reds indicate higher potential suitable area loss or gain. Results are derived from binary model output and have been normalized based on present-day suitability.
Figure S1.1.13 Cumulative potential suitable area loss and gain over three time slices (2021–2040, 2041–2060 and 2081–2100) for the extreme scenario of change (RCP 8.5). Darker reds indicate higher potential suitable area loss or gain. Results are derived from binary model output and have been normalized based on present-day suitability.
Appendix S1.1d. Nomenclatural note: *Conus anabathrum*

*Conus floridanus* Gabb, 1869 is a junior synonym of *Conus anabathrum* Crosse, 1865. Nevertheless, most museum specimens of this taxon are identified as *C. floridanus*, and that is the name we used in our online database searches.
Appendix S1.2

Appendix S1.2 Supporting information on environmental variables and their contributions to model development (Figure S1.2.1, Tables S1.2.1–1.2.3).

Sensitivity testing of predictor variables

We examined whether the exclusion of bathymetry alters the conclusions of our modeling efforts; in other words, without bathymetry, are dramatic reductions in suitable area still obtained under future climate scenarios. As indicated by the ‘no bathy’ column in Table S1.2.1, reductions of suitable area are similar to those when bathymetry is included. However, without bathymetry, some species present a reverse trend from that with bathymetry. Notably, reverse patterns are predicted for Conus spurius, Crassostrea virginica and Bulla occidentalis. Conus spurius is projected to gain suitable area rather than lose suitable area under MAXENT. The opposite is true for C. virginica, which is predicted to lose suitable area when bathymetry is omitted under both modeling algorithms, but gain suitable area when all variables are used. Under GARP, B. occidentalis is predicted to suffer declines in suitable area without bathymetry for RCP 2.6, whereas this species is predicted to gain suitable area with bathymetry. The same situation is occasioned for the MAXENT RCP 8.5 scenario.

We also assessed whether the number of variables and correlation among them (see Fig. S1.2.1) artificially induced the declines in suitable area observed under future climate change scenarios. To do so, we modeled the species using a less correlated subset of the predictor variables (i.e. bathymetry, diatom phytoplankton concentration, nitrogen concentration, sea surface temperate and sea surface salinity). For most species, significant declines in suitable area are still obtained using the reduced variable set, although the losses are often less dramatic than when all variables are used (as, for example, for Conus anabathrum, Dinocardium robustum, Oliva sayana and Strombus alatus). The patterns diverge more for RCP 2.6 than for RCP 8.5. As with models run without bathymetry, Crassostrea virginica
loses, rather than gains, suitable area under both algorithms. Similarly, *Conus spurius* gains rather than loses suitable area using GARP (for RCP 2.6) and MAXENT (for RCP 8.6).

These analyses suggest that the results for *Conus spurius* and *Crassostrea virginica* may be more dependent on variable selection, and that gain and loss in suitable area, respectively, are likely for these species when a reduced variable set is used and when bathymetry is excluded.
Figure S1.2.1 Pearson correlation of the environmental variables used in this study, performed with the ‘cor’ function in R.
Table S1.2.1  Percentage decrease in suitable area from the present to each of three time slices under RCP 2.6 and 8.5, using: all, all environmental variables; no bathy, all variables except bathymetry; red., a reduced set of variables that included bathymetry, diatom phytoplankton concentration, nitrogen concentration, sea surface temperature and sea surface salinity.
Table S1.2.2 Changes in suitable area for 14 mollusk species in the western Atlantic Ocean under different models. Data are for MAXENT models. Species names are as in Table S1.2.1. Present Δ, percent change in suitable area from the present-day model when the designated variable is set to future conditions and all others kept at present-day conditions; future Δ, percent change in suitable area from the RCP 2.6 2081-2100 projection when designated variable is held constant at present-day conditions (with all other variables set at future conditions); alkal., total alkalinity; bathy., bathymetry; DIC, dissolved inorganic carbon; D phyt., diatom phytoplankton concentration; ND phyt., non-diatom phytoplankton concentration; SSS, sea surface salinity; SST, sea surface temperature; zoopl., zooplankton concentration.

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Table S1.2.3 Percentage contribution of each environmental variable to the MAXENT model. Alkal., total alkalinity; bathy., bathymetry; DIC, dissolved inorganic carbon; D phyt., diatom phytoplankton concentration; ND phyt., non-diatom phytoplankton concentration; SSS, sea surface salinity; SST, sea surface temperature; zoopl., zooplankton concentration.

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Appendix S1.3

Appendix S1.3 Supporting information for model extrapolation analyses: (a) mobility-oriented parity surfaces (Fig S1.3.1, Table S1.3.1); and (b) environmental overlap analyses (Fig S1.3.2).

Appendix S1.3a. Mobility-oriented parity surfaces (MOP)

MOP consistently identifies the mid-Atlantic and the south-west corner of the projection region (Pacific Ocean) as containing values outside those in the calibration region. Interestingly, these areas are also predicted to be suitable in many of our models (Table S1.3.1), a case of algorithm extrapolation, and this suitability is likely an artefact of unrealistic model response curves. Out-of-range environments also occur off the coast of Brazil, near Rio de Janeiro, for both the present-day and future projections – a region deemed suitable for many of our species – such that predictions in these areas should be treated with appropriate caution. The northern reaches of our study region contain values for environmental variables outside those of the calibration region for most species analyzed. Suitable area for these species, however, do not overlap with the masked regions, with the exception of a few pixels for *Anomia simplex* d’Orbigny, 1853, *Conus spurius* Gmelin, 1791 and *Dinocardium robustum* Lightfoot, 1786 (Table S1.3.1) – too few to affect our conclusions. These out-of-range values do not limit suitability in a northward direction, however, because a buffer (area of non-suitability) exists between predicted suitable area and the out-of-range environmental space for most species.
Figure S1.3.1 MOP values for all species comparing the training-region environment with the present-day projection (top) and the RCP 8.5 emission scenario 2081–2100 time slice (bottom). Comparisons are made using the environmentally-closest 5% of pixels in the training region to a given pixel in the projection region. Values close to one (greens to blues) indicate high environmental dissimilarity, whereas values close to zero (orange to brown) indicate high environmental similarity. Note that the present-day and future projections are scaled independently of each other. See Table S1.3.1 for species names.
Table S1.3.1 Indication of model extrapolation in specified regions. Crosses indicate cases where the model predicts suitable area in that region, but the area also contains values for environmental variables that are outside those found in the training region. For most species, only a few suitable pixels are implicated in the respective regions.

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<td>x</td>
</tr>
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<td></td>
<td>x</td>
</tr>
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<td>Mercenaria campechiensis</td>
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<td>x</td>
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<tr>
<td>Gastropoda</td>
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<td>Terebra dislocata</td>
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Appendix S1.3b. Environmental overlap masks

Results from these analyses indicate present-day projections are largely unaffected by novel combinations of environmental parameters, with the exception of the areas outside the ranges of values altogether (MOP) (e.g., the region off the coast of Brazil). Conversely, future time slices possess a large number of pixels with novel environmental combinations (Figs S1.3.2). As expected, the RCP 8.5 2081–2100 time slice contains the greatest number of novel climatic combinations, with virtually no expected analogue pixels. The absence of analogue pixels compared to the present-day calibration region is somewhat surprising; however, the
extreme nature of this climate change scenario should also be considered. GARP predicts virtually no suitable area for the majority of species under the RCP 8.5 2081–2100 time slice, whereas MAXENT typically predicts at least some suitable areas. The two algorithms diverge most dramatically in this scenario and time slice, which can be explained in part by the non-analogue climatic conditions. This discrepancy diminishes under MAXENT without extrapolation, as the model truncates suitability at the edge of known environmental values (or, potentially, combinations of pixels) like GARP.
**Figure S1.3.2** Environmental overlap masks for all species for present-day and RCP 2.6 and RCP 8.5 2081–2100 time slices. Blue indicates analogous environmental combinations, whereas purple indicates novel environmental combinations. Note that the RCP 8.5 2081–2100 time slice contains virtually no analogous environment, meaning that future combinations of variables all differ from those in the present-day training region (although the values are not necessarily outside the range of values within the training region). See Table S1.3.1 for species names.
Appendix S2.1

Appendix S2.1 Supporting information on model results and distributional data (Figures S2.1.1–S2.1.5, Tables S2.1.1–2.1.2).

Figure S2.1.1 Ecological niche models for the present, LIG, and mPWP time slices for *Bulla occidentalis*, *Crassostrea virginica*, *Crepidula fornicata*, and *Dinocardium robustum*. Binary and continuous predictions are presented, with binary predictions thresholded using the mean suitability value from the continuous output. For the binary predictions, yellow=suitable and dark blue=unsuitable, whereas for the continuous predictions, darker grays indicate higher suitability.
Figure S2.1.2 Ecological niche models for the present, LIG, and mPWP time slices for *Lucina pensylvanica*, *Mercenaria campechiensis*, *Neverita duplicata*, and *Terebra dislocata*. Binary and continuous predictions are presented, with binary predictions thresholded using the mean suitability value from the continuous output. For the binary predictions, yellow=suitable and dark blue=unsuitable, whereas for the continuous predictions, darker grays indicate higher suitability.
Figure S2.1.3 Distributional data for Anomia simplex, Bulla occidentalis, Crassostrea virginica and Crepidula fornicata for the three time slices: mid-Pliocene Warm Period (mPWP; ~3.1 Ma), Last Interglacial (LIG; ~130 Ka), and present-day (PI).
Figure S2.1.4 Distributional data for *Dinocardium robustum*, *Lucina pensylvanica*, *Mercenaria campechiensis* and *Neverita duplicata* the three time slices: mid-Pliocene Warm Period (mPWP; ~3.1 Ma), Last Interglacial (LIG; ~ 130 Ka), and present-day (PI).
Figure S2.1.5 Distributional data for *Oliva sayana* and *Terebra dislocata* for the three time slices: mid-Pliocene Warm Period (mPWP; ~3.1 Ma), Last Interglacial (LIG; ~130 Ka), and present-day (PI).
Table S2.1.1 Data on climatic preference and larval strategy for the species analyzed. Distributional data are shown for each time slice: mid-Pliocene Warm Period (mPWP; ~3.1 Ma), Last Interglacial (LIG; ~130 Ka), and present-day (PI). The “all” column indicates the total number of distributional records for each time slice/species, and the “unique” column specifies the spatially explicit distributional records used for modeling.

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Table S2.1.2 Model evaluation results. P-values were obtained with the jackknife procedure of (Pearson et al., 2007) for time slices/species that had < 25 occurrence points (single rows), and with the partial Receiver Operating Characteristic Analysis (Peterson et al., 2008) for time slices/species that had > 25 occurrence points. All models were statistically significant.

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Appendix S2.2

Appendix S2.2 Supporting information on Neogene stratigraphy of the Atlantic Coastal Plain, with correlational chart (Figure S2.2.1) and table on Pliocene to recent geological units (Tables S2.2.1–2.2.2).

The Neogene stratigraphy of the Atlantic Coastal Plain is complex. Although numerous papers have been published on the subject, different stratigraphers have proposed quite different stratigraphic relationships. Part of the confusion stems from how these stratigraphers have diagnosed and applied terminology to the stratigraphic units (e.g., whether they did so based on morphology/elevation, lithology or biostratigraphy). Additional confusion can arise because geologic names have been applied to stratigraphic units and later expanded to terraces and vice versa (Colquhoun et al., 1968). Moreover, in many instances, we simply lack reliable age constraints and knowledge of the geological relationships of the region, and many more years of detailed study are needed to elucidate the stratigraphic framework of the Neogene Atlantic Coastal Plain.

Here, we attempt to provide an up-to-date compilation on Pliocene—recent stratigraphy of the Atlantic Coastal Plain. These data have been compiled from extensive literature review and detailed discussions with stratigraphers. We stress that they in no way represent a consensus opinion on the Pliocene—recent stratigraphy of the Atlantic Coastal Plain. The chart is provided as a schematic only, and is not intended to relate information regarding unconformities, hiatuses, or facies. Note that, when possible, we used the updated Berggren zonations from Wade et al. (2011). The “~” indicates that the age range is approximate and was determined from stratigraphic position or from the ages of associated units. I hope that this stratigraphic chart and
Table 2.2.1 Table of viable formations used for the mPWP and LIG time slices in this study.

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<th>LIG (~130 Ka) Formations</th>
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<td>Canepatch</td>
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<td>Coffee Mill Hammock</td>
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Table of viable formations used for the mPWP and LIG time slices in this study.
Figure 2.2.1 Correlational chart of Pliocene to recent geological units of the Atlantic Coastal Plain.
Table S2.2.2: Part 1. Northwest Florida

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<th>Unit (Ma)</th>
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<td></td>
<td>The Prairie Fm (135-60 Ma) (Meins 2000; Ottos 2005, 2009; Shen et al 2008); Silko Fm (232-116 Ma) (Ottos 2005, 2012, 2015), and Gulfport Fm (232-118 Ma) (Ottos 2015) are not valid formations according to the Florida Geological Survey (Means, pers comm 2013). These formations were based on elevation and not named following stratigraphic guidelines. According to Ottos (1993), the Prairie Fm deposits interfinger with transgressive Silko units; they cover Silko deposits and the landward flank of the Gulfport Belt. According to Ottos (2009, 2013), the Silko is partially correlated with the above-lying Gulfport Fm. Kolbe et al. (2011) cite these as present in NW Florida. Huddleston (pers comm 2013) also indicated the Silko Fm of Ottos is present in the coastal area as far east as St. George Island and is in the same stratigraphic position as the Saffite Fm of GA.</td>
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| Miccosukee | Cooke and Mason (1937); Ottos (1998) | ~3.3-2.6 | Found in E and Citronelle to W. Miccosukee Fm is more clayer; the transition between these two units occurs around central Gladstone County (Means, pers comm 2013); unit could be a member or facies of the Citronelle Fm. Huddleston (pers comm 2013) indicated he has no reasonable evidence that the Citronelle, Miccosukee, and Jackson Bluff Fms are anything but lithofacies of one depositional event: the Citronelle/Miccosukee Fms are a shore/shelfface deposit or lithofacies, whereas the Jackson Bluff Fm is an offshore, shelf bottom deposit or lithofacies. The Intracoastal Fm represents a farther offshore deposit or lithofacies, where only minor siliciclastics are present but may dominate in some beds (the siliciclastics having been deposited closer to shore). | Age is uncertain, as deposit is fairly eosioclastic; age range is thus an estimate and inferred from stratigraphic position; Kolbe et al. (2011) indicated a slightly younger age for both the Citronelle and Miccosukee Fms (2.4-1.7 Ma). | Considered time-equivalent of Cypresshead Fm (GA) and correlated in part with Naushe Fm in N. Florida (Huddleston 1988); time equivalent with Citronelle Fm (Hupper 1990; Ottos 1988, 1998). Huddleston (pers comm 2013) indicated Miccosukee, Citronelle, Jackson Bluff, Cypresshead and Intracoastal Fms are time equivalents. | Note that in this compilation, the Miccosukee Fm is only partially correlated with the Cypresshead Fm. |

| Citronelle | Stringfield and LaMonaca (1967); Huddleston (1988); Ottos (1988); Means (2009) | ~3.3-2.6* | Citronelle found only in the uplands from 56A to TX (Ottos 1998, 2004). There is a questionable, thin bed that may be younger and perhaps olistostat atop the Citronelle Fm. Huddleston (pers comm 2013) indicated he has no reasonable evidence that the Citronelle, Miccosukee, and Jackson Bluff Fms are anything but lithofacies of one depositional event: the Citronelle/Miccosukee Fms are a shore/shelfface deposit or lithofacies, whereas the Jackson Bluff Fm is an offshore, shelf bottom deposit or lithofacies. The Intracoastal Fm represents a farther offshore deposit or lithofacies, where only minor siliciclastics are present but may dominate in some beds (the siliciclastics having been deposited closer to shore). Ottos (1992) indicated that in the western panhandle of FL and southern AL, the unit unconformably overlies the Perdido Key Fm, but this formation is not recognized by the Florida Geological Survey (Means, pers comm 2013). Means (pers comm 2013) indicated that in the central FL panhandle, the unit unconformably overlies the Jackson Bluff Fm; however, Huddleston (pers comm 2013) indicated the Citronelle and Jackson Bluff Fms are time-equivalent. | *Age range is an estimate. Age of the Citronelle Fm has been debated for years because of the lack of index fossils and has been variously assigned to the Miocene, Pliocene or Pleistocene (Hupper 1990; see Means (2009) for a review. Authors cited within the "supporting references" section all indicate a Pliocene age. Means (2009) indicated the age is no later than Late Miocene, but this was before the Pliocene/Pleistocene boundary change. Markewich et al. (1992) and Kolbe et al. (2011) cited a slightly younger age (2.4 and 2.5-1.7 Ma, respectively). |

<p>|        | Cooke and Mason (1939); Ottos (1998) |            | Fm grades into Miccosukee Fm (Cooke and Mason 1939); correlated with Cypresshead Fm (Huddleston 1988, Ottos 1988, 1998; Means 2009); Huddleston (pers comm 2013) indicated the Miccosukee, Citronelle, Jackson Bluff, Cypresshead and Intracoastal Fms are time equivalents. | Note that in this compilation, the Citronelle Fm is only partially correlated with the Cypresshead Fm. |            |            |            |</p>
<table>
<thead>
<tr>
<th>Region</th>
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<th>Age (Ma)</th>
<th>Unit</th>
<th>Formation</th>
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<tr>
<td>Midwest Florida</td>
<td></td>
<td>3.94±0.6</td>
<td>Ancestral Bluff</td>
<td>Middle - Early Mississippian</td>
</tr>
<tr>
<td>Northeast Florida</td>
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<td>3.94±0.6</td>
<td>Ancestral Bluff</td>
<td>Middle - Early Mississippian</td>
</tr>
<tr>
<td>Southeast Florida</td>
<td></td>
<td>3.94±0.6</td>
<td>Ancestral Bluff</td>
<td>Middle - Early Mississippian</td>
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</table>

**Table S2.2.2: Part 2, Northwest Florida**

**Table S2.2.2: Part 2, Northeast Florida**

**Table S2.2.2: Part 2, Southeast Florida**

**Table S2.2.2: Part 2, Ancestral Bluff**

**Table S2.2.2: Part 2, Middle \- Early Mississippian**
Table S2.2.2: Part 3. Southwest Florida

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<th>Correlation</th>
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<th>General regional notes</th>
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<tbody>
<tr>
<td>Lake Flint</td>
<td>Formation &amp;</td>
<td>Coffee Mill Hammock</td>
<td>0.14-0.11</td>
<td>Port and Vanstrum (1969); Lyons (1991)</td>
<td>Considered a unit of the Ft. Thompson Fm, although others have argued for an erosional status (e.g., Brooks 1966, 1974; Lyons 1991). The validity of the Ft. Thompson Fm as a lithological unit has been debated by the Florida Geological Survey in their most recent map of Florida (2001).</td>
<td>Petush and Roberts (2007) indicated the Coffee Mill Hammock Member and the Ft. Thompson Fm are younger (from 0.6-0.01 Ma).</td>
<td>Correlated with the Princess Anne Fm (Lyons 1991) (this Fm is included within the Nassau Fm by Hubbard (1988) and is correlated in part in this compilation). Lyons (1991) indicated the Socastee, Pamlico (in part), Norfolk (now Shirley, Tidoh or Accutale Fms.), Sandbridge, Princess Anne, Silver Bluff, and Anastasia Fms. have been cited within Blackwelder interval zone M1, which Lyons (1991) does not agree with. Lyons (1991) argued only the Princess Anne Fm and Coffee Mill Hammock Member of the Ft. Thompson Fm are in interval M1.</td>
<td>Ward and Blackwelder (1977) considered the Ft. Thompson Fm (including the Coffee Mill Hammock) as correlative with the Socastee Fm, but Lyons (1991) disagreed; however, in this report, the Ft. Thompson does correlate in part with the Socastee Fm. The Ft. Thompson, Anastasia, and Key Large Fms. are equivalent (Dubar 1992). The Ft. Thompson Fm grades into the Anastasia Fm in the E and the Miami Limestone to the SW (Kittie and Portell 2010).</td>
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<td></td>
<td></td>
<td>Fort Thompson</td>
<td>&lt;0.1</td>
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<td></td>
<td></td>
<td>Undifferentiated</td>
<td>0.6-0.12</td>
<td>Whelihan and Schnap (1978); Kowalewski et al. (1998); Moxham (2001a); Atikey et al. (2010); Musial and Wise (2012)</td>
<td>The Ft. Thompson Fm has also been said to include the Chuararock Member, but the Florida Geological Survey is skeptical about using the Ft. Thompson as a lithological unit in general, and thus this member is not presented here.</td>
<td>Hickey et al. (2010) indicated that reliable dates for the Ft. Thompson Fm are difficult to obtain, but placed the interval around 0.6-0.4 Ma; Brooks (1974) cited an age of 0.22 4+/-Ma; others cited slightly older ages: 0.95-0.95 Ma (Wesol et al. 1988) and 0.9-0.1 Ma (Kolbe et al. 2011). Petush and Roberts (2007) cited a younger top age for the Fm (0.01 Ma).</td>
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<tr>
<td>Bermost</td>
<td></td>
<td></td>
<td>1.6-1.1</td>
<td></td>
<td>Hubert and Moger (1969); Webb et al (1989); Campbell and Moger (1985); Knorr and Harnes (2006); Kolbe et al (2011)</td>
<td>The unit is only found in southern Florida.</td>
<td>Younger ages have been cited previously for the Bermost Firm, including: 1.0-0.5 Ma (Duller 1974; Willard et al 1991); 1.6-0.5 Ma (Mitterer 1974; 1975); however, these younger ages may be suspect for a number of reasons, see Lyons (1991); Pettach and Roberts (2000) also indicated a younger top age for the firm (of 0.4 Ma).</td>
<td>Partially correlated with the James City and Waccamaw Firms (NC and SC) (Ward et al 1991).</td>
<td>Dullar (1991) indicated that the unit correlates with the Canoeport Firm (SC), but this is not supported in this compilation, with the Canoeport Firm younger than the Bermost Firm here.</td>
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<tr>
<td>Caloosahatchee</td>
<td></td>
<td>2.3-1.7</td>
<td></td>
<td></td>
<td>Cunningham et al (2001), Missimer (2001a,b), Kelab et al (2011), Missimer and Wise (2013)</td>
<td>A “lower” and “upper” Caloosahatchee have been referred to in publications, but the firm in places (e.g., the Sarasota area) can have 2 to 3 discontiguities/unconformities.</td>
<td>Missimer (2001a) cited an age of 2.1 to 1.7 Ma for 0.6 Ma, but the latter age does not accord with other dates for the Caloosahatchee Firm or with other formations in the sequence. Furthermore, a more up-to-date 55A abstract (Missimer and Wise 2012) indicated the firm straddles the Geisler-Calabrian boundary. Older ages cited for the firm include: 1.85-1.71 and 0.3-0.2 Ma in the same publication (Missimer et al. 1991), 2.5-1.8 Ma (Willard et al. 1993). There was no provenance data for the sample (Bender 1972; 1975; Lyons 1991): 2.55-2.35 Ma for the lower Caloosahatchee and 1.91.1.7 Ma for the upper Caloosahatchee (Campbell and Campbell 1995).</td>
<td>Correlated with the Waccamaw and Nashua Firms (Dullar 1991) (only partially correlated with the Nashua Firm in this compilation; here, the Nashua Firm is primarily older); correlated with the James City and Waccamaw Firms (Blackwell 1991a; Allmon et al 1995a).</td>
<td>Dullar (1991) indicated the firm is correlated with the Nashua Firm, but the Nashua Firm is primarily older in this report; Lyons (1991) indicated the firm is correlated with the Chauvin River Firm (NC and VA), but the unit is younger here; Missimer (1993) indicated the lower Caloosahatchee is correlated with the lower Anastasia, which is not supported in this compilation; the Anastasia Firm is younger here.</td>
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<td>Region</td>
<td>Formation</td>
<td>Member</td>
<td>Unit</td>
<td>Age (Ma)</td>
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<tr>
<td>Southwest Florida</td>
<td>Pinecrest Sand</td>
<td></td>
<td></td>
<td>2.9-2.1</td>
<td>Almond et al (13966); Jones et al (1991)</td>
<td>Beds versus Petuch (1982) and modified by Zullo and Harris (1992) placed the Petuch’s Unit (3) in the Caloosahatchee Frm, and Units 2 through 9 in the upper Tamiami Frm. The authors also subdivided the units into the upper Pinecrest Beds (Units 2 and 3) and lower Pinecrest Beds (Units 4 through 9). Petuch’s Unit 10 and 13 were placed into the lower Tamiami Formation. *Indicates this unit was no longer included in the Pinecrest (Unit 10 and 13) (Petrucci et al 2002).</td>
<td>Campbell and Campbell (1995) cited an age of 3.0-2.8 Ma for Beds 3-1; Almond et al (1996a) cited a slightly younger age of 2.9-2.8 Ma (Midocene Chron).</td>
<td>The &quot;upper Pinecrest&quot; correlates with the Chokran River Fm (VA and Carolinas) Jones et al (1991); DeWeese and Cronin 1996; Williams et al (2001).</td>
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<td></td>
<td>Pinecrest Sand</td>
<td></td>
<td>3.5-2.6</td>
<td></td>
<td>Almond et al (13966); Jones et al (1991)</td>
<td></td>
<td>Orenin (1991) indicated an age of 3.5-3.6 Ma for Beds 10-5; Campbell and Campbell (1995) cited an age of 3.5-3.1 Ma for the &quot;middle bed&quot; of the Pinecrest. Knowles et al (2000) and Williams et al (2001) have the Pinecrest Beds 10-5 at 3.7-3.2 Ma.</td>
<td></td>
<td>The unit is correlated with the Duplin Fm (NC, SC, GA) and Jackson Bluff Fm (Florida) Worstall (DeWeese and Cronin 1996); the &quot;lower Pinecrest&quot; correlated with the Duplin and Rappahannock Fms (NC, SC, and GA) and Bushmore, Megan’s Beach and Moore House Members of the Yorktown Fm (Cronin 1991); correlated with the lower and upper Yorktown of VA and NC (Lyons 1995) [In this report correlated primarily with the upper]; lower Pinecrest correlated with the Jackson Bluff, Duplin, and Rappahannock Fms, and the Bushmore and Megan’s Beach Members of the Yorktown Fm (Almond et al 1996a).</td>
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<tr>
<td></td>
<td>Pinecrest Sand</td>
<td></td>
<td>4.6-3.8</td>
<td></td>
<td>Orenin et al (1991); Lyons (1991)</td>
<td></td>
<td>Knowles et al (2000) and Williams et al (2001) placed this unit at 4.2-3.6 Ma, suggesting the authors did not revise the age of interval zone. Campbell and Campbell (2000) placed the age of 4.05-3.16 Ma for Beds 10 and 11.</td>
<td></td>
<td>Jones et al (1991), Willard et al (1995), and Williams et al (2000) indicated the firm is equivalent to the Sunkland Meadow Member of the Yorktown Fm, but this correlation is not supported in this compilation; here, the Sunkland Meadow Member is older; others (e.g., Scott 1995) indicated the Sunkland Meadow Member is not correlated with any Tamiami sediments, at least not in Florida.</td>
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### Table S2.2.2: Part 6. Southwest Florida

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<tr>
<td>Tamiami</td>
<td>Undiffer-</td>
<td>3.2-2.2</td>
<td></td>
<td></td>
<td>Missimer (2001a, b);</td>
<td>Missimer (2001a) indicated the “Pinocrest” is 3.2-2.15 Ma; however, when Beds 10 and 11 are removed from traditional definitions of the “Pinocrest”, this age range seems to match the ages of the sequences fairly well; Missimer and Wise (2003) indicated the Pinocrest is 3-2 Ma.</td>
<td></td>
<td>Correlated with the Bear Bluff (NC, SC, and GA) and Chewah River Fmns (Caledon Beach and Edenhouse Member) Fmns (VA and NC) (Cronin 1991).</td>
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<tr>
<td>Ochopee Limestone</td>
<td>Cunningham et al (2001)</td>
<td>3.83-3.62</td>
<td></td>
<td></td>
<td></td>
<td>The Ochopee Limestone is present in southern Florida, an undifferentiated sand body above it, which is probably equivalent to the Long Key Fm of the Keys or the Pinocrest Beds (Kuninnen et al. 2001); Hunter (1968) suggested that the Pinocrest Sand, Ochopee Limestone and Buckingham Limestone were lateral equivalents, but Missimer (1992) indicated that the unit consisted of at least 9 mappable facies. Portell (pers. comm. 2013) indicated the Ochopee and Pinocrest appear time equivalent based on the molluscan assemblages.</td>
<td>Petch and Roberts (2001) placed the Ochopee Limestone as younger than 3.6 Ma and equivalent to the Pinocrest Beds. Conversely, Missimer (1990) and others cited the Ochopee Limestone as older than the Pinocrest Beds.</td>
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<tr>
<td>Buckingham Limestone</td>
<td>Missimer (1990)</td>
<td>3.6-3.8</td>
<td></td>
<td></td>
<td></td>
<td>Missimer (1990, 1992) indicated that the Buckingham Limestone is the lowermost facies of around 9 total facies and is probably equivalent in age to the clay and sand facies, however, Hunter (1968) suggested that the Pinocrest Sand, Ochopee Limestone and Buckingham Limestone are lateral equivalents.</td>
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<td>Region</td>
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<td>Southwest Florida</td>
<td>Missimer (1994); Moore (1997); Missimer (1998); Scott (1998); Missimer (1999); Misumi (2001); Cunningham et al. (2003); Knowles et al. (2006); Williams et al. (2009); Kibler et al. (2011)</td>
<td>4.3-2.1</td>
<td>11-4.5</td>
<td>4.3-2.1</td>
<td>According to Missimer (2005, 1993), the definition of the Newcomb is used to establish the base of the Tamiami Fm. It is established using the Beulah Member or the H. Thompson Fms. Missimer (1999) defined 9 or more members of the Tamiami Fm., however, correlation among them is problematic. These units can be mapped on the basis of different stratigraphic markers, including the Pinecrest Sand Member, the unnamed limestone facies, the Golden Gate Reef Member (of Missimer 1986), the Port Royal facies, the Okeechobee Limestone Member, the sand facies, the Buckingham Limestone Member, and the fine clay and sand facies. Only 1 or 4 of these occur in a vertical stratigraphic section at any given locality. In contrast to Missimer (1990, 1993), Krumen (1969) indicated the Pinecrest Sand, Okeechobee Limestone and Buckingham Limestone were later equivalents. Missimer (1999), on the other hand, indicated the Buckingham Limestone is the lowermost facies and is probably equivalent in age to the clay and sand facies. The Tamiami Fm. additionally has been broken into at least three other members (Martin, Golden Gate Reef, and Bonita Springs Member), each younger or older by Missimer (1997) and Patalch and Roberts (2010), but these remain controversial. Missimer (1995) did not formally define the Golden Gate Reef Member in terms of the stratigraphy and relationships with other major lithological units. Missimer (1996) and Missimer (1996) informally suggested the Bonita Springs Member. Much controversy concerning facies surrounds the surface and near-surface deposits of southern Florida, especially the Tamiami Fm. This is for a variety of reasons, see Jones et al. (1975) and Scott (1998) for details. Based on the sequence stratigraphic framework of Zullo and Harris (1992) at the AICPA and SMR Pts. the authors concluded that Pelto's Units 0-1 belong to the Caloosahatchee Fm. and Units 2-2.1 were within the Tamiami Fm. Units 2-9 were divided into the upper Tamiami Fm., and Units 2-11 were within the lower Tamiami Fm. Further subdivision placed Units 2-3 into the upper Pinecrest Beds, and Units 4-8 into the lower Pinecrest Beds. Pelto and O'Malley (1991), however, now consider Units 2-4 to belong to the Prudhoe Member (Tamiami Fm). Units 2-9 to belong to the Bonita Member (Tamiami Fm). Unit 10 to belong to the Tamiami Member (Tamiami Fm) and Unit 11 to be the Suwanee Member (Marineck Station Fm). The unconformities between the Peace River Fm. and the overlying Tamiami Fm. have been dated as 4.3 Ma (Kibler et al. 2011), an age which Guertin et al. (2000) also cited.</td>
<td>The lower Tamiami and lower Pinecrest Beds are correlative with the Jackson Bluff Fm. (Zullo and Harris 1992; Zullo and Portier 1993) (note that the lower Tamiami Fm., depending on the definition, does not correlate with the Jackson Bluff Fm. in this compilation).</td>
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## Table S2.2.2: Part 8. Southern Florida

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<tr>
<td></td>
<td>Miami Limestone</td>
<td></td>
<td></td>
<td>0.13-0.09</td>
<td>Breckner and Thurber (1953); Osmond et al (1955); Guenther et al (2000); Neal et al (2008); Hickey et al (2010)</td>
<td>The Miami Limestone sits above the Ft. Thompson Fm., previously considered part of the Key Largo Fm. (Hickey et al 2010).</td>
<td>Kolbe et al (2011) cited an older age of 0.9-0.1 Ma, while Scott (2011) indicated a younger age of 0.01 Ma.</td>
<td>Dvornik (1993) indicated the Miami Limestone interfingers with the Anastasia Fm. in the N. the Key Largo Fm. in the S, and the Ft. Thompson Fm. is the NW, but according to Neal et al (2008) and Hickey et al (2010), the unit sits above the Ft. Thompson Fm.; here the Ft. Thompson is above and partially interfingers/correlates. Hickey et al (2010) indicated the unit is a lateral equivalent to the upper part of the Key Largo Limestone.</td>
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<td>0.132-0.07</td>
<td>Osmond et al (1970); Marshby (1973); Mitterer (1974); McNeil (1981); Portell et al (2003); Banks et al (2007); Burdette et al (2008); Burdette (2010)</td>
<td>Portell (pars comm 2013) indicated the unit is present from St. Augustine to southern Palm Beach County.</td>
<td>Kolbe et al (2011) cited an older age for this Fm. (0.9-0.1 Ma); publications such as Osmond et al (1970), Murphey (1973), and Mitterer (1974) cited slightly younger ages (around 113 to 118 Ka) compared to the others of around 118 to 113 Ka (e.g., Banks et al 2007; Finke et al 2000; Burdette 2010); Petch and Roberts (2007) indicated an age of 0.1-0.01 Ma.</td>
<td>The Miami Dolomite of the Miami Limestone is considered contemporaneous with the Anastasia Fm. (Cooker and Mossom 1929); the Anastasia Fm. interfingers with the Miami Limestone at the top of the section and probably correlates with the Caloosahatchee Fm. at the top of the section.</td>
<td>Wasmier et al (2000) indicated the unit probably correlates with the Caloosahatchee and Ft. Thompson Fms., but the Caloosahatchee Fm is too old in this compilation to correlate. If congruent with OIS 5a, the unit correlates with the Biloxi and Gulfport Fms (ME).</td>
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Table S2.2.2: Part 9. Southern Florida

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<tr>
<td>Southern Florida</td>
<td>Key Largo</td>
<td></td>
<td></td>
<td>1.3-0.09</td>
<td>Broecker and Thurler (1962); Osmund et al (1965); Muller et al (2002);</td>
<td>The Key Largo Fm is a fossil coral reef that forms the Florida Keys from Soldier Key southwest to the New Found Harbor Channel (Dulaa 1991). The age may not be as old as 0.3 Ma, as there tends to be a bias towards older dates in U-series dating (Muller et al 2002); Agnos found single data points of 0.139 Ma (Harman et al 1979), 0.145 Ma (Siabao and Nalley 1981), 0.146 Ma ± 10 ka (Muhs et al 1992); 0.136–0.125 Ma (Trujillo et al 2000), but these dates have error bars of probably 5 ka; a generally accepted age is 0.125 Ma (Shin 2000); Meehan pers comm 2013, but recent work indicates 0.135 Ma (Henderson and Stover 2006), Peterson and Roberts (2007) cited an older age (0.6 Ma) for the base; Scott (2011) cited a younger age for the top (0.01 Ma).</td>
<td>The upper part of the Key Largo limestone is the same age as the Miami Limestone (Dulaa 1991); the Ft. Thompson Fm is recognized as a lateral equivalent of the Key Largo limestone (Kenneboum et al 1998).</td>
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<td></td>
<td>Limestone</td>
<td></td>
<td></td>
<td>1.0-1.71</td>
<td>Guerin (1998); Messimer (1997); Guerin et al (2000);</td>
<td>*Placed around 2 Ma and referred to as Ft. Thompson and Colosassatchee Fm equivalents (Guerin et al 2000), and thus the upper age boundary is set at 0.4 Ma, which is within the Ft. Thompson Fm.</td>
<td></td>
<td></td>
<td>Suggested to be a Ft. Thompson-Colosassatchee equivalent (Messimer 1997; Guerin 1998; Guerin et al 2000).</td>
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<tr>
<td>Region</td>
<td>Formation</td>
<td>Member</td>
<td>Unit</td>
<td>Age (Ma)</td>
<td>Supporting References</td>
<td>Notes</td>
<td>Other age details or opinions</td>
<td>Correlation</td>
<td>Other opinions on correlations</td>
<td>General regional notes</td>
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<tr>
<td>Nashua</td>
<td></td>
<td></td>
<td></td>
<td>3.0-1.9</td>
<td>Huddleston (1988); Markewich et al (1992); Scott (1992)</td>
<td>Cooke and Mossam (1929) abandoned the Nashua farm name and used the Caloosahatchee instead.</td>
<td>Note: to be within Berggren zone 4LJ (~3-2.3 Ma), based on updated stratigraphy from Wade et al (2011) and a Cypresshead equivalent (Huddleston 1988). Markewich et al (1992); Kotb et al (2011) cited a younger age (2.4-1.7 Ma), as does Peltier and Roberts (2007) (~2.5-1.6 Ma). Cited age differs from Scott (2001) (~3.3-1.8 Ma), but Scott's (2011) age has been revised in the most up-to-date stratigraphic column by the Florida Geological Survey (Means pers comm 2013).</td>
<td>The Cypresshead (and thus Cronolite) and Bear Bluff (SC) Fms are equivalents (Huddleston 1988; Markewich et al 1992; Means pers comm 2013).</td>
<td>Dular (1992) indicated the unit is correlative with the Waccamaw Fm., but the Waccamaw Fm. is younger in this compilation.</td>
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<tr>
<td>Stock Island (West)</td>
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<td></td>
<td></td>
<td>4.5-2.0</td>
<td>Cunningham et al (1998); Guerin et al (1998)</td>
<td>Fine-grained limestone underlying the lower part and part of the middle of the Florida Keys (Guerin et al 2000).</td>
<td>Correlated with a portion of the Long Key Fm. and with the Ochoppee Limestone (Cunningham et al 1998; Cunningham et al 2001).</td>
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<tr>
<td>Long Key (East)</td>
<td></td>
<td></td>
<td></td>
<td>5.6-2.0</td>
<td>Warrenski et al (1996); Guerin et al (1998); Guerin et al (1999); Guerin et al (2003)</td>
<td>The Long key Fm. has three depositional intervals (Guerin et al 2000).</td>
<td>Correlated with the Ochoppee Limestone and with the Stock island Fm (Cunningham et al 1998; Cunningham et al 2001); the Long Key Fm. has three intervals, which correlate with the Peace River Fm., the Tamiami Fm., and the Pineland Member of the Tamiami Fm (Guerin et al 2000).</td>
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<tr>
<td>Region</td>
<td>Formation</td>
<td>Member</td>
<td>Unit</td>
<td>Age (Ma)</td>
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<td>Other age details or opinions</td>
<td>Correlation</td>
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<td>General regional notes</td>
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<td>Qu</td>
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<td>&lt;0.090</td>
<td>According to Parker and Cooke (1944), the Satilla Fm overlies the Anastasia Fm in Florida, but Marine Series (comn 2013) indicated the Satilla Fm is only in Georgia. Scott (2011) does not include the Anastasia Fm in the N Florida stratigraphic column and instead placed the unit in S Florida. However, the unit is present in N Florida versus Scott (1992).</td>
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<tr>
<td></td>
<td>Anastasia</td>
<td></td>
<td></td>
<td>0.132-0.1</td>
<td>Osmond et al (1970); Murphy (1971); McNett (1985); Portell et al (2003); Banks et al (2007); Bannister (2010)</td>
<td></td>
<td>Kobe et al (2011) cited an older age for this Fm (0.9-1.1 Ma), publications such as Osmond et al (1970); Murphy (1979); McNett (1974) cited a slightly younger age (around 90 to 102 Ka) compared to others of 115 to 116 Ka (e.g., Banks et al 2007; Riney et al 2009; Bannister 2010)</td>
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<tr>
<td></td>
<td>Sutliff</td>
<td></td>
<td></td>
<td>~0.126-0.1</td>
<td>Huddleston (1988); Miller et al (2008); Huddleston (pers comm 2013)</td>
<td></td>
<td>The Satilla Fm in GA, SC and FL includes the Pamlico Fm of Cooke (1943); the Princess Anne Fm and the Silver Bluff Fms (Halls and Noy 1969) and Holocene shoreline complexes, as redefined by Huddleston (1988); these were rejected by Huddleston (1988) because they simultaneously referred to terrace plains - e.g., geomorphic features - and lithostratigraphic units. Huddleston (pers comm 2013) indicated the relationship between the Sutliff Fm and the Princess Anne, Silver Bluff and Pamlico terraces is still unclear. Portell (pers comm 2013) indicated the units mapped as &quot;Sutliff Fm&quot; in NE Florida were based on lithostratigraphy. Parker and Cooke (1944) also indicated the unit is present in FLorida and this was accepted by Huddleston (1988).</td>
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The Miami Oolite of the Miami Limestone is contemporaneous with the Anastasia Fm (Cooke and Moss 1928); the Anastasia Fm interferes with the Miami Limestone at the top of the section and probably correlates to the Caloosahatchee and Ft. Thompson Fms (Ottmerser et al 2000). However, the Caloosahatchee Fm is too old in this compilation to correlate, if cognate with OIS 6, the unit correlates with the St. Johns and Gulfport Fms (McN.).

Ottmerser et al (2000) indicated the unit probably correlates to the Caloosahatchee and Ft. Thompson Fms, but the Caloosahatchee Fm is too old in this report.
Table S2.2.2: Part 12. Northeast Florida

<table>
<thead>
<tr>
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<th>Member</th>
<th>Unit</th>
<th>Age (Ma)</th>
<th>Supporting References</th>
<th>Notes</th>
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<th>Correlation</th>
<th>Other opinions on correlations</th>
<th>General regional notes</th>
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<tr>
<td>Northeast Florida</td>
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<tr>
<td>Nashua</td>
<td>Huddleston (1968); Markewich et al. (1992); Scott (1992)</td>
<td></td>
<td>3.0-1.5</td>
<td></td>
<td>Cookie and Messina (1929) abandoned the Nashua name and used Calcenaclilithiina instead, but Huddleston (1988) reintroduced the Nashua name of Matson and Clapp (1969); the formation is conformable overlies the Cross Creek Shale in the coastal area, the formation may be overlain by the Satilla Shale (Huddleston 1988). Kolbe et al. (2011) defined the Tannant Formation as a unit below the Cypresshead/Nashua Fms in NE Florida, but the unit is not included in this region by Scott (2011) and Fountain (2010). Noted to be within the Benggen zone FL2 (~9.2-3 Ma), based on updated biostratigraphy from Wade et al. (2001) and a Cypresshead Shale equivalent (Huddleston 1988; Markewich et al. 1992; Kolbe et al. 2011) cited a younger age (2.4-1.7 Ma), as does Fichter and Roberts (2007) (~2.3-1.6 Ma). The early age differs from Scott (2011) (~3.0-1.8 Ma), but Scott's (2011) age has been revised in the most up-to-date stratigraphic column by the Florida Biological Survey (Means pers comm 2013).</td>
<td></td>
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<td>The Cypresshead Shale (and thus the Citronelle) and the Bear Bluff Fm (SC) are equivalents (Huddleston 1988; Markewich et al. 1992; Means pers comm 2013).</td>
<td></td>
<td>Dular (1991) indicated the unit is correlated with the Waxamaeer Fm, but the Waxamaeer Fm is younger in this compilation.</td>
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<tr>
<td>Cypresshead</td>
<td>Huddleston (1968); Fountain (2010)</td>
<td></td>
<td>~4.4-2.6</td>
<td></td>
<td>Sediments in peninsular Florida probably belong to the Cypresshead Fm, not the Citronelle Fm (Scott 1988). Means (2009). The formation is found in coastal GA and NE Florida (Orsus 1938); reworking of the unit occurred from 1.8-1.8 Ma (Fountain 2010). The Cypresshead Fm contains both Citronelle-type and Mississippian-type faunas (Huddleston pers comm 2013). The age differs from that cited by Krantz (1991) (2.5-1.9 Ma), Albert et al. (2003) (3.6-1.0 Ma) and Scott (2011) (3.3-1.8 Ma). Dating the interval is difficult due to the lack of fossil material (Means pers comm 2013). The unit is coeval with the Citronelle and Mississippian Fms, overlies the Naylor Fm, and correlates with the Talbot of the Carolinas (Orsus 1938). Campbell and Campbell (1995) argued that the unit is coincident with the Waccamaw Fm, that Wad and Gilinsky (1953) disagreed (the unit is not correlated in this report); equivalent to the Nashua Fm (Huddleston 1988; Markewich et al. 1992); the unit underlies the Satilla Fm (Albert et al. 2003); Huddleston (pers comm 2013) indicated the Miossissippian, Citronelle, Jackson Bluff, Cypresshead and Intracoastal Fms are time equivalents.</td>
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<td>Krantz (1991) indicated the unit is correlated with the Chocowinity River and Bear Bluff Fms, but this is not supported in this compilation; these formations are younger than the Cypresshead Fm here; Markewich et al. (1992) indicated the Cypresshead Fm is not correlated with the Bear Bluff Fm in the Carolinas, but this is not supported in this compilation, with the Cypresshead Fm older here. Orsus (1938) indicated the Cypresshead Fm is correlated with the Talbot Fm of the Carolinas; otherwise referred to as the Caney Creek Fm (the Talbot Fm in SC VA), but the Fm is not correlated in this report.</td>
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Table S2.2.2: Part 13. Northeast Florida

<table>
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<tr>
<th>Region</th>
<th>Formation</th>
<th>Member</th>
<th>Unit</th>
<th>Age (Ma)</th>
<th>Supporting References</th>
<th>Notes</th>
<th>Other age details or opinions</th>
<th>Correlation</th>
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<th>General regional notes</th>
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<tr>
<td>Tamlam equivalent</td>
<td></td>
<td></td>
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<td>*4.3-8</td>
<td>Hordell (pers comm 2013)</td>
<td>Quarries in Palatka are known to contain Tamlam-aged fossils (mostly Eocene tormatites); whether the unit below the Nashua Fm at this site is biologically the Tamlam Fm has not yet been confirmed (Hordell, pers comm 2013); Kola et al (2011) included the Tamlam Fm as a unit below the Cypresshead/Nashua Fms in NE Florida, but this has not been confirmed by the Florida Geological Survey.</td>
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<tr>
<td>Wacoso Beds</td>
<td></td>
<td></td>
<td></td>
<td>*5.5-4.3</td>
<td>Huddleston (1988); Markewich et al (1992)</td>
<td>The Wacoso Beds is an informal term applied to lower Miocene, phosphatic, calcareous, and microfossiliferous, variably argillaceous, silty, fine-grained to very fine grained sand in the subsurface of the coastal area of GA, southern SC, and eastern Fl. (Huddleston 1988); Scott (2001) indicated the Wacoso Beds are also within the upper Miocene strata at a variety of locations, but that they do not outcrop at the surface. The Wacoso Beds were treated as formational rank by Krantz (1991), but there seems to be no evidence for this, although Huddleston (pers comm 2013) would like to see them formalized.</td>
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**Table S2.2.2: Part 14. Georgia**

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<th>Member</th>
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<th>Supporting References</th>
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<th>Correlation</th>
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<th>General regional notes</th>
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<td>Qu</td>
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<td></td>
<td>0.0017</td>
<td>Huddleston (1988); Alber et al (2003); Huddleston (pers comm 2013)</td>
<td>The Fino-Pleistocene sediments in GA and SC were limited, transgressive sections and lacked embayments (Markewich, pers comm 2013). The Pleistocene material up to 25 m thick very similar, which is why Huddleston (1988), using a lithostratigraphic framework, placed all units within the Satilla Fm. The framework of Huddleston (1988) is adopted here, but work is only beginning to tease apart the complexities of the region, and this current framework is used for illustrative purposes only. The Satilla Fm in GA, SC and Fl, includes the Pamlico Fm of Cooke (1983), the Princess Anne and the Silver Bluff Fms (Hulse and Hoyt 1969), and the Holocene shoreline complex, restated by Huddleston (1988); these were rejected by Huddleston (1988) because they simultaneously referred to terrace planes—geomorphic feature—and lithostratigraphic units. Huddleston (pers comm 2013) indicated the relationship between the Satilla Fm and the Princess Anne, Silver Bluff and Pamlico terraces is still unclear.</td>
<td><em>Markewich et al (1992), pers comm 2013</em> preferred a different interpretation to Huddleston’s (1988), pers comm 2013) usage of only the Satilla and Cypresshead Fms, one which is more aligned to McGarri et al (1984, 1980) for SC. There have been varying interpretations of Pleistocene stratigraphy of GA and southern South Carolina; see chart summarizing relationships in Markewich et al (2013). Definition of formations depends on whether one takes a morphostratigraphic, lithostratigraphic or biostratigraphic interpretation. Huddleston’s (1988) framework (here adopted) does not define units on morphological features, as does Cooke (1936, 1945) or Hoyt and Hulse (1974). Huddleston (pers comm 2013) indicated the terraces above the Cypresshead Fm are merely overprinted on the older Cypresshead Fm and not genetically related to the Fm. Huddleston has not been able to determine discrete lithostratigraphic units uniquely related to specific marine terraces in GA.</td>
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Table S2.2.2: Part 15. Georgia

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<th>Correlation</th>
<th>Other opinions on correlations</th>
<th>General regional notes</th>
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<tbody>
<tr>
<td></td>
<td>Cypresshead</td>
<td></td>
<td></td>
<td>3.4 - 2.0</td>
<td>Huddleston (1988); Fountain (2010)</td>
<td>*No age data are available for Cypresshead sediments in Georgia outcrops (Markewich et al. 1992). Markewich (pers comm 2013) indicated the Cypresshead Firm is at least middle Miocene in age. She suggested the upper part of what Huddleston (1988) mapped as the Cypresshead Firm is called the Wacacumay Firm, and correlates with the Talbot Firm of the Carolinas (Olson 1998); Campbell and Campbell (1993) think the unit is coincident with the Wacacumay Firm, but Ward and Gillen (1993) disagreed (the unit is not correlated in this report); considered a Nanticoke equivalent (Huddleston 1988; Markewich et al. 1992); the unit underlies the Talbot Firm (Alber et al. 2003); Huddleston (pers comm 2013) indicated the Wacacumay, Cypresshead, Jackson Bluff, Cypresshead and Intercalated Fms are time equivalents.</td>
<td>Equivalent with the Cypresshead and Mississippi Fms, overlies the Kayar Fm, and correlates with the Talbot Fm of the Carolinas (Olson 1998); Campbell and Campbell (1993) think the unit is coincident with the Wacacumay Fm, but Ward and Gillen (1993) disagreed (the unit is not correlated in this report); considered a Nanticoke equivalent (Huddleston 1988; Markewich et al. 1992); the unit underlies the Talbot Fm (Alber et al. 2003); Huddleston (pers comm 2013) indicated the Wacacumay, Cypresshead, Jackson Bluff, Cypresshead and Intercalated Fms are time equivalents.</td>
<td>Krantz (1991) indicated that the unit is correlated with the Choctaw River and Bear Bluff Fms, but this relationship is not supported in this compilation; these formations are younger than the Cypresshead Fm here; Markewich et al (1992) also indicated the Fm is coincident with the Bear Bluff Fm in the Carolinas, but this is not supported in this compilation, with the Cypresshead Fm older here. Olson (1998) indicated the unit is correlated with the Talbot Fm of the Carolinas, otherwise referred to as the Canepathla Firm (or the Talbot Fm in SE VA), but the Fm is not correlated in this report.</td>
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Table S2.2.2: Part 16. Georgia

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<th>Unit</th>
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<th>Supporting References</th>
<th>Notes</th>
<th>Other age details or opinions</th>
<th>Correlation</th>
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<th>General regional notes</th>
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<tr>
<td>Rayser</td>
<td></td>
<td></td>
<td>1.8-1.1</td>
<td></td>
<td>Huddleston (1998); Ward and Huddleston (1988); Cronin (1993); Markewich et al. (1995); Campbell and Campbell (1995); Campbell (pers comm 2013) (for lower date)</td>
<td>Razer (1929) originally named the Rayser Marl for deposits in SC that are older than the Duplin Marl (he considered them to be Upper Miocene in age). Rayser deposits were left behind from eroding Miocene shoreline and are spotty in Georgia (Huddleston pers commun 2013); these deposits are also referred to as the Duplin Fm (possibly time-equivalent) (Markewich pers comm 2013); Poyntz et al. (1924) initiated the Rayser Marl sediments (neustatographe) designated by Blackwell and Ward (1995) are lithostratigraphically similar to the Goose Creek Limestone (Eocene) and should be abandoned. Campbell (1993) rejected the Rayser Fm on the basis that the only known locality that matches the original type description is hidden by a diatoma, but this rejection is not in use even by those authors in subsequent publications (e.g. Campbell and Campbell 1995).</td>
<td>The Rayser is thought to be within zone P.3 of Degeger or N220 (Huddleston 1988; Cronin 1991).</td>
<td>Correlated with the Duplin and Bluegrass Members of the Yorktown Fm (Cronin et al. 1994; Ward and Huddleston 1988) and to the Jacksontown Member of the Yorktown Fm (Huddleston 1988); Rayser Fm interfingers with the continental Duplin Fm in SC and extends southward into GA (Ward et al. 1993);correlated with the lower Pinecrest Beds, Jacksontown Member of the Yorktown Fm (Cronin et al. 1994);correlated with the Yorktown and Duplin Fms on the basis of foraminifera (Oswell and Wilga 1982); Rayser Fm was placed below the Duplin Fm in Woods and Lewis (2002); Campbell and Campbell (1995) argued that the Goose Creek and Rayser Fms are older than the Duplin Fm at the natural Well stratotype section. The Rayser Fm is equivalent to the upper Goose Creek Fm and overlaps the lower Goose Creek Fm. Ward and Huddleston (1988); the Rayser Fm is placed above the Goose Creek Fm (but the authors later reversed their opinions, pers comm). The Rayser, Cyanella, and Jackson snail Fms are correlated (Huddleston pers comm 2013).</td>
<td>Kranz (1951) correlated the lower Duplin with the Rayser Fm, but here the Duplin Fm is correlated with the upper Rayser Fm. Kratz (1951) placed the Duplin and Rayser Fms as correlative with the Yorktown Fm, but with the Yorktown Fm younger than the Duplin and Rayser Fms. However, in this compilation, the Duplin and Rayser Fms correlate with the upper part of the Yorktown Fm.</td>
<td>The Plio- Pleistocene fossil record of Georgia and South Carolina is still uncertain, partially due to the lack of fossil material in these sediments (Markewich 1993); the definition of formations depends on whether one takes a regional or lithostratigraphic interpretation. Huddleston's (1988) framework has been adopted, but work is ongoing and this does not necessarily represent consensus opinion. The Duplin Fm does not define units on morphological features, as did Hoyt and Halls (1974) or Dupin (1972, 1979).</td>
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</table>

| Waibasso Beds | Huddleston (1988); Markewich et al. (1995); Campbell and Campbell (1995) | 3.5-4.3 | | | | | | Correlated with the lower Duplin Fm as time equivalent of the Waibasso Beds. The Waibasso Beds were named as a formal unit by Krantz (1991), but there are no additional data that support this. The Waibasso Beds are correlated with the lower Duplin Fm in SC and with the upper Waibasso Beds in GA. | | | The unit is correlated with the Waibasso Beds, but this is not supported in the compilation. Here the Waibasso Beds are younger than the Waibasso Beds and the San Joaquin Member, and the Saukian Meadow Member. | | |

The two columns labeled "Other age details or opinions" and "Correlation" are empty except for one entry. The rest of the columns are filled with various geological and historical information.
### Table S2.2.2: Part 17. Southeast and central South Carolina

<table>
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<th>General regional notes</th>
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<td>0.070</td>
<td>McCartney et al (1980); McCartney et al (1988); Stabu (1983)</td>
<td>Youngest of SC coastal region (Soller and Mills 1991). McCartney et al (1980) indicated the Wando Fm includes deposits formerly within the Pamblico, Princess Anne and Silver Bluff Fmms; the authors argued that these names should not be used in S Carolina. The Wando Fm is divided into an upper and lower unit by Wehmiller et al (1980) equivalent to (respectively) the Princess Anne and Pamlico Terraces of Ceilidhoun. *Age of unit is unclear; if younger ages for the Socastee and Copsepatch Fmms are assumed (see discussion below), then the dates indicated for the Wando Fm do not match this compilation. Stabu (1980) found ages of 120,000 +/- 10,000 for the lower Wando Fm and 87,000 +/- 4000 for the upper Wando Fm. The unit has generally been identified as latest Pleistocene in age (McCartney et al 1990), with dates of 126-67 Ka (McCartney et al 1988). Isotope ages Su-18O data (Soller and Mills 1991), and an older age of 230 Ka (Wehmiller and Sellnow 1982, but these authors correlated the Wando Fm with the Socastee and Flanner Beach Fmms, so their definition of formations may have differed. All of MIS 5 may be recorded in the Wando Fm (Maris et al 2003), and there is evidence for multiple amino acids present, but these cannot be directly associated with U-series ages (Corrado et al 1988; Harris 2000; York et al 2001; see Maris et al 2003). Wando is 80-130 Ka (Andrus et al 2009).</td>
<td>The unit may correlate with the Core Creek Sand ofMixon and Pirkey (1975) in northeastern NC (Soller and Mills 1991), but Corrado et al (1988) do not share this interpretation; the unit is also tentatively correlated with the Lighthouse Member of the Tobb Fm of Johnson and Pooles (1980) (Soller and Mills 1991).</td>
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<tr>
<td></td>
<td>Wando</td>
<td>lower</td>
<td></td>
<td>0.129</td>
<td>McCartney et al (1980); McCartney et al (1988); Stabu (1983); Soller and Mills (1991)</td>
<td>Unconformably overlies the Cooper Fm or the Santee Limestone and underlies Holocene coastal deposits (McCartney et al 1980); the unit may correlate with the Core Creek Sand (Mixon and Pirkey 1975) in NC and tentatively correlated with the Lighthouse Member of the Tobb Fm (Johnson and Pooles 1980; Soller and Mills 1991).</td>
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Wenthon and Sellnow (1982) correlated the Wando Fm with the Socastee and Flanner Beach Fms, which supposedly underlie the Wando Fm in this report; the definitions of these formations may have changed or may differ from those of the authors, leading to this discrepancy.
Table S2.2.2: Part 18. Southeast and central South Carolina

<table>
<thead>
<tr>
<th>Region</th>
<th>Formation</th>
<th>Member</th>
<th>Unit</th>
<th>Age (Ma)</th>
<th>Supporting References</th>
<th>Notes</th>
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<th>Correlation</th>
<th>Other opinions on correlations</th>
<th>General regional notes</th>
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</thead>
<tbody>
<tr>
<td>Socastee</td>
<td>McCarron et al (1942); Wohlenberg et al (1988); Soller and Mills (1991)</td>
<td>~0.24-0.1</td>
<td></td>
<td></td>
<td>Dockal (1996) indicated the Neuse Firm has priority over the Socastee firm and the two units are synonymous, but the &quot;Socastee&quot; name is still in use for sediments of this age in SC.</td>
<td>*Age is still fairly unclear in spite of years of study, with part of the problem stemming from different definitions of various units within the region: the firm is typically assigned an age of ~40-180 ka (McCarron et al 1982; Wohlenberg et al 1988; Soller and Mills 1991). But, O'Hara and Heritage (1990) indicated the age is younger, dating to late isotope stage 5 (~40-70 ka), which conforms with what Dockal (1996) found for the age of the Neuse Firm (Keefer Formation) in southern NC, which is thought to be synonymous with the Socastee Firm (~75-50 ka). Mills et al (2003) indicated the dates of O'Hara and Heritage (1990) would be consistent with an astronomically calibrated comparison with the Sea Island VGP data.</td>
<td>Correlated with the Hampton Beach (NC), Norfolk (VA), and Shirley, Tabb or Wedge Falls (MD) Firms (McCarron et al 1982); correlated with the Hampton Beach Firm and the Shirley Firm and the Wedgefield Member of the Tabb Firm (Soller and Mills 1991); correlated with the Hampton Beach Firm (Harr 1996; Dockal 1996; Soller and Mills 1991).</td>
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<tr>
<td>Ladson</td>
<td>McCarron et al (1990)</td>
<td>~0.45-0.40</td>
<td></td>
<td></td>
<td>Named by Mackie (1959) in the Charleston area, may be equivalent to the Canepatch Firm of the Myrtle Beach area of Durr (1971), but the &quot;Ladson&quot; name is older and thus retained (Wetmore et al 1994). The unit is interpreted as a fluvial/deltaic deposit (Wohlenberg et al 1988). Like the Canepatch Firm, the unit is also referred to as unit 4B (Wetmore et al 1994; Bowen 2009).</td>
<td></td>
<td>Equivalent to the upper Talmadge terrace of Colquhoun (1974) (Wohlenberg et al 1988); considered a Charleston area equivalent of the Canepatch Firm of Myrtle Beach (Corrado et al 1996; Wetmore et al 1994; Bowen 2009).</td>
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Table S2.2.2: Part 19. Southeast and central South Carolina

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<th>Correlation</th>
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<th>General regional notes</th>
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<tbody>
<tr>
<td>Southeast &amp; central SC</td>
<td>Pringlestown beds</td>
<td></td>
<td>&lt;3.1 &amp; 3.2</td>
<td></td>
<td>Wissms et al. (1994) indicated Placocene and early Miocene age; the age cited here was determined via stratigraphic position and based on ages of other units.</td>
<td>Informal unit named by Wissms et al. (1994) for sediments near Charleston; considered an extension to sapon deposit.</td>
<td>The unit may underlie the Waccamaw/Firm and overlie the Raylor Firm (Wissms et al. 1994).</td>
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<tr>
<td>Raylor</td>
<td></td>
<td></td>
<td>3.0-4.1</td>
<td></td>
<td>Ward and Huddleston (1998) Markewich et al. (1990); Campbell and Campbell (1995). Campbell (pers comm 2013) (For lower data)</td>
<td>Cooke (1936) originally named the Raylor Mill as deposits in SC that are older than the Duplin. It is considered to be a lower Miocene age. Raylor deposits were left behind from eroding Miocene shoreline and are similar in age to the Goose Creek Limestone and should be abandoned. Campbell (1992) rejected the Raylor Firm on the basis that the only known locality that matches the original type description is hidden by a swamp, but this has not been newly by these authors in subsequent publications. (E.g. Campbell and Campbell 1995). L. Campbell (pers comm 2013) indicated the lower Goose Creek Limestone as found at the type section lies stratigraphically under the Raylor beds, and the Raylor equivalent strata to the east are referred to as “upper Goose Creek Limestone”, which include the “Upper Millstone Deposit”. The Raylor Firm is thought to be within some 9 of Argonne or N20 (Huddleston 1990; Crenin 1991).</td>
<td>Correlated with the Duplin Firm and exposed member of the Yorktown Firm (Crane et al. 1994; Ward and Huddleston 1998) and to the Jackson Bluff Firm (Huddleston 1990); the Raylor Firm interfingers with the correlative Duplin Firm in SC and extends southward into GA (Ward et al. 1994); correlated with the lower Pinecrest Beds, Jackson Bluff, Duplin and Raylor firms and the Rushmore and Morgants Beach Members of the Yorktown Firm (Crane 1995). Allmendinger et al. (1996) correlated with Yorktown and Duplin Firms on the basis of evidence (Bosworth and Wigglesworth 1992); the Raylor Firm was placed above the Duplin Firm in Wissms and Lewis (2001); Campbell and Campbell (1992) argued that the Goose Creek and Raylor Firms are older than the Duplin Firm at the Natural Well stratigraphic section. The Raylor Firm is equivalent to the upper Goose Creek Firm and overlies the lower Goose Creek Firm, in Ward and Huddleston (1998); the Raylor Firm is deposited at below the Goose Creek Firm (but the authors later revised their opinions, pers comm.). The Raylor, Duplin and Jackson Bluff Firms are correlated (Huddleston pers comm 2013).</td>
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Table S2.2.2: Part 20. Southeast and central South Carolina

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<th>Correlation</th>
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<th>General regional notes</th>
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<tbody>
<tr>
<td>Goose Creek</td>
<td>Limestone</td>
<td>Upper</td>
<td>3.75-3.55</td>
<td>Campbell and Campbell (1995); Ward and Huddleston (1988)</td>
<td>The unit was originally mapped from Charleston, SC (Taylor 1848; Wemers et al 1982); Campbell and Campbell (1995) indicated the unit is found in NE GA, eastern SC and SE NC. Campbell and Campbell (1995) suggested the Kauror Marl unconformably overlies the Goose Creek Limestone, which is a reversed relationship from previous publications. According to Campbell and Campbell (1995), the Kauror Firm and upper Goose Creek Limestone firm appear to be coeval lithofacies distinct from and older than the Duplin Firm at the Natural KC stratotype. L. Campbell (pers comm 2013) indicated the lower Goose Creek Limestone as found at the type section lies stratigraphically under the Kauror sands, and Kauror equivalent strata to the east are referred to as &quot;upper Goose Creek Limestone&quot; and include the &quot;Bear Bluff&quot; deposits. Ward (pers comm 2012) does not support the name Goose Creek.</td>
<td>According to Campbell and Campbell (1995), the upper Goose Creek Limestone firm and the Kauror Firm appear to be laterally equivalent, coeval lithofacies, and both are older than the Duplin Firm. Here, the Duplin Firm is wholly equivalent to the Kauror Firm. Ward and Huddleston (1988) placed the Goose Creek Firm above the Kauror Firm in their stratigraphic chart, which Huddleston (pers comm 2013) indicated was incorrect and was reversed in later publications by these authors.</td>
<td>According to Campbell and Campbell (1995), the Duplin Marl unconformably overlies the lower Goose Creek Limestone, a reversal of the inferred stratigraphic sequence presented in other reports.</td>
<td>The Bear Bluff is congruent with the upper Goose Creek Limestone Firm (Campbell and Campbell 1995); this relationship is not supported in this compilation, with the Bear Bluff Firm younger than the Goose Creek Firm here.</td>
<td>The Bear Bluff is complicated by a lack of fossils within the deposits and by differing definitions of stratigraphic units (e.g., should they be defined based on morphology/elision vs. lithology vs. biostratigraphy); work has just begun to address these questions. As a result, although numerous papers have been published on the Pleistocene stratigraphy of the South Carolina Coastal Plain, different groups of stratigraphers have proposed quite different stratigraphic correlations using different mixes of data. For example, Duer (2008) indicated the following formations for the Pliocene of SC: and SE VA: Westville, Indianola, Tom Blakes Hill Beds, Pamlico, Princess Anne and Silver Bluff.</td>
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<tr>
<td></td>
<td></td>
<td>Lower</td>
<td>4.0-3.3</td>
<td>Campbell and Campbell (1995)</td>
<td>The Wabasso Beds is an informal name applied to lower Pliocene, phosphatic, colorless, and minute flintiferous, varably argillaceous, silty, fine-grained to very fine grained sand in the subsurface of the coastal areas of GA, southern SC, and eastern FL (Huddleston 1988). Scott (2001) indicated the Wabasso Beds are also in the Pool River firm in S Florida, but that they do not overstep at the surface. The Wabasso Beds were treated as a formal unit by Krantz (1991), but there seems to be no evidence for this, although Huddleston (pers comm 2013) would like to see them formalized.</td>
<td>The unit is included within zone P.3 or in N.18 (Huddleston 1988); the unit is considered no older than 5.7 Ma and no younger than 4.2-4.0 Ma (Markewich et al 1992).</td>
<td>The unit is probably time equivalent to the Sunken Meadow Member of the Yorktown Firm in SE VA and NE NC.</td>
<td>Grantz (1993) indicated the lower Duplin Firm is time equivalent to the Sunken Meadow Member of the Yorktown Firm and Wabasso Beds, but this relationship was not supported in this compilation; here, the Duplin Firm is younger than the Wabasso Beds and the Sunken Meadow Member.</td>
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Table S2.2.2: Part 21. Central/northeast SC & southeast North Carolina

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<th>Correlation</th>
<th>Other opinions on correlations</th>
<th>General regional notes</th>
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<tbody>
<tr>
<td>Neuse/Seascape/</td>
<td></td>
<td></td>
<td>0.2-0.1</td>
<td></td>
<td>Strata of this age are referred to by various names in the region; the Neuse Unit &amp; Southeastern Riasocene deposits in NC. However, Mienz and Hildreth (1971) and Villard and Wheeler (1974) unit contain many different lithologies and was not used by these authors, with the type section redefined as the Neuse Unit. Backwell (1984) also included sediments assigned to the Neuse Unit and abandoned the Neuse Unit. Docks (1996) indicated the name Neuse Unit, which includes the Cape Fear Group, has priority over the Neuse Unit and should be in use. The Neuse Unit is still used in publications for sediments in NC, while other authors use these sediments as the Neuse/Beaufort firm as even the Neuse/Beaufort firm.</td>
<td>Age unclear in spite of years of study (see Muijs et al. 2003); Muijs et al. (1986) using amino acid racemization analysis found an age for St. Johns Complex of 329 ka or even older, with a further study (Muir et al. 1975) indicating an age of 330-350 ka. Prasad (1995) performed U-series dating on shell of the Neuse Cut and obtained an age of 62 ka. Docks (1996) did not assign these deposits to the Neuse Cut material and found an age of 28-34 ka (Docks 1996), but those dates are probably too young according to the authors with an actual age closer to 72-75 ka. Muijs and Hildreth (1990) assigned the Neuse Unit in SC and indicated an age younger than typically assigned, around 80 ka. Muijs et al. (1993) indicate the dates of Hildreth and Muijs (1990) would be consistent with amino acid racemization with the Sea Islands VSP data.</td>
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<tr>
<td>Neuse/Beaufort/</td>
<td></td>
<td></td>
<td>0.6-0.31</td>
<td></td>
<td>Named for deposits near Hart County. The unit lies above the Penfield/Glacial Terrace (Dollar and Wells 1971). The Neuse Unit is the first to occur in time along the Intracoastal Waterway (Docks 1996), and thus was not used by Hildreth (1996). However, the Neuse Unit is still in use today. Deposits of the Neuse Unit are referred to as SC or the South Carolina Formation by Muijs et al. (1991) and Wells et al. (1989). According to Villard and Wheeler (1974), the unit occurs in C and SC; Buddington (pers. comm. 2013) indicated the Neuse Unit also occurs in the Neuse River basin and, as such, is not in favor of the name.</td>
<td><em>In spite of many years of study, serious ambiguities about the age of the Neuse Unit &amp; Southeastern Riasocene deposits remain unresolved</em> (Muijs et al. 2003, p. 111). Typically, the upper age was cited as the middle Neuseocene (Dollar 1975) or ~300 ka e.g., Muijs et al. (1986) 360-370 ka, Cowin et al. (1983) 530 ka, Wells (1989).</td>
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<tr>
<td>Neuse/Beaufort/</td>
<td></td>
<td></td>
<td>0.4-0.31</td>
<td></td>
<td>Named for deposits near Hart County. The unit lies above the Penfield/Glacial Terrace (Dollar and Wells 1971). The Neuse Unit is the first to occur in time along the Intracoastal Waterway (Docks 1996), and thus was not used by Hildreth (1996). However, the Neuse Unit is still in use today. Deposits of the Neuse Unit are referred to as SC or the South Carolina Formation by Muijs et al. (1991) and Wells et al. (1989). According to Villard and Wheeler (1974), the unit occurs in C and SC; Buddington (pers. comm. 2013) indicated the Neuse Unit also occurs in the Neuse River basin and, as such, is not in favor of the name.</td>
<td><em>In spite of many years of study, serious ambiguities about the age of the Neuse Unit &amp; Southeastern Riasocene deposits remain unresolved</em> (Muijs et al. 2003, p. 111). Typically, the upper age was cited as the middle Neuseocene (Dollar 1975) or ~300 ka e.g., Muijs et al. (1986) 360-370 ka, Cowin et al. (1983) 530 ka, Wells (1989).</td>
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<tr>
<td>Neuse/Beaufort/</td>
<td></td>
<td></td>
<td>0.4-0.31</td>
<td></td>
<td>Named for deposits near Hart County. The unit lies above the Penfield/Glacial Terrace (Dollar and Wells 1971). The Neuse Unit is the first to occur in time along the Intracoastal Waterway (Docks 1996), and thus was not used by Hildreth (1996). However, the Neuse Unit is still in use today. Deposits of the Neuse Unit are referred to as SC or the South Carolina Formation by Muijs et al. (1991) and Wells et al. (1989). According to Villard and Wheeler (1974), the unit occurs in C and SC; Buddington (pers. comm. 2013) indicated the Neuse Unit also occurs in the Neuse River basin and, as such, is not in favor of the name.</td>
<td><em>In spite of many years of study, serious ambiguities about the age of the Neuse Unit &amp; Southeastern Riasocene deposits remain unresolved</em> (Muijs et al. 2003, p. 111). Typically, the upper age was cited as the middle Neuseocene (Dollar 1975) or ~300 ka e.g., Muijs et al. (1986) 360-370 ka, Cowin et al. (1983) 530 ka, Wells (1989).</td>
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<tr>
<td>Neuse/Beaufort/</td>
<td></td>
<td></td>
<td>0.4-0.31</td>
<td></td>
<td>Named for deposits near Hart County. The unit lies above the Penfield/Glacial Terrace (Dollar and Wells 1971). The Neuse Unit is the first to occur in time along the Intracoastal Waterway (Docks 1996), and thus was not used by Hildreth (1996). However, the Neuse Unit is still in use today. Deposits of the Neuse Unit are referred to as SC or the South Carolina Formation by Muijs et al. (1991) and Wells et al. (1989). According to Villard and Wheeler (1974), the unit occurs in C and SC; Buddington (pers. comm. 2013) indicated the Neuse Unit also occurs in the Neuse River basin and, as such, is not in favor of the name.</td>
<td><em>In spite of many years of study, serious ambiguities about the age of the Neuse Unit &amp; Southeastern Riasocene deposits remain unresolved</em> (Muijs et al. 2003, p. 111). Typically, the upper age was cited as the middle Neuseocene (Dollar 1975) or ~300 ka e.g., Muijs et al. (1986) 360-370 ka, Cowin et al. (1983) 530 ka, Wells (1989).</td>
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### Table S2.2.2: Part 22. Central/northeast SC & southeast North Carolina

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<th>Correlation</th>
<th>Other opinions on correlations</th>
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<tbody>
<tr>
<td>Waccamaw</td>
<td>upper</td>
<td></td>
<td></td>
<td>1.7-1.5</td>
<td>Graybill et al. (2009); Badryka et al. (2010)</td>
<td>The youngest change in polarity (Matayama Reversal Chron to Sherwood Normal Chron at about 0.7 Ma) occurs between the Waccamaw (Krause) and Campaspaton (normal) formations near Myrtle Beach, SC (Usatoff 2002).</td>
<td>Bybells (1990) indicated an age range of 1.8-1.4 Ma, which is close to that cited here; same for Aker et al. (1972) of 1.6-0.7 Ma, which is younger, and Bybells (1981a,b) and unpub data cited within Lyons (1993) of 1.6-1.1 Ma. Campbell (1993) and Campbell and Campbell (1995) indicated an older age for both the lower and upper Waccamaw Fm (2.2-1.9 Ma or 2.4-1.5 Ma for the upper), but this is contrary to the recent dating work done (Graybill et al. 2009 and Badryka et al. 2010) and not used here. Mabey and Thayer (2001) indicated a late Pleistocene age of 130-10 ka.</td>
<td>The unit underlies the Canocochclidean Fm, overlies the lower Bluff Fm, and correlates with the James City Fm (Krause et al. 1991); Buckwelder and Ward 1979; correlative with the Galoshatchie Fm based on faunal similarity (Lyons 1993). Campbell and Campbell (1993) agreed that the upper Waccamaw Fm is correlated with the Santee Fm of the James City and Galoshatchie Fms (Krause et al. 1991); the James City Fm is a correlate (Krause 1996).</td>
<td>Campbell (1992) indicated this unit is essentially equivalent with the Cypresshead Fm, which is not supported in this report, as the Cypresshead is older here.</td>
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| Waccamaw                         | lower  |           |        | 2.1-1.7   | Graybill et al. (2009); Badryka et al. (2010); Mcdarph et al. (2011) | The Waccamaw is divided into a lower and upper unit by an unconformity (Krause 1992; Aker 1972; Ward et al. 1994; Campbell and Campbell 1993). | Graybill et al. (2009) is listed in support, but these authors found a highly younger age for the lower Waccamaw Fm of 1.55 Ma, in addition to an age of 2 Ma and 1.8 Ma; Campbell (1993) and Campbell and Campbell (1995) indicated an older age for both the lower and upper Waccamaw Fm (2.5 or 2.4 Ma for the lower), but this is contrary to the recent dating work done and is not used here. Aker (1972) and Krantz (1991) indicated an age of 1.9-1.7 Ma, which is similar to the age cited here. | The lower Waccamaw Fm is correlated with the Bacon Castle Fm (Krause 1991). |}
Table S2.2.2: Part 23. Central/northeast SC & southeast North Carolina

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<th>Age (Ma)</th>
<th>Supporting References</th>
<th>Notes</th>
<th>Other age details or opinions</th>
<th>Correlation</th>
<th>Other opinions on correlations</th>
<th>General regional notes</th>
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<tbody>
<tr>
<td>Central/northeast SC</td>
<td>Bear Bluff</td>
<td></td>
<td></td>
<td>2.6-2.1</td>
<td>McCarron et al (1993); Krantz (1993); Markewich et al (1992); Campbell (1992)</td>
<td>The Bear Bluff Fm is of southeastern NC and northeastern SC, lies above the Duplin Fm. Markewich et al (1992). Campbell (1992) concluded that the upper Goose Creek Limestone and the type Bear Bluff are the same unit based on faunal and lithological similarity and recommended that the Bear Bluff Fm be abandoned (the authors argued that the unit is actually part of the upper Goose Creek Limestone at the stratotype of the Bear Bluff Fm), but the Bear Bluff Fm is still in use by the USGS. Campbell and Campbell (1995) similarly argued that the Bear Bluff stratotype is pre-Natural W. Duplin Fm in age, which is contrary to other stratigraphic opinions, and is similar to the upper Goose Creek Limestone. Campbell (pers comm 2013) indicated that the name “Bear Bluff” has generally been misapplied to facies and lithologically dissimilar beds that in fact are much younger, after the 2.5 Ma boundary, equivalent to the Chown River Fm (old Chasometown). L. Campbell (pers comm 2013) indicated that the placement of the Bear Bluff Fm is younger than the Razor Fm is based on Dabar including the lower Wisconsinan Fm argonitic beds as the datable material in his composite “Bear Bluff”, and that the unit is actually similar to the upper Goose Creek Limestone and/or Razor Fm.</td>
<td>All ages roughly point to about 2.5 Ma, with some minor differences: McCarron et al (1992) cited an age of 2.4-3.8 Ma; Krantz (1991) cited an age of 2.5-1.9 Ma; Campbell (1993) cited an age of 2.5 Ma, and suggested older ages obtained (e.g., 3.7 Ma) were from older sediments like the Goose Creek Limestone. McCarron et al (1992) cited an age of PLS (roughly equivalent to somewhere within 3.1-2.5 Ma); L. Campbell (pers comm 2013) noted that the Bear Bluff Fm is as old as 3.8 Ma or older and equivalent to the Razor Fm. Correlated with the Chown River Fm (Ward et al 1991); correlated with the Chown River Fm and Cypresshead Fm (Krantz 1991) (note that the Cypresshead Fm is older in this compilation, and thus not correlated with the Bear Bluff Fm here); the Bear Bluff Fm is correlated with the Chown River Fm and also potentially with the upper Pinecrest Beds of Florida (Allmon et al 1996a); Moolman (pers comm 2013) indicated the Bear Bluff Fm is younger than the Citronelle or Cypresshead Fms and not correlated with the Citronelle Fm.</td>
<td>Campbell (1993) indicated the molluscan fauna are younger than that of the Pinecrest Beds but older than that in the Caloosahatchee Fm, however, here the Pinecrest Beds are partially equivalent to the Bear Bluff Fm; Markewich et al (1992) indicated the unit lies above the Duplin Fm and is equivalent to the Cypresshead Fm (GA) and Nanuki Fm of NE FL, but while partially time equivalent with the Noshap Fm, the unit is younger than the Cypresshead Fm in the compilation.</td>
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Table S2.2.2: Part 24. Central/northeast SC & southeast North Carolina

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<th>Other age details or opinions</th>
<th>Correlation</th>
<th>Other opinions on correlations</th>
<th>General regional notes</th>
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<tbody>
<tr>
<td>Durbin</td>
<td>3.3-3.1</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Members of the Yorktown Fm are mapped as far south as the Neuse River in NC, but south of the river they cannot be differentiated and are placed in the Durbin Fm (Krantz 1991). The Yorktown Fm is equivalent to the Beaufort Fm in SC. Correlate with the Yorktown Fm in SC and the Beaufort Fm in NC.</td>
<td>Krantz (1991) indicated the lower Durbin Fm is 3.3-3.2 Ma.</td>
<td></td>
<td></td>
<td>The Pensacola Fm (Owen 1989) was abandoned by Harkness (1988) but reinterpreted by Wescott and Lemoine (1999) and used by Soller and Mills (1991). Unit is not included in this column because the North Carolina Geological Survey does not subscribe to using terrace formation names when naming units, however, changing stratigraphic understanding and nomenclature could reintroduce units.</td>
</tr>
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Table S2.2.2: Part 25. Central/northeast SC & southeast North Carolina

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<th>Correlation</th>
<th>Other opinions on correlations</th>
<th>General regional notes</th>
</tr>
</thead>
<tbody>
<tr>
<td>Goose Creek Limestone</td>
<td>upper</td>
<td></td>
<td>3.75-3.55</td>
<td>Ward and Hudleston (1988); Campbell and Campbell (1995)</td>
<td>The unit was originally mapped from Charleston, SC, by Tsureyama (1966a). Weems et al. (1982). Campbell and Campbell (1995) indicated the unit is found in northeastern SC and SE NC. Campbell and Campbell (1995) suggested that the Razor Marl unconformably overlies the Goose Creek Limestone, which is a reversed relationship to previous publications. According to Campbell and Campbell (1995), the Razor Marl and upper Goose Creek Limestone appear to be coeval lithofacies distinct from and older than the Dupo Fm at the Natural Well stratotype. J. Campbell (pers. comm. 2003) indicated that the upper Goose Creek Limestone is found at the type section lies stratigraphically under the Razor sands, and is the east, Razor-equivalent strata are referred to as &quot;upper Goose Creek Limestone&quot; and include the &quot;Bear Bluff&quot; deposits.</td>
<td>Age cited at 3.5-3.2 Ma or zone NK 13 to mid-NK 14 (Hykell 1990).</td>
<td>According to Campbell and Campbell (1995), the upper Goose Creek Limestone and the Razor Marl appear to be laterally equivalent, coeval lithofacies, and both are older than the Dupo Fm. The current compilation has the Dupo Fm only equivalent to the Razor Marl. Ward and Hudleston (1988) placed the Goose Creek above the Razor Fm and in their stratigraphic chart, which Hudleston (pers. comm. 2013) indicated is incorrect and was reversed in later publications by these authors.</td>
<td>The Bear Bluff Fm is congruent with the upper Goose Creek Limestone (Campbell and Campbell 1995); however, this relationship is not supported by this compilation, as the Bear Bluff Fm is younger than the Goose Creek Limestone.</td>
<td>Table 2.13: Quaternary zone NN 21 of Martini (1971) around 970 ka (Weems et al. 1994); equivalent beds in the Stallville Quadrangle yield J to middle NN 21 ages of 700 ka (Sanders 1985). The Fosheley Fm is said to overlie the lower Wisconsinan Fm and underlie the upper Wisconsinan Fm and with unit QS of McCarron et al. (1986) and Cristoforetti (1957) (from Solier and Mills 1991). See overview of stratigraphic naming issues and associated problems of dating formations in Corrada et al. (1986).</td>
</tr>
<tr>
<td>Goose Creek Limestone</td>
<td>lower</td>
<td></td>
<td>4.0-3.8</td>
<td>Ward and Hudleston (1988); Campbell and Campbell (1995)</td>
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Table S2.2.2: Part 26. Central and northeast North Carolina

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<th>Unit (Ma)</th>
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<th>Correlation</th>
<th>Other opinions on correlations</th>
<th>General regional notes</th>
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<tbody>
<tr>
<td>Core Creek Sand (informal unit) &amp; Ozo</td>
<td></td>
<td></td>
<td>&lt;0.18</td>
<td></td>
<td>Numerous names have been applied to middle and upper Pleistocene units between the Cape Fear and Neuse Rivers in NC, including the Scoutsaw, Campbark, and Flanner Beach Fms (Harms 1996). Older and fossiliferous (1963) named the “Pleistocene” deposits the Flanner Beach Fm and rejected the usage of the Pleistocene Fm (Ward 2008). Fallaw and Wheeler (1932) rejected usage of the Flanner Beach Fm and indicated that the Flanner Beach Fm includes deposits of Koury Clay and Croatan Fms and is not a distinct lithological unit. Mean and Hickey (1979) adopted the Flanner Beach Fm for use by the USGS and restricted the unit to exclude the Manseetee Ridge sand and younger Pleistocene beds. Blackwelder (1981) reused the Flanner Beach Fm to include sediments previously assigned to the Koury Fm and abandoned usage of the Neuse Fm.</td>
<td>*The Flanner Beach Fm is typically assigned to the middle Pleistocene (Harms 1996; Dorris et al. 1939; Dorris 1939), with an age of 240-280 ka (McCartan et al. 1982; Miller 1985). However, younger dates for correlative sediments of the Scoutsaw and Nuese Fms suggest that the age of the Flanner Beach Fm may be younger, around the Sangamonian interglacial (~125-75 ka), which Phillips (1950) used as an age for the Fm. Dorris et al. (1939) cited a middle Pleistocene age for lower Croatan sediments, but also indicated a possible age of 2.5-2.6 Ma. This older age could result from the Croatan Fm = James City Fm, as the name has been in use. Crexie et al. (2001) found an age of 1.5 Ma for a coral from this Fm, but the corals may have been reworked from lower units. Britell et al. (2001) discussed some of the ambiguities in dating Quaternary Fms in the Atlantic Coastal Plains.</td>
<td>Correlated with the Scoutsaw, Norfolk (new Shinnecock Fm) and Nuese Fms (McCartan et al. 1982). Correlated with the Great Bridge Fm of southeastern VA (new Acaralana Fm and with the Scoutsaw Fm of southeastern NC and northeastern SC (Miller 1985). Correlated with the Nuese Fm.</td>
<td>Correlated with the Nuese Fm.</td>
<td>Miller (1955) indicated the Great Bridge Fm of southeastern VA (new Acaralana Fm) is correlable, but the unit is younger than the Flanner Beach Fm in this completion.</td>
</tr>
<tr>
<td>Flanner Beach</td>
<td></td>
<td></td>
<td>&lt;0.14-0.16</td>
<td></td>
<td>*The Flanner Beach Fm is typically assigned to the middle Pleistocene (Harms 1996; Dorris et al. 1939; Dorris 1939), with an age of 240-280 ka (McCartan et al. 1982; Miller 1985). However, younger dates for correlative sediments of the Scoutsaw and Nuese Fms suggest that the age of the Flanner Beach Fm may be younger, around the Sangamonian interglacial (~125-75 ka), which Phillips (1950) used as an age for the Fm. Dorris et al. (1939) cited a middle Pleistocene age for lower Croatan sediments, but also indicated a possible age of 2.5-2.6 Ma. This older age could result from the Croatan Fm = James City Fm, as the name has been in use. Crexie et al. (2001) found an age of 1.5 Ma for a coral from this Fm, but the corals may have been reworked from lower units. Britell et al. (2001) discussed some of the ambiguities in dating Quaternary Fms in the Atlantic Coastal Plains.</td>
<td>Correlated with the Scoutsaw, Norfolk (new Shinnecock Fm) and Nuese Fms (McCartan et al. 1982). Correlated with the Great Bridge Fm of southeastern VA (new Acaralana Fm and with the Scoutsaw Fm of southeastern NC and northeastern SC (Miller 1985). Correlated with the Nuese Fm.</td>
<td>Correlated with the Nuese Fm.</td>
<td>Correlated with the Nuese Fm.</td>
<td>Correlated with the Nuese Fm.</td>
</tr>
<tr>
<td>James City</td>
<td></td>
<td>lower</td>
<td>2.1-1.9</td>
<td></td>
<td>The James City Fm was initially called the Croatan Fm by Doll (1929), and this name is probably still valid (Rado 1989), but the “James City” name has predominated. Blackwelder (1981) renamed the lower Croatan deposits as the Chocowa Fm and the upper Croatan deposits as the James City Fm. The Croatan name is still in use by some (e.g., Dorris et al. 1999). According to Ward et al. (1999), correlative deposits are assigned to the Waccamaw Fm south of New Jersey, and the James City Fm actually contains several beds of slightly different ages of similar lithology, but with different mollusk assemblages, all within the early Pleistocene. This was later echoed by Ward (2008), when he stated that the James City Fm is divided into two deposits, both of which are roughly equivalent to the two Waccamaw Fm deposits. However, H. Campbell (pers. comm. 2015) indicated Ward and Blackwelder (1987) mislabeled the name James City at Aurora, and the unit in question is an equivalent to the upper Waccamaw (and older than the stratotype of the James City Fm). Campbell also indicated the James City is not a Seaboard Fm equivalent (2.1-1.1 Ma), as is shown here, since none of the distinctive index fossils that mark the Seaboard Fm have been found in the James City Fm; thus, the dates here may be too old for the upper or type James City Fm. The type James City equivalent both in South Carolina are often called the Waccamaw Fm (L. Campbell pers. comm. 2015).</td>
<td>Slightly younger ages are cited by Miller (2001) of 1.4-0.7 Ma, and by McCartney et al. (1982) of 1.6-1.1 Ma. The James City Fm unconformably overlies the Chocowa Fm in NC (Ward and Blackwelder 1987; Rado 1989), but the unit correlates with the Waccamaw Fm (Blackwelder and Ward 1979; Blackwelder 1981b; Campbell 1990b).</td>
<td>The James City Fm correlates with the Waccamaw Fm.</td>
<td>The James City Fm is not a Seaboard Fm equivalent (2.1-1.1 Ma), as is shown here, since none of the distinctive index fossils that mark the Seaboard Fm have been found in the James City Fm; thus, the dates here may be too old for the upper or type James City Fm. The type James City equivalent both in South Carolina are often called the Waccamaw Fm (L. Campbell pers. comm. 2015).</td>
<td>Campbell (pers comm 2015) indicated the James City and Seaboard Fms are not equivalent and do not share characteristic index fossils, but here they are shown as time equivalent.</td>
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Table S2.2.2: Part 27. Central and northeast North Carolina

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<th>Notes</th>
<th>Other age details or opinions</th>
<th>Correlation</th>
<th>Other opinions on correlations</th>
<th>General regional notes</th>
</tr>
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<tbody>
<tr>
<td>Bacon's Castle</td>
<td></td>
<td></td>
<td>-2.1-2.0</td>
<td></td>
<td>Ramsey (1886, 1902); Crown (1901)</td>
<td>Johnson and Bergquist (1989) indicated age determination is difficult because there are no shell fossils or radiometrically datable material, but indicated a Pleistocene age; Minn (1989) and Radz and Evers (1985) both considered the unit to be of late Pleistocene age.</td>
<td>Krantz (1991) indicated an age of 1.5-1.7 Ma, but dating was tentative; Ramsey (1992) indicated an age of 2.3-2.0 Ma.</td>
<td>The Bacon's Castle Fm. unconformably overlies the Yorktown and Chowan River Fms. in eastern VA (Krantz, 1991); the unit correlates with the upper Beaver Dam Fm. (Ramsey, 1992); correlates with the lower Waccamaw Fm (Krantz, 1991).</td>
<td>The chart of Carter et al (2003) indicated the Bacon's Castle Fm is equivalent to the Chowan River Fm, but Krantz (1991) indicated the unit overlies the Chowan River Fm.</td>
<td>Many of the Tidewater units in North Carolina are not fossiliferous, either a pseudo or as a result of trenching, and thus correlation and dating on these units is difficult. The stratigraphy has been one of flux, with many units having been named and re-named. Work is ongoing in the region, and thus this particular compilation is sure to change in the future. These Tidewater Fms. are mapped as Walltown (1990) in southeastern Virginia, was abandoned by Youell (1988) and is now called Old Tidewater Formation (Johnson and Bergquist, 1989); however, the unit name is still in use in NC by some (e.g., Dennison et al. 1993); see Wehmeier et al. (2004a,b) and Wehmeier et al. (2010, 2011) for further information on Quaternary units and dating issues in N Carolina.</td>
</tr>
<tr>
<td>Colerain</td>
<td></td>
<td></td>
<td>2.6-2.1</td>
<td></td>
<td></td>
<td>Aged have been obtained anywhere from 3 to 1.9 Ma; see discussion in “Other age details or opinions” section.</td>
<td>Aged have been obtained anywhere from 3 to 1.9 Ma; Ags have centered around 2.5 or 2.1 Ma, but have also been found as old as 2.8 or 3.5 Ma. 2.4-1.9 Ma. (Bender unpublished data, from Blackwellder, 1985a,b); 2.2-1.9 Ma (Cromin, et al. 1961); 2.8 Ma (Grono, 1991). 2.1-2.1 Ma (Krantz, 1991). 2.3 Ma (Ramsey, 1988, 1992); 2.3 Ma (Campbell, 1993); 3.2 Ma from strat chart (Pascall, 1981); 3.2 Ma (Campbell and Campbell, 1995); 2.40-1.9 Ma (Holbrook, 2004).</td>
<td>Correlated with the Eustis Bluff and Cypresshead Fms (Krantz, 1991). Node that in this report, the Cypresshead and Eustis Bluff Fms. are not time equivalent, correlations and deposits in SC known as the Eustis Bluff Fm. Krantz (1991), correlate with Pinocott Rocks 2 and 3 of the ARIC Pit (Campbell, 1993); the Chowan River Fm. is older than the lower Waccamaw Fm., but younger than the Duplin River Fm. (Campbell and Campbell, 1995); the upper Pinocott Rocks units (units 4-2 sensu Altenm et al. 1996a) are separated by a horizon that may be equivalents of the Chowan River Fms. of VA and NC Carolinas (Dowsett and Wardill, 1995; Jones et al., 1992); the upper Bluff (SC), Caloosahatchee (FL) and Chowan River Fms. are equivalent (Blackwellder, 1985a,b; Ward and Blackwelder, 1987) (note that the Caloosahatchee Fm. is younger than the Chowan River Fm. in this report), equivalent to the Lower Waccamaw Fm. (Krantz, 1990).</td>
<td>Correlated with the Eustis Bluff and Cypresshead Fms (Krantz, 1991)</td>
<td>Colerain (1993) correlated the unit in part with the Moore House Member of the Yorktown Fm. of Krantz (1991) and Ward et al. (1991), which is restricted to 3.5 Ma, but the Yorktown Fm. (Moore House Member) is below the Chowan River Fm. in this compilation. Ward and Gillinsky (1991) did not agree with Campbell (1993). In equating the Moore House Member of the Yorktown Fm. with the Chowan River bed (Campbell and Campbell, 1993). Evidence suggests that the Chowan River Fm. is younger than 3.5 Ma.</td>
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<td>Central and northeastern North Carolina</td>
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Table S2.2: Part 28. Central and northeastern North Carolina
Table S2.2.2: Part 29. Central and northeast North Carolina

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<tr>
<td>Sunken Meadow</td>
<td></td>
<td></td>
<td>4.8-4.6</td>
<td>Cronin et al. (1991); Ward and Huddleston (1988); Krantz (1991).</td>
<td>The lowest initial transgressive deposit, the Sunken Meadow Member of the Yorktown Formation contains a somewhat different mollusk assemblage from the rest of the Yorktown Formation and is separated from the other units by a depositional hiatus (Blackwelder 1981).</td>
<td>Krantz (1991) indicated the Sunken Meadow Member is time equivalent with the Wabasso Beds and the lower Duplin Beds; the latter relationship is not supported here, but the Sunken Meadow Member is correlated with the Wabasso Beds.</td>
<td>Jones et al. (1991) and Williams et al. (2000) indicated the Sunken Meadow Member is equivalent to Unit 11 of the lower Pimlico, but this is not supported in this compilation; others (e.g., Scott 1995) indicated the Sunken Meadow Member is not correlated with any terrane sequences, at least not in S. Florida.</td>
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### Table S2.2.2: Part 30. Southeastern Virginia

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<th>Correlation</th>
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<th>General regional notes</th>
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<tr>
<td>Powellis Crossing</td>
<td></td>
<td></td>
<td></td>
<td>Oaks and Coch (1963); Spencer and Campbell (1967); it now includes the Sand Bridge at top and Sandbar Bridge, which were reduced to member rank.</td>
<td>The Sand Bridge Fm, now part of Powellis Crossing, has a radiocarbon age of 40 Ka (Oaks and Coch 1963); the Sand Bridge is Wisconsin in age (96-40 Ka) (Coch 1953).</td>
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<tr>
<td>Acroclade</td>
<td></td>
<td></td>
<td></td>
<td>Oaks and Coch (1963); Spencer and Campbell (1967)</td>
<td>Little information could be found on this Fm, which is not used extensively in the literature; the Kynnsville, Norfolk, and Great Bridge Fms were reduced to member rank and assigned to the Acroclade Fm in the Virginia Beach area (Spencer and Campbell 1967).</td>
<td>Very few papers are available on this Fm; Oaks and Coch (1963) indicated a middle or late Pliocene age for the Fm; Spencer and Campbell (1967) indicated a late Pliocene age.</td>
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<tr>
<td>Tabb</td>
<td></td>
<td></td>
<td></td>
<td>Saiko (1995); Johnson and Benquist (1999); Johnson and Hobbs (1990); Mirmak et al (1995); Scott et al (2010)</td>
<td>The Tablo Fm, as mapped by Worthing (1950) in southeastern VA, is now called the Tablo Fm (Johnson and Benquist 1999); the unit is also mapped as the Norfolk Fm by Bick and Coch (1969) and others (see Hobbs 2004).</td>
<td>Saiko (1995) found an age for the Norfolk Fm of 71-85 Ka (The Norfolk Fm was divided into the Shirley and Tablo Fms); Mirkal et al (1995) (thought 72 Ka average for the Norfolk Fm was too young and resulted from loss of thorium due to burial in permeable, water-saturated deposits); however, these dates may be appropriate for younger units (Tablo Fm). Rather than the Shirley Fm, Mirkal et al (1995), Paraglio (1993), and Radioc (1999) cited a late Pliocene age; Johnson and Benquist (1999) indicated Mirkal (1982) dated sediments correlating with the Sedgefield Member at 71-85 Ka; correlating sediments at the Goma Pb in Norfolk, VA, were dated 125-80 Ka (Mirkal et al 1995); the majority of ages averaged around 70 Ka for the Sedgefield Member of the Tablo Fm (Scott et al 2002); Johnson and Hobbs (1990) suggested a 65-ka for the Pooquonsett Member of the Tablo Fm; Scott et al (2010) found OSL dates of 88-6-6.5 Ka and 45+4-5.2 Ka for the Pooquonsett Members; overall, the Fm appears to have been deposited during 115-3 or 135-40 Ka (Swift et al 2003, Scott et al 2010).</td>
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<td>Region</td>
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<td>Member</td>
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<td>Virginia</td>
<td>Shenandoah</td>
<td>&amp; Virginian</td>
<td>~3.9-4.0</td>
<td>S2</td>
<td>This formation was previously mapped as a series of the Shenandoah and Virginia formations (Sturt 1975)</td>
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<td>&amp; York</td>
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<td>~3.9-4.0</td>
<td>S2</td>
<td>This formation was previously mapped as a series of the Shenandoah and Virginia formations (Sturt 1975)</td>
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<tr>
<td></td>
<td>&amp; James</td>
<td></td>
<td>~3.9-4.0</td>
<td>S2</td>
<td>This formation was previously mapped as a series of the Shenandoah and Virginia formations (Sturt 1975)</td>
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<tr>
<td></td>
<td>&amp; Elizabeth</td>
<td></td>
<td>~3.9-4.0</td>
<td>S2</td>
<td>This formation was previously mapped as a series of the Shenandoah and Virginia formations (Sturt 1975)</td>
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<tr>
<td></td>
<td>&amp; Chickahominy</td>
<td></td>
<td>~3.9-4.0</td>
<td>S2</td>
<td>This formation was previously mapped as a series of the Shenandoah and Virginia formations (Sturt 1975)</td>
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<tr>
<td></td>
<td>&amp; York</td>
<td></td>
<td>~3.9-4.0</td>
<td>S2</td>
<td>This formation was previously mapped as a series of the Shenandoah and Virginia formations (Sturt 1975)</td>
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<tr>
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<td>&amp; James</td>
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<td>S2</td>
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<tr>
<td></td>
<td>&amp; Elizabeth</td>
<td></td>
<td>~3.9-4.0</td>
<td>S2</td>
<td>This formation was previously mapped as a series of the Shenandoah and Virginia formations (Sturt 1975)</td>
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<tr>
<td></td>
<td>&amp; Chickahominy</td>
<td></td>
<td>~3.9-4.0</td>
<td>S2</td>
<td>This formation was previously mapped as a series of the Shenandoah and Virginia formations (Sturt 1975)</td>
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Table S2.2.2: Part 32. Southeastern Virginia

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<th>Correlation</th>
<th>Other opinions on correlations</th>
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<tr>
<td>Southeastern Virginia</td>
<td>Windsor</td>
<td></td>
<td></td>
<td>2.0-1.9</td>
<td>Johnson and Bergquist (1989); Groot (1991); Pazzaglia (1993)</td>
<td>The unit was previously mapped as part of the Wisconsinian Fm by Clark and Miller (1950, 1952) and Wentworth (1951), and as the Kilby Fm by Moore (1956). The Windsor Fm was also formerly referred to as the Iberian Fm of Coch (1965), but the unit was abandoned by Coch (1968) and replaced with the Windsor Fm (Richards 1969). The Windsor Fm is said to overlie the Solley Fm, the Bacon Castle Fm, or the Yorktown Fm (Koch 1968), but the Solley Fm was abandoned by Johnson and Bergquist (1989), because the unit is composed primarily of unsorted and weathered material. The Fm was mapped into the Carolinas but has spotty outcrops (Boiler and Mills 1991). The lower part of the Windsor Fm as mapped by Bilic and Coch (1969) was redefined as the Bacon Castle Fm by Johnson and Bergquist (1989). The age is uncertain (Robbins 2004); dates for the lower James City Fm are provided here, given that the unit is a potential correlate (Krantz 1991). The Windsor Fm is potentially early Pleistocene (Johnson and Bergquist 1989; Groot 1991; Pazzaglia 1993), late or early Pleistocene (Rader and Evans 1993), or lower Pleistocene or upper Pliocene (Milligan et al. 2010). The Fm was placed at 0-400 ft below the chart in Swift et al. (2003), which seems too young.</td>
<td>Potentially correlated with the James City Fm (Krantz 1991).</td>
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<tr>
<td>Bacon Castle</td>
<td></td>
<td></td>
<td></td>
<td>2.1-2.0</td>
<td>Romsey (1988, 1992); Groot (1991)</td>
<td>Johnson and Bergquist (1989) indicated age determination for this unit is difficult because there are no shell fossils or radiometrically datable material, but suggested a Pliocene age; Mink et al. (1988) and Rader and Evans (1989) both considered the unit to be late Pleistocene.</td>
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</table>

The Bacon Castle unconformably overlies the Yorktown and Chowan River Fms in eastern VA (Krantz 1991); the unit is correlated with the lower Beaver Dam Fm (Raney 1992); correlated with the lower Waccamaw Fm (Krantz 1991). The Carter Chart indicates that Bacon Castle Fm is equivalent with the Chown River Fm, but Krantz (1991) indicated the unit overlies the Chowan River Fm.
### Table S2.2.2: Part 33. Southeastern Virginia

<table>
<thead>
<tr>
<th>Region</th>
<th>Formation</th>
<th>Member</th>
<th>Unit</th>
<th>Age (Ma)</th>
<th>Supporting References</th>
<th>Notes</th>
<th>Other age details or opinions</th>
<th>Correlation</th>
<th>Other opinions on correlations</th>
<th>General regional notes</th>
</tr>
</thead>
<tbody>
<tr>
<td>Chowan River</td>
<td></td>
<td>Colorado</td>
<td></td>
<td>2.4-2.1</td>
<td>Ages have been obtained anywhere from 3 to 1.9 Ma. Ages have centered around 2.5 or 2.1 Ma, but have been found as old as 2.8 or 3 Ma. 2.4-1.9 Ma (Bender unpublished data, from Blackwelder 1981a,b); 2.3-2.4 Ma (Kreis et al. 1988); 2.8 Ma (Groves 1991); 2.9-2.6 or 2.6-2.1 Ma (Kreis 1991); 2.5 Ma (Ramsay 1982); 2.5 Ma (Kreis et al. 1988); 3.4-2 Ma from their stratigraphic chart (Pazzaglia 1993); 3-2.8 Ma (Campbell and Campbell 1993); 2.40-1.9 Ma (Noble 2004).</td>
<td>Correlated with the Bear Bluff and Cypresshead Fms (Kreis 1991) [note that in this report, the Cypresshead and Bear Bluff Fms are not time equivalent]; correlated with deposits in SC known as the Bear Bluff Fm (Ward et al. 1991); correlated with Pinhook Beds 2 and 3 of the APAC Pit (Campbell 1993); the Chowan River fauna is older than the lower Waccamaw Fm, but younger than the Dublin Fm (Campbell and Campbell 1993); the upper Pinhook Beds (Kreis 1991); the upper Pinhook Beds (Groves 1991); the upper Pinhook Beds (Campbell and Campbell 1993); the upper Pinhook Beds (Kreis 1991); the upper Pinhook Beds (Campbell and Campbell 1993); the upper Pinhook Beds (Kreis 1991); the upper Pinhook Beds (Campbell and Campbell 1993); the upper Pinhook Beds (Kreis 1991); the upper Pinhook Beds (Campbell and Campbell 1993); the upper Pinhook Beds (Kreis 1991); the upper Pinhook Beds (Campbell and Campbell 1993); the upper Pinhook Beds (Kreis 1991); the upper Pinhook Beds (Campbell and Campbell 1993); the upper Pinhook Beds (Kreis 1991); the upper Pinhook Beds (Campbell and Campbell 1993); the upper Pinhook Beds (Kreis 1991).</td>
<td>Campbell (1993) correlated the unit in part with the Moore House Member of the Yorktown Fm of Kreis (1991) and Ward et al. (1991), which is restricted to 3.5 Ma, but the Yorktown Fm (Moore House Member) is below the Chowan River Fm in this compilation. Ward and Illinsky (1995) did not agree with Campbell (1993) in equating the Moore House Member of the Yorktown Fm with the Chowan River beds (Campbell and Campbell 1993). Evidence suggests that the Chowan River Fm is younger than 3.5 Ma,</td>
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### Table S2.2.2: Part 34. Southeastern Virginia

<table>
<thead>
<tr>
<th>Region</th>
<th>Formation</th>
<th>Member</th>
<th>Unit</th>
<th>Age (Ma)</th>
<th>Supporting References</th>
<th>Notes</th>
<th>Other age details or opinions</th>
<th>Correlation</th>
<th>Other opinions on correlations</th>
<th>General regional notes</th>
</tr>
</thead>
<tbody>
<tr>
<td>Moore House</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Hazel (1983); Snyder et al. (1985); Croxson (1991); Dowsett and Cronin (1990); Kranz (1991); Dowsett and Wiggs (1992)</td>
<td>Campbell [1992] indicated the members proposed by</td>
<td>4.8-2.8 Ma, with the upper limit near the middle of zone N21.</td>
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<tr>
<td>Mergants Beach</td>
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<td></td>
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<td></td>
<td></td>
<td></td>
<td></td>
<td>4.6-3.1</td>
<td></td>
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</tr>
<tr>
<td>Yorktown</td>
<td></td>
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<td></td>
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<tr>
<td>Rathsmore</td>
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</table>

The Moore House Member is the youngest unit and does not seem to be correlated with anything in SC or GA [Kranz, 1991]: the Yorktown Fm is the same age as the Duplin and Rayor Fms [Cronin et al, 1984; Ward and Huddleston, 1980; Dowsett and Wiggs, 1990]. The Jackson Bluff Member is younger than 3.5 Ma [Harris, 1995] and is equivalent to those members of the Yorktown Fm (only partially in this report).

References:
- Campbell (1993) correlated the Moore House Member of Ward et al (1991) with the Chowan River Fm, which is restricted to 3.5 Ma, but the Yorktown Fm (Moore House Member) is below the Chowan River Fm in this compilation. Ward and Gilinsky (1983) did not agree with Campbell (1993) in equating the Moore House Member of the Yorktown Fm with the Chowan River Fm [Campbell and Campbell, 1995]. Evidence suggests that the Chowan River Fm is younger than 3.5 Ma [Harris, 1995] and the Moore House Member is the youngest unit and does not seem to be correlated with anything in SC or GA [Kranz, 1991].
### Table S2.2.2: Part 35. Southeastern Virginia

<table>
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<tr>
<th>Region</th>
<th>Formation</th>
<th>Member</th>
<th>Unit</th>
<th>Age (Ma)</th>
<th>Supporting References</th>
<th>Notes</th>
<th>Other age details or opinions</th>
<th>Correlation</th>
<th>Other opinions on correlations</th>
<th>General regional notes</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sunken Meadow</td>
<td></td>
<td></td>
<td></td>
<td>4.8-4.6</td>
<td>Connin et al (1984); Ward and Huddleston (1983); Krantz (1991), although he cited a range from 4.8-3.5 Ma for this member</td>
<td>The lowest initial transgressive deposit, the Sunken Meadow Member of the Yorktown Fm., contains a somewhat different molluscan assemblage from the rest of the Yorktown Fm. and is separated from the other units by a depositional hiatus (Buchwelder 1981a).</td>
<td>Krantz (1991) indicated the Sunken Meadow Member is time equivalent with the Wabasso Beds and the lower Duplin Fm.; the latter relationship is not supported here, but the Sunken Meadow Member is correlated with the Wabasso Beds.</td>
<td>Jenny et al. (1986) Williams et al. (1998) and Williams et al. (2005) indicated the Sunken Meadow Member is equivalent to Unit 11 of the lower Piney Point, but this is not supported in this compilation; others (e.g., Scott 1995) indicated the Sunken Meadow Member is not correlated with any Tantamai sediments, at least not in S Florida.</td>
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</tbody>
</table>
### Table S2.2.2: Part 36. Lower Delmarva Peninsula, Chesapeake Bay Coast

<table>
<thead>
<tr>
<th>Region</th>
<th>Formation</th>
<th>Member</th>
<th>Unit</th>
<th>Age (Ma)</th>
<th>Supporting References</th>
<th>Notes</th>
<th>Other age details or opinions</th>
<th>Correlation</th>
<th>Other opinions on correlations</th>
<th>General regional notes</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Washapogue</td>
<td></td>
<td></td>
<td>0.06-0.02</td>
<td>Owens and Denby (1979); Skulski et al. (1984); Zinkinsh and Kearny (1988); Pattich et al. (2000); Scott et al. (2010)</td>
<td>The unit unconformably overlies the Yorktown Fm; in other places, it transgresses and/or overlies the Omar and Nassawadox Fms (Mixon 1985). The age is uncertain (Toscano and York 1992; Hobbs 2004): Mixon (1985) cited radiocarbon ages of greater than 33 ka, U-series of 129 ka, and amino acid racemization dates of 82 ka; according to Scott et al. (2010), the 129 ka is too old. Skulski et al. (1984) obtained dates of 73, 20, and 360 ka, which according to Toscano and York (1992), suggested contamination; Zinkinsht and Kearny (1988) presented similar dates of 36-28 ka, but these are also controversial according to Toscano and York (1992); Toscano and York (1992) placed the unit in older in MF3.1 (specifically Sd-e), equivalent to “115-84 ka; Owens and Denby (1979) indicated dates of 30 +/- 1 ka for the stratigraphic equivalent Kent Island Fm, and Pattich et al. (2005) found dates of 37 +/- 6.1 ka from DSi dating for the Kent Island Fm; Scott et al. (2010) found OLS ages of 46.9 +/- 6.9 and 38.9 +/- 5.5 ka, and Scott et al. (2010) placed the unit within MS-3 (80-02 ka).</td>
<td>Correlated with the upper member of the Sand Bridge Fm [new Powell's Crossroads Fm] and potentially with the [Sinepuxent Fm as discussed by Owens and Denby (1979); Mixon 1985; Hobbs 2004] considered a stratigraphic equivalent to the Kent Island Fm [Scott et al. 2010]; correlated with the Tabb and Nassawadox Fms (Toscano and York 1992).</td>
<td>For an overview of the history of stratigraphic nomenclature in the Chesapeake Bay area, see Toscano and York (1992) and Hobbs (2004).</td>
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<td></td>
<td>Scott et al. (2010)</td>
<td>The Joyeys Neck Sand truncates and unconformably overlies the Assateague Member of the Omar Fm (Mixon 1985).</td>
<td>The age is uncertain (Hobbs 2004; Rader and Evans 1993) placed the unit as latest Pleistocene. Toscano and York (1992) indicated the unit was deposited during isotopically Stage 5 d and e, which is 1533-145 ka, while Scott et al. (2010) indicated the unit was deposited after MS-5 and before the middle of MS-3.</td>
<td>The unit may be correlated with the upper lens of the Assateague Member of the Omar Fm (Hobbs 2004).</td>
<td></td>
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</tr>
<tr>
<td>Lower Delmarva Peninsula, Chesapeake Bay Coast</td>
<td>Joyeys Neck Sand</td>
<td></td>
<td></td>
<td>~0.07-0.06</td>
<td>Owens and Denby (1979); Skulski et al. (1984); Zinkinsht and Kearny (1988); Pattich et al. (2000); Scott et al. (2010)</td>
<td>The unit unconformably overlies the Yorktown Fm; in other places, it transgresses and/or overlies the Omar and Nassawadox Fms (Mixon 1985). The age is uncertain (Toscano and York 1992; Hobbs 2004): Mixon (1985) cited radiocarbon ages of greater than 33 ka, U-series of 129 ka, and amino acid racemization dates of 82 ka; according to Scott et al. (2010), the 129 ka is too old. Skulski et al. (1984) obtained dates of 73, 20, and 360 ka, which according to Toscano and York (1992), suggested contamination; Zinkinsht and Kearny (1988) presented similar dates of 36-28 ka, but these are also controversial according to Toscano and York (1992); Toscano and York (1992) placed the unit in older in MF3.1 (specifically Sd-e), equivalent to “115-84 ka; Owens and Denby (1979) indicated dates of 30 +/- 1 ka for the stratigraphic equivalent Kent Island Fm, and Pattich et al. (2005) found dates of 37 +/- 6.1 ka from DSi dating for the Kent Island Fm; Scott et al. (2010) found OLS ages of 46.9 +/- 6.9 and 38.9 +/- 5.5 ka, and Scott et al. (2010) placed the unit within MS-3 (80-02 ka).</td>
<td>Correlated with the upper member of the Sand Bridge Fm [new Powell's Crossroads Fm] and potentially with the [Sinepuxent Fm as discussed by Owens and Denby (1979); Mixon 1985; Hobbs 2004] considered a stratigraphic equivalent to the Kent Island Fm [Scott et al. 2010]; correlated with the Tabb and Nassawadox Fms (Toscano and York 1992).</td>
<td>For an overview of the history of stratigraphic nomenclature in the Chesapeake Bay area, see Toscano and York (1992) and Hobbs (2004).</td>
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</table>
Table S2.2.2: Part 37. Lower Delmarva Peninsula, Chesapeake Bay Coast

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<thead>
<tr>
<th>Region</th>
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<th>Member</th>
<th>Unit</th>
<th>Age (Ma)</th>
<th>Supporting References</th>
<th>Notes</th>
<th>Other age details or opinions</th>
<th>Correlation</th>
<th>Other opinions on correlations</th>
<th>General regional notes</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lower Del</td>
<td>Omer</td>
<td></td>
<td></td>
<td>0.1-0.2</td>
<td>Minion (1983); Cronin et al (1983); Kronin and Kacheman (2002); Ward and Embry (1986); DeJong and Cronin (1990); Cronin (1991); Ervin (1992); DeJong and Wiggs (1992)</td>
<td>The unit is composed of multiple depositional packages with unconformities between Tuscarora and York (1992). Minion (1983) indicated the oldest Pleistocene unit, the Accomack Member of the Omer Fm., is between 200 and 500 ka; Cronin and Kacheman (1979) indicated an age of 125-300 ka; Cronin et al (1983) found amino acid dates of 100, 200 and 500 ka Tuscarora and York (1993) indicated the unit placed within MIS 179 the 13, which is an age of 400200 ka; and Denny et al (2000) cited ages of 400-325 Ka.</td>
<td>Correlated with the Shirley Fm (Tuscarora and York 1992) [note that it is only partially correlated here].</td>
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<tr>
<td></td>
<td>Yorktown</td>
<td></td>
<td>~4.8-3.1</td>
<td></td>
<td></td>
<td>See notes and references for individual members in the &quot;SE Virginia&quot; and &quot;C &amp; N North Carolina&quot; sections; this is a composite age for all of the Yorktown Fm.</td>
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</table>
Table S2.2.2: Part 38. Lower Delmarva Peninsula, Atlantic Coast

<table>
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<tr>
<th>Region</th>
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<th>Member</th>
<th>Unit (Ma)</th>
<th>Supporting References</th>
<th>Notes</th>
<th>Other age details or opinions</th>
<th>Correlation</th>
<th>Other opinions on correlations</th>
<th>General regional notes</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lower Delmarva Peninsula, Atlantic Coast</td>
<td>Kent Island</td>
<td></td>
<td>&lt;0.06</td>
<td>Owens and Denny (1978); Markewich et al. (1987)</td>
<td>The Kent Island firm refers to a pale gray to yellowish gray sand bordering the east side of the Chesapeake Bay.</td>
<td>Age is cited as: 32-36 Ka (Owens and Denny 1979) and 28-45 ka-6.6 ka (Markewich et al. 1987). The age is somewhat disputed because Mars (1997) indicated the unit is about 60-40 Ka based on stratigraphic correlations and loam and age &gt;10 Ka (from Markewich et al. 1987); Fewick et al. (2006) found an age of 37 +/- 6.4 Ka from Os dating; Ramsey (2010) indicated the unit is between 120 and 80 Ka, which is older than the other ages cited.</td>
<td>Correlated with the Sinequanta Firm.</td>
<td></td>
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<tr>
<td></td>
<td>Nassawadox</td>
<td></td>
<td>0.125-0.673</td>
<td>Vlcek et al. (1982); Tonscane and York (1992)</td>
<td>Surficial sandy and gravelly deposits of narrow, flat upland and adjacent bayside terraces (Ruder and Evans 1993).</td>
<td>Age is cited as: 125-60 Ka (Mason et al. 1982); Sec-a (130-70 Ka) (Tonscane and York 1992); 125 Ka (Swift et al. 2006). The upper member correlates with the Tabb Firm (Vlcek 1985); correlated with the Tabb and Wachapreague Firms (Tonscane and York 1992).</td>
<td></td>
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<td>For overview of the history of stratigraphic nomenclature in the Chesapeake Bay, see Webb (2004) and Tonscane and York (1992).</td>
</tr>
<tr>
<td></td>
<td>Omar</td>
<td></td>
<td>0.5-0.2</td>
<td>Vlcek (1983); Groot et al. (1990); Tonscane and York (1992)</td>
<td>The Oamar Firm contains multiple depositional packages with interleaving disconformities (Tonscane and York 1992).</td>
<td>Vlcek (1983) indicated the oldest Mississippian unit, the Ascumark Member of the Oamar Firm, is 120-116 Ka (Owens and Denny 1979); Groot et al. (1990) found amino acid dates of 116, 200, and 550 Ka; Tonscane and York (1993) indicated MIS 7/9 (235 ka), which is &lt;538-200 Ka; 000-200 Ka (Swift et al. 2006); 500-350 Ka (Ramsey 2010).</td>
<td>Correlated with the Shi-Way Firm (Tonscane and York 1992).</td>
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<tr>
<td></td>
<td>Yorktown</td>
<td></td>
<td>&gt;4.8-3.1</td>
<td>Hazel (1983); Snyder et al. (1983); Stover and Croon (1990); Croon (1991);, Wann (1991);, Croon (1991),, Sheldon and Wigg (1992)</td>
<td>See notes and references for individual members in “Shi Virginia” and “C &amp; N: North Carolina” sections; this is a composite age for all of the Yorktown Firms.</td>
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</table>
References


Brooks, H.K. (1968) The Plio-Pleistocene of Florida, with special references to the strata outcropping on the Caloosahatchee River. *Late Cenozoic stratigraphy of southern


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Appendix S2.3

Appendix S2.3 Supplemental data files for niche comparison tests for: (a) environmental comparisons using a PCA applied to all six variables, (b) environmental comparisons using a PCA applied to the three most important variables, (c) environmental comparisons using raw temperature variables, (d) geographic comparisons using projections from ecological niche models (ENMs), (e) maximum temperature comparisons, and (f) minimum temperature comparisons.

Appendix S2.3a. Environmental comparisons using a PCA applied to all six variables

Results from niche comparison tests for a principle component analysis (PCA) applied to three most important environmental variables (maximum and minimum surface temperature and maximum surface salinity) using script of Broennimann et al. (2012). The first two panels represent the niche of the species along the first two axes of the PCA in the respective time periods. The solid and dashed lines represent 100% and 50% of the available (background) environment, respectively. The bottom left panel represents the contribution of the climatic variables to the two axes of the PCA and the percentage of inertia explained by the two axes. The top histogram is the simulated similarity values (D) and observed similarity value (red bar) for the niche equivalency test. The bottom two histograms are the simulated and observed (red bar) similarity values for the niche similarity tests. Observed values falling within the null distribution do not allow for discrimination of similarity or differences based on the environment available to the entities in question. If the observed value falls to the right of the histogram, niches are statistically more similar than expected given the environmental background, whereas if the observed value falls to the left of the histogram, niches are statistically more different than expected given the environmental background.
**Anomia simplex: LIG—mPWP**

**PCA-env – LIG**

**PCA-env – mPWP**

**correlation circle**

**Equivalency**

- niche overlap: $D = 0.45$
- $D$ p.value = 0.002

**Similarity mPWP→LIG**

- $D$ p.value = 0.05794

**Similarity LIG→mPWP**

- $D$ p.value = 0.002
Anomia simplex: LIG—PI

PCA-env – LIG

PCA-env – PI

correlation circle

nich overlap:
D= 0.693

Equivalency

Similarity PI→LIG

Similarity LIG→PI

axis1 = 44.18 % axis2 = 28.88 %

p.value = 0.002

D

p.value = 0.002

D

p.value = 0.004

D

p.value = 0.004

p.value = 0.002
Anomia simplex: PI — mPWP

PCA-env – PI

PCA-env – mPWP

correlation circle

niche overlap:
D = 0.434

Equivalency

p.value = 0.002

Similarity mPWP->PI

p.value = 0.002

Similarity PI->mPWP

p.value = 0.03996

axis1 = 46.5 % axis2 = 27.75 %
**Bulla occidentalis: LIG—mPWP**

**PCA-env – LIG**

**PCA-env – mPWP**

**correlation circle**

- **Equivalency**
  - niche overlap: $D = 0.344$

- **Similarity mPWP→LIG**
  - Frequency
  - $D$ p.value = 0.10589

- **Similarity LIG→mPWP**
  - Frequency
  - $D$ p.value = 0.004

axis1 = 45.78% axis2 = 27.97%
**Bulla occidentalis: LIG—PI**

**PCA-env — LIG**

**PCA-env — PI**

**Correlation circle**

niche overlap: 
D= 0.733

**Equivalency**

p.value = 0.002

**Similarity PI→LIG**

p.value = 0.002

**Similarity LIG→PI**

p.value = 0.002
Bulla occidentalis: PI—mPWP

PCA-env - PI

PCA-env - mPWP

Correlation circle

axis1 = 46.5 % axis2 = 27.75 %

Equivalency

niche overlap:
D= 0.362

p.value = 0.002

Similarity mPWP->PI

Similarity PI->mPWP

Frequency

D
p.value = 0.15784
p.value = 0.002
Crassostrea virginica: LIG—mPWP

**PCA-env – LIG**

**PCA-env – mPWP**

**Correlation circle**

**Equivalency**

nich overlap: $D = 0.355$

**Similarity mPWP→LIG**

**Similarity LIG→mPWP**

axis1 = 45.78% axis2 = 27.97%

$D$ p.value = 0.04595

$D$ p.value = 0.00799
Crassostrea virginica: LIG—PI

PCA-env – LIG

PCA-env – PI

Correlation circle

Niche overlap:
\( D = 0.539 \)

Equivalency

Similarity PI→LIG

Similarity LIG→PI

axis1 = 44.18 % axis2 = 28.88 %
Crassostrea virginica: PI—mPWP

PCA-env – PI

PCA-env – mPWP

correlation circle

Equivalency

nich overlap:
D= 0.427

Similarity mPWP→PI

Similarity PI→mPWP

axis1 = 46.5 % axis2 = 27.75 %

p.value = 0.002

p.value = 0.02797

p.value = 0.002

0.0 0.2 0.4

0.0 0.2 0.4

0.0 0.2 0.4

0.0 0.2 0.4
Crepidula fornicata: LIG—mPWP

PCA-env – LIG

PCA-env – mPWP

correlation circle

Equivalency

niche overlap: D= 0.372

Similarity mPWP–>LIG

Similarity LIG–>mPWP

axis1 = 45.78 % axis2 = 27.97 %

p.value = 0.10589
d

p.value = 0.002
Crepidula fornicata: LIG—PI

PCA-env – LIG

PCA-env – PI

correlation circle

Equivalency

niche overlap:
D= 0.523

Similarity PI→LIG

Similarity LIG→PI

axis1 = 44.18 % axis2 = 28.88 %

p.value = 0.00599

p.value = 0.002
Crepidula fornicata: PI—mPWP

**PCA-env – PI**

**PCA-env – mPWP**

**Correlation circle**

- niche overlap: $D = 0.333$
- p.value = 0.002

**Equivalency**

**Similarity mPWP->PI**

- Frequency
- $D$ = 0.333
- p.value = 0.01199

**Similarity PI->mPWP**

- Frequency
- $D$ = 0.333
- p.value = 0.00599

axis1 = 46.5 % axis2 = 27.75 %
Dinocardium robustum: LIG—mPWP

**PCA-env – LIG**

**PCA-env – mPWP**

**correlation circle**

**Equivalency**

nische overlap:
D= 0.494

**Similarity mPWP→LIG**

**Similarity LIG→mPWP**

axis1 = 45.78 % axis2 = 27.97 %

D
p.value = 0.32368

D
p.value = 0.002

214
Dinocardium robustum: LIG—PI

PCA-env – LIG

PCA-env – PI

Correlation circle

Equivalency

nich overlap:
D = 0.626

p.value = 0.002

Similarity PI->LIG

Similarity LIG->PI

axis1 = 44.18 % axis2 = 28.88 %

D
p.value = 0.004

D
p.value = 0.004
**Dinocardium robustum: PI—mPWP**

**PCA-env – PI**

**PCA-env – mPWP**

**Correlation Circle**

niche overlap: $D = 0.8$

$D$ = 0.6

$p$-value = 0.02

**Similarity mPWP→PI**

$D$ = 0.01399

$p$-value = 0.002

**Similarity PI→mPWP**

$D$ = 0.002

$p$-value = 0.01399

axis1 = 46.5% axis2 = 27.75%
Lucina pensylvanica: LIG—mPWP

PCA-env – LIG

PCA-env – mPWP

correlation circle

niche overlap: D= 0.497

Equivalency

p.value = 0.002

Similarity mPWP->LIG

Similarity LIG->mPWP

axis1 = 45.78 % axis2 = 27.97 %

p.value = 0.15784

D

p.value = 0.002
Lucina pensylvanica: LIG—PI

PCA-env – LIG

PCA-env – PI

correlation circle

niche overlap: D= 0.494

Equivalency

axis1 = 44.18 % axis2 = 28.88 %

Similarity PI→LIG

Similarity LIG→PI

D p.value = 0.08791

D p.value = 0.002
Lucina pensylvanica: PI—mPWP

PCA–env – PI

PCA–env – mPWP

correlation circle

axis1 = 46.5 % axis2 = 27.75 %

Equivalency

niche overlap:
D = 0.401

p.value = 0.002

Similarity mPWP→PI

p.value = 0.13586

Similarity PI→mPWP

p.value = 0.002
**Mercenaria campechiensis: LIG—mPWP**

PCA-env – LIG

PCA-env – mPWP

**Equivalency**

niche overlap:  
\[ D = 0.377 \]

**Similarity mPWP→LIG**

\[ D = 0.14785 \]

**Similarity LIG→mPWP**

\[ D = 0.002 \]

axis1 = 45.78 %  
axis2 = 27.97 %
Mercenaria campechiensis: LIG—PI

PCA-env – LIG

PCA-env – PI

Correlation circle

axis1 = 44.18 % axis2 = 28.88 %

Equivalency

niche overlap:
D= 0.766

p.value = 0.002

Similarity PI→LIG

D
p.value = 0.004

Similarity LIG→PI

D
p.value = 0.002
Mercenaria campechiensis: PI–mPWP

PCA–env – PI

PCA–env – mPWP

Correlation circle

Equivalency

nich overlap:

D = 0.464

p.value = 0.002

Similarity mPWP->PI

Similarity PI->mPWP

axis1 = 46.5 % axis2 = 27.75 %
*Neverita duplicata: LIG—mPWP*

**PCA-env – LIG**

**PCA-env – mPWP**

**correlation circle**

niche overlap:  
D = 0.362

D  
p.value = 0.002

**Equivalency**

**Similarity mPWP→LIG**

**Similarity mPWP→LIG**

axis1 = 45.78 % axis2 = 27.97 %
*Neverita duplicata: LIG–PI*

**PCA-env – LIG**

**PCA-env – PI**

**Correlation circle**

- **Niche overlap:**
  - \( D = 0.681 \)
  - \( \text{p.value} = 0.002 \)

**Equivalency**

**Similarity PI→LIG**

- \( D = \) —
  - \( \text{p.value} = 0.002 \)

**Similarity LIG→PI**

- \( D = \) —
  - \( \text{p.value} = 0.002 \)

**Axes:**
- \( \text{axis1} = 44.18\% \text{ axis2} = 28.88\% \)
Neverita duplicata: PI—mPWP

PCA-env – PI

PCA-env – mPWP

correlation circle

equivalency

niche overlap:
D = 0.443

Similarity mPWP→PI

Similarity PI→mPWP

axis1 = 46.5 % axis2 = 27.75 %

Frequency

Frequency

D
D

p.value = 0.05195
p.value = 0.002

p.value = 0.002

p.value = 0.002
Oliva sayana: LIG—mPWP

PCA–env – LIG

PCA–env – mPWP

correlation circle

Equivalency

niche overlap:
D= 0.396

Similarity mPWP→LIG

Similarity LIG→mPWP

axis1 = 45.78 % axis2 = 27.97 %
Oliva sayana: LIG—PI

PCA–env – LIG

PCA–env – PI

correlation circle

Equivalency

niche overlap:
D = 0.692

Similarity PI→LIG

Similarity LIG→PI

axis1 = 44.18 % axis2 = 28.88 %

D
p.value = 0.002

D
p.value = 0.002
Oliva sayana: PI—mPWP

PCA–env – PI

PCA–env – mPWP

correlation circle

Equivalency

niche overlap:
D= 0.445

p.value = 0.002

Similarity mPWP→PI

p.value = 0.02997

Similarity PI→mPWP

p.value = 0.002

axis1 = 46.5 % axis2 = 27.75 %
Terebra dislocata: LIG—mPWP

PCA–env – LIG

PCA–env – mPWP

Correlation circle

Equivalency

niche overlap:
D= 0.38

D
p.value = 0.002

Similarity mPWP→LIG

Similarity LIG→mPWP

axis1 = 45.78 % axis2 = 27.97 %

p.value = 0.05594

p.value = 0.00599
**Terebra dislocata: LIG – PI**

**PCA-env – LIG**

**PCA-env – PI**

**Correlation Circle**

axis1 = 44.18% axis2 = 28.88%

**Equivalency**

niche overlap: D = 0.612

p.value = 0.002

**Similarity PI→LIG**

D = 0.004

p.value = 0.002

**Similarity LIG→PI**

D = 0.004

p.value = 0.002
Terebra dislocata: P1 — mPWP

PCA-env - PI

PCA-env - mPWP

Equivalency

nich overlap:
D= 0.418

p.value = 0.002

Similarity mPWP→P1

Similarity PI→mPWP

axis1 = 46.5 % axis2 = 27.75 %

p.value = 0.01199

p.value = 0.002
Appendix S2.3b. Environmental comparisons using a PCA applied to the three most important variables

Results from niche comparison tests for a principle component analysis (PCA) applied to the three most important environmental variables (maximum and minimum surface temperature and maximum surface salinity) using the script of Broennimann et al. (2012). The first two panels represent the niche of the species along the first two axes of the PCA in the respective time periods. The solid and dashed lines represent 100% and 50% of the available (background) environment, respectively. The bottom left panel represents the contribution of the climatic variables to the two axes of the PCA and the percentage of inertia explained by the two axes. The top histogram is the simulated similarity values (D) and observed similarity value (red bar) for the niche equivalency test. The bottom two histograms are the simulated and observed (red bar) similarity values for the niche similarity tests. Observed values falling within the null distribution do not allow for discrimination of similarity or differences based on the environment available to the entities in question. If the observed value falls to the right of the histogram, niches are statistically more similar than expected given the environmental background, whereas if the observed value falls to the left of the histogram, niches are statistically more different than expected given the environmental background.
Anomia simplex: LIG—mPWP

PCA-env – LIG

PCA-env – mPWP

correlation circle

Equivalency

nich overlap:
D= 0.327

d p.value = 0.002

Similarity mPWP→LIG

Similarity LIG→mPWP

axis1 = 81.77 % axis2 = 13.74 %
Anomia simplex: LIG—PI

PCA—env – LIG

PCA—env – PI

Correlation circle

Equivalency

niche overlap:
D = 0.672
p.value = 0.002

Similarity PI→LIG

Similarity LIG→PI

axis1 = 80.81% axis2 = 15.07%
Anomia simplex: PL—mPWP

PCA-env – PI

PCA-env – mPWP

correlation circle

Equivalency

niche overlap: 
D= 0.426

Similarity mPWP→PI

Similarity PI→mPWP

axis1 = 82.63 % axis2 = 13.89 %

D
p.value = 0.00799

D
p.value = 0.002
Bulla occidentalis: LIG—mPWP

PCA-env – LIG

PCA-env – mPWP

correlation circle

Equivalency

niche overlap:  
D= 0.291

Similarity mPWP→LIG  
Frequency

D  
p.value = 0.34166

Similarity LIG→mPWP  
Frequency

D  
p.value = 0.54346

axis1 =  81.77 % axis2 = 13.74 %
Bulla occidentalis: LIG—PI

PCA-env – LIG

PCA-env – PI

correlation circle

Equivalency

niche overlap:
D= 0.373

D
p.value = 0.002

Similarity PI→LIG

Similarity LIG→PI

axis1 = 80.81 % axis2 = 15.07 %

D
p.value = 0.1019

D
p.value = 0.28971
Bulla occidentalis: PI—mPWP

PCA-env – PI

PCA-env – mPWP

correlation circle

Equivalency

niche overlap:
D= 0.432

p.value = 0.002

Similarity mPWP→PI

Similarity PI→mPWP

axis1 = 82.63 % axis2 = 13.89 %

Frequency

Frequency

D

D

p.value = 0.30769

p.value = 0.2018
Crassostrea virginica: LIG—mPWP

PCA-env – LIG

PCA-env – mPWP

Correlation circle

Equivalency

niche overlap:
D = 0.459

Frequency

0
0.2
0.4

D
p.value = 0.002

Frequency

0
100

D
p.value = 0.03796

Similarity mPWP→LIG

Similarity LIG→mPWP

axis1 = 81.77 % axis2 = 13.74 %
Crassostrea virginica: LIG—PI

PCA–env – LIG

correlation circle

axis1 = 80.81 % axis2 = 15.07 %

PCA–env – PI

Equivalency

nich overlap: 
D= 0.38

p.value = 0.002

Similarity PI→LIG

p.value = 0.02797

Similarity LIG→PI

p.value = 0.002
**Crassostrea virginica: PI—mPWP**

**PCA-env – PI**

**PCA-env – mPWP**

**correlation circle**

axis1 = 82.63 % axis2 = 13.89 %

**Equivalency**

niche overlap: D= 0.314

D

p.value = 0.002

**Similarity mPWP→PI**

D

p.value = 0.002

**Similarity PI→mPWP**

D

p.value = 0.002
Crepidula fornicata: LIG—mPWP

**PCA-env – LIG**

**PCA-env – mPWP**

**correlation circle**

axis1 = 81.77 % axis2 = 13.74 %

**Equivalency**

niche overlap:

D= 0.344

p.value = 0.002

**Similarity mPWP→LIG**

**Similarity LIG→mPWP**

D

p.value = 0.02997

D

p.value = 0.002
Crepidula fornicata: LIG—PI

PCA–env – LIG

PCA–env – PI

Correlation circle

Equivalency

Niche overlap: D = 0.455

Similarity PI→LIG

Similarity LIG→PI

Axis 1 = 80.81% axis 2 = 15.07%
Crepidula fornicata: PL—mPWP

PCA–env – PL

PCA–env – mPWP

Correlation circle

axis1 = 82.63 % axis2 = 13.89 %

Equivalency

niche overlap:
D= 0.158
p.value = 0.002

Similarity mPWP→PI

D
p.value = 0.29371

Similarity PL→mPWP

D
p.value = 0.58342
Dinocardium robustum: LIG—mPWP

PCA-env – LIG

PCA-env – mPWP

Correlation circle

Equivalency

niche overlap: D= 0.519

Similarity mPWP→LIG

Similarity LIG→mPWP

axis1 = 81.77% axis2 = 13.74%
Dinocardium robustum: LIG—PI

PCA-env – LIG

PCA-env – PI

correlation circle

Equivalency

niche overlap: 
D= 0.529

Similarity PI→LIG

Similarity LIG→PI

axis1 = 80.81 % axis2 = 15.07 %
Dinocardium robustum: PI→mPWP

PCA-env – PI

PCA-env – mPWP

Equivalency

niche overlap:
D = 0.466

p.value = 0.002

Similarity mPWP→PI

Similarity PI→mPWP

axis1 = 82.63 % axis2 = 13.89 %
Lucina pensylvanica: LIG—mPWP

PCA-env – LIG

PCA-env – mPWP

correlation circle

Equivalency

niche overlap:
D= 0.302

Similarity mPWP→LIG

Similarity LIG→mPWP

axis1 = 81.77 % axis2 = 13.74 %
Lucina pensylvanica: LIG—PI

PCA-env – LIG

PCA-env – PI

correlation circle

Equivalency

niche overlap: D= 0.422
p.value = 0.002

Similarity PI->LIG

Similarity LIG->PI

axis1 = 80.81 % axis2 = 15.07 %

D p.value = 0.002
D p.value = 0.002
Lucina pensylvanica: PL—mPWP

PCA-env – PI

PCA-env – mPWP

correlation circle

niche overlap:
D = 0.311

Equivalency

Similarity mPWP→PI

Similarity PI→mPWP

axis1 = 82.63 % axis2 = 13.89 %
**Mercenaria campechiensis: LIG—mPWP**

**PCA-env – LIG**

**PCA-env – mPWP**

**correlation circle**

- axis1 = 81.77% axis2 = 13.74%

**Equivalency**

- niche overlap: D= 0.434
- p.value = 0.002

**Similarity mPWP->LIG**

- D = 0.01199
- p.value = 0.002

**Similarity LIG->mPWP**

- D = 0.002
- p.value = 0.002
Mercenaria campechiensis: LIG—PI

PCA-env – LIG

PCA-env – PI

correlation circle

Equivalency

niche overlap:
D= 0.476
p.value = 0.002

Similarity PI–>LIG

Similarity LIG–>PI

axis1 = 80.81 % axis2 = 15.07 %
Mercenaria campechiensis: PI—mPWP

PCA–env – PI

PCA–env – mPWP

correlation circle

niche overlap: D = 0.5

Equivalency

Similarity mPWP→PI

Similarity PI→mPWP

axis1 = 82.63 % axis2 = 13.89 %
Neverita duplicata: LIG—mPWP

PCA-env – LIG

PCA-env – mPWP

Correlation circle

Equivalency

niche overlap:  
D= 0.407

Similarity mPWP->LIG

Similarity LIG->mPWP

axis1 = 81.77 % axis2 = 13.74 %

D  
p.value = 0.07792

D  
p.value = 0.002
Neverita duplicata: LIG—PL

PCA-env – LIG

PCA-env – PL

correlation circle

Equivalency

niche overlap:
D = 0.404

test

p.value = 0.002

Similarity PL→LIG

p.value = 0.00599

Similarity LIG→PL

p.value = 0.43956

axis1 = 80.81 % axis2 = 15.07 %
Neverita duplicata: PI—mPWP

PCA-env – PI

PCA-env – mPWP

correlation circle

niche overlap:
D= 0.511

Equivalency

Similarity mPWP→PI

Similarity PI→mPWP

axis1 = 82.63 % axis2 = 13.89 %
Oliva sayana: LIG—PI

PCA-env – LIG

PCA-env – PI

Correlation circle

niche overlap:
\( D = 0.43 \)

Equivalency

Similarity PI→LIG

Similarity LIG→PI

axis1 = 80.81 % axis2 = 15.07 %
Oliva sayana: LIG—mPWP

PCA-env – LIG

PCA-env – mPWP

correlation circle

Frequency

Equivalency

niche overlap:
D = 0.446

D
p.value = 0.002

Similarity mPWP→LIG

Similarity LIG→mPWP

Frequency

D
p.value = 0.01798

D
p.value = 0.002

axis1 = 81.77 % axis2 = 13.74 %
Oliva sayana: PL—mPWP

PCA-env – PL

PCA-env – mPWP

correlation circle

Equivalency

nich overlap: D= 0.37

Similarity mPWP→PI

Similarity PL→mPWP

axis1 = 82.63 % axis2 = 13.89 %

D p.value = 0.004

D p.value = 0.002
**Terebra dislocata: LIG—mPWP**

**PCA-env – LIG**

**PCA-env – mPWP**

**correlation circle**

axis1 = 81.77 % axis2 = 13.74 %

**Equivalency**

niche overlap: 
D= 0.286

p.value = 0.002

**Similarity mPWP—>LIG**

p.value = 0.01798

**Similarity LIG—>mPWP**

p.value = 0.002
Terebra dislocata: LIG—PI

PCA–env – LIG

-2 0 2 4 6 PC1

PCA–env – PI

-2 0 2 4 6 PC1

correlation circle

axis1 = 80.81 % axis2 = 15.07 %

Equivalency

niche overlap:
D = 0.39

p.value = 0.002

Similarity PI→LIG

D
p.value = 0.002

Similarity LIG→PI

D
p.value = 0.00599

Frequency

0 0.2 0.4

Frequency

0 0.2 0.4

Frequency

0 0.2 0.4

Frequency

0 0.2 0.4
**Terebra dislocata: Pl—mPWP**

**PCA-env – Pl**

**PCA-env – mPWP**

**Correlation Circle**

axis1 = 82.63 % axis2 = 13.89 %

**Equivalency**

nich overlap: D= 0.428

**Similarity mPWP→PI**

D: 0.002

**Similarity PI→mPWP**

D: 0.002
Appendix S2.3c. Environmental comparisons using raw temperature variables

Results from niche comparison tests using raw average bottom temperature and maximum surface temperature conducted with a modified script of Broennimann et al. (2012). The histograms are the simulated and observed (red bar) similarity values (D). Observed values falling within the null distribution do not allow for discrimination of similarity or differences based on the environment available to the entities in question. If the observed value falls to the right of the histogram, niches are statistically more similar than expected given the environmental background, whereas if the observed value falls to the left of the histogram, niches are statistically more different than expected given the environmental background.
Appendix S2.3d. Geographic comparisons using projections from ecological niche models

Results from niche comparison tests using ENMTools (Warren et al., 2008, 2010) on projections of ecological niche models. The histograms are the simulated and observed (red bar) similarity values (D). Observed values falling within the null distribution do not allow for discrimination of similarity or differences based on the environment available to the entities in question. If the observed value falls to the right of the histogram, niches are statistically more similar than expected given the environmental background, whereas if the observed value falls to the left of the histogram, niches are statistically more different than expected given the environmental background.
Appendix S2.3e. Maximum temperature comparisons

Results from comparison of maximum temperature tolerances using script of Broennimann et al. (2012). The right histogram is the simulated similarity values (D) and observed similarity value (red bar) for the niche equivalency test. The left two histograms are the simulated and observed (red bar) similarity values for niche similarity tests. Observed values falling within the null distribution do not allow for discrimination of similarity or differences based on the environment available to the entities in question. If the observed value falls to the right of the histogram, niches are statistically more similar than expected given the environmental background, whereas if the observed value falls to the left of the histogram, niches are statistically more different than expected given the environmental background.
Anomia simplex: LIG → mPWP

Max temp – LIG

Max temp – mPWP

Similarity mPWP→LIG

Similarity LIG→mPWP

Equivalency

nich overlap: D= 0.598

D
p.value = 0.03996

D
p.value = 0.004

D
p.value = 0.002
Anomia simplex: LIG—PI

Max temp – LIG

Max temp – PI

Similarity PI→LIG

Similarity LIG→PI

Equivalency

nich overlap: $D = 0.69$

D
p.value = 0.002

D
p.value = 0.002

D
p.value = 0.01598
Anomia simplex: PI–mPWP

Max temp – PI

Max temp – mPWP

Similarity mPWP→PI

Similarity PI→mPWP

Equivalency

D
p.value = 0.002

D
p.value = 0.002

niche overlap:
D= 0.619

D
p.value = 0.002
**Bulla occidentalis: LIG—mPWP**

**Temp max – LIG**

**Temp max – mPWP**

---

**Similarity mPWP→LIG**

**Similarity LIG→mPWP**

**Equivalency**

\[
\text{niche overlap: } \quad D = 0.63
\]

\[
\text{p.value = 0.002}
\]

\[
\text{p.value = 0.004}
\]

\[
\text{p.value = 0.002}
\]
**Bulla occidentalis: LIG—PI**

**Max temp—LIG**

**Max temp—PI**

**Similarity PI→LIG**

**Similarity PI→LIG**

**Equivalency**

nich overlap: D= 0.646

D

p.value = 0.002
**Bulla occidentalis: PI—mPWP**

**Temp max – PI**

**Temp max – mPWP**

---

**Similarity mPWP→PI**

**Similarity PI→mPWP**

**Equivalency**

- **mPWP→PI**
  - Frequency
  - D
  - p.value = 0.95504

- **PI→mPWP**
  - Frequency
  - D
  - p.value = 0.01798

- **Equivalency**
  - Frequency
  - D
  - p.value = 0.002

---

nich overlap: D= 0.26
**Crassostrea virginica: LIG—mPWP**

**Temp max – LIG**

**Temp max – mPWP**

**Similarity mPWP→LIG**

**Similarity LIG→mPWP**

**Equivalency**

- **n**ich overlap: 
  \[ D = 0.488 \]
  
  - **D**
  - **p.value = 0.004**

- **D**
  - **p.value = 0.002**

- **D**
  - **p.value = 0.002**
Crassostrea virginica: LIG—PI

Temp max – LIG

Temp max – PI

Similarity PI→LIG

Similarity LIG→PI

Equivalency

nich overlap:

D = 0.479

D
p.value = 0.002

D
p.value = 0.01598

D
p.value = 0.002
Crepidula fornicata: LIG→mPWP

Temp max – LIG

Temp max – mPWP

Similarity mPWP→LIG

Similarity LIG→mPWP

Equivalency

n niche overlap: D= 0.746

D p.value = 0.002

D p.value = 0.002

D p.value = 0.03996
Crassostrea virginica: PI—mPWP

Temp max – PI

Temp max – mPWP

Similarity mPWP→PI

Similarity PI→mPWP

Equivalency

niche overlap: 

D = 0.55

p.value = 0.002

p.value = 0.00599

p.value = 0.002

D

D

D

p.value = 0.002
Crepidula fornicata: LIG → PI

**Temp max – LIG**

**Temp max – PI**

**Similarity PI→LIG**

**Similarity LIG→PI**

**Equivalency**

nich overlap: $D = 0.655$

Frequency

<table>
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<th>0.6</th>
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<tr>
<td>p.value</td>
<td>0.02</td>
<td></td>
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Frequency

<table>
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<tr>
<th>Frequency</th>
<th>0.1</th>
<th>0.3</th>
<th>0.5</th>
<th>0.7</th>
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<tbody>
<tr>
<td>p.value</td>
<td>0.02</td>
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</table>

Frequency

<table>
<thead>
<tr>
<th>Frequency</th>
<th>0.7</th>
<th>0.9</th>
</tr>
</thead>
<tbody>
<tr>
<td>p.value</td>
<td>0.02</td>
<td></td>
</tr>
</tbody>
</table>
Crepidula fornicata: PI—mPWP

Temp max – PI

Temp max – mPWP

Similarity mPWP→PI

Similarity PI→mPWP

Equivalency

nich overlap: 
D = 0.387

Frequency

Frequency

Frequency

D
p.value = 0.00999

D
p.value = 0.002

D
p.value = 0.002

287
Dinocardium robustum: LIG—mPWP

Temp max – LIG

Temp max – mPWP

Similarity mPWP→LIG

Similarity LIG→mPWP

Equivalency

nich overlap: 
D= 0.698

D
p.value = 0.02597

D
p.value = 0.004

D
p.value = 0.004
Dinocardium robustum: LIG—PI

Temp max – LIG

Temp max – PI

Similarity PI→LIG

Similarity LIG→PI

Equivalency

D

p.value = 0.002

D

p.value = 0.002

D

p.value = 0.00599

niche overlap: D= 0.712
*Dinocardium robustum: PI—mPWP*

**Temp max – PI**

**Temp max – mPWP**

**Similarity mPWP→PI**

**Similarity PI→mPWP**

**Equivalency**

- **nich overlap:** $D = 0.456$
- $p$-value = 0.002

- $D$
  - $p$-value = 0.09391
- $D$
  - $p$-value = 0.002
Lucina pensylvanica: LIG—mPWP

Temp max – LIG

Density of occurrence

PC1

Temp max – mPWP

Density of occurrence

PC1

Similarity mPWP→LIG

Frequency

D
p.value = 0.002

Similarity LIG→mPWP

Frequency

D
p.value = 0.004

Equivalency

Frequency

n niche overlap:
D= 0.683

p.value = 0.002
Lucina pensylvanica: LIG—PI

Temp max – LIG

Temp max – PI

Similarity PI→LIG

Similarity LIG→PI

Equivalency

nich overlap: D = 0.576

D

p.value = 0.002

D

p.value = 0.002

D

p.value = 0.002
Lucina pensylvanica: PI—mPWP

Temp max – PI

Temp max – mPWP

Similarity mPWP→PI

Similarity PI→mPWP

Equivalency

nich overlap: $D = 0.356$

$D$

$p\text{-value} = 0.80919$

$D$

$p\text{-value} = 0.41558$

$D$

$p\text{-value} = 0.002$
Mercenaria campechiensis: LIG—mPWP

Temp max – LIG

Temp max – mPWP

Similarity mPWP→LIG

Similarity LIG→mPWP

Equivalency

nich overlap: 
D = 0.726

D
p.value = 0.01199

D
p.value = 0.002

D
p.value = 0.00599
Mercenaria campechiensis: LIG—PI

Temp max – LIG

Temp max – PI

Similarity PI→LIG

Similarity LIG→PI

Equivalency

niche overlap: 
D= 0.527

D
p.value =  0.002

D
p.value =  0.02597

D
p.value =  0.002
**Mercenaria campechiensis: PI-mPWP**

**Temp max – PI**

**Temp max – mPWP**

**Similarity mPWP→PI**

**Similarity PI→mPWP**

**Equivalency**

Niche overlap: $D = 0.681$

$p$-value = 0.004

$p$-value = 0.002

$p$-value = 0.002
*Neverita duplicata: LIG—mPWP*

**Temp max – LIG**

**Temp max – mPWP**

**Similarity mPWP→LIG**

**Similarity LIG→mPWP**

**Equivalency**

- **Density of occurrence**
- **Frequency**
- **Niche overlap:**
  - $D = 0.745$
  - $p$-value = 0.00799

- **D**
  - $p$-value = 0.002

- **D**
  - $p$-value = 0.00799
Neverita duplicata: LIG—PI

Temp max – LIG

Temp max – PI

Similarity PI→LIG

Similarity LIG→PI

Equivalency

nich overlap: 
D = 0.472

D
p.value = 0.002

Frequency
0 300
0.0 0.2 0.4

D
p.value = 0.06394

Frequency
0 200
0.0 0.4 0.8

D
p.value = 0.002
Neverita duplicata: PI—mPWP

**Temp max – PI**

![Graph showing PC1 density of occurrence for Temp max – PI](image)

**Temp max – mPWP**

![Graph showing PC1 density of occurrence for Temp max – mPWP](image)

**Similarity mPWP→PI**

![Bar chart showing similarity between mPWP and PI](image)

\[ \text{D} \]

\[ \text{p.value} = 0.002 \]

**Similarity PI→mPWP**

![Bar chart showing similarity between PI and mPWP](image)

\[ \text{D} \]

\[ \text{p.value} = 0.002 \]

**Equivalency**

![Bar chart showing equivalency between mPWP and PI](image)

\[ \text{D} \]

\[ \text{p.value} = 0.00799 \]
Oliva sayana: LIG—mPWP

**Temp max – LIG**

**Temp max – mPWP**

**Similarity mPWP→LIG**

**Similarity LIG→mPWP**

**Equivalency**

necit overlap: $D = 0.724$

D

p.value = 0.002

D

p.value = 0.002

D

p.value = 0.01399

300
Oliva sayana: LIG → PI

Temp max – LIG

Temp max – PI

Similarity PI → LIG

Similarity LIG → PI

Equivalency

nich overlap: D = 0.4

D
p.value = 0.002

D
p.value = 0.0799

D
p.value = 0.15185

D
p.value = 0.00799

D
p.value = 0.15185
Oliva sayana: PL→mPWP

**Temp max – PI**

```
<table>
<thead>
<tr>
<th>Frequency</th>
<th>0.0</th>
<th>0.4</th>
<th>0.8</th>
</tr>
</thead>
<tbody>
<tr>
<td>D</td>
<td>0.53946</td>
<td></td>
<td></td>
</tr>
<tr>
<td>p.value</td>
<td>0.002</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
```

**Temp max – mPWP**

```
<table>
<thead>
<tr>
<th>Frequency</th>
<th>0.0</th>
<th>0.4</th>
<th>0.8</th>
</tr>
</thead>
<tbody>
<tr>
<td>D</td>
<td>0.297</td>
<td></td>
<td></td>
</tr>
<tr>
<td>p.value</td>
<td>0.002</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
```

**Similarity mPWP→PI**

```
<table>
<thead>
<tr>
<th>Frequency</th>
<th>0.0</th>
<th>0.4</th>
<th>0.8</th>
</tr>
</thead>
<tbody>
<tr>
<td>D</td>
<td>0.53946</td>
<td></td>
<td></td>
</tr>
<tr>
<td>p.value</td>
<td>0.002</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
```

**Similarity PI→mPWP**

```
<table>
<thead>
<tr>
<th>Frequency</th>
<th>0.0</th>
<th>0.4</th>
<th>0.8</th>
</tr>
</thead>
<tbody>
<tr>
<td>D</td>
<td>0.297</td>
<td></td>
<td></td>
</tr>
<tr>
<td>p.value</td>
<td>0.002</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
```

**Equivalency**

```
<table>
<thead>
<tr>
<th>Frequency</th>
<th>0.3</th>
<th>0.6</th>
<th>0.9</th>
</tr>
</thead>
<tbody>
<tr>
<td>D</td>
<td>0.002</td>
<td></td>
<td></td>
</tr>
<tr>
<td>p.value</td>
<td>0.002</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
```
**Terebra dislocata: LIG - mPWP**

**Temp max - LIG**

![Graph showing PC1 density of occurrence for Temp max - LIG]

**Temp max - mPWP**

![Graph showing PC1 density of occurrence for Temp max - mPWP]

**Similarity mPWP -> LIG**

- Frequency
  - D
  - p.value = 0.002

**Similarity LIG -> mPWP**

- Frequency
  - D
  - p.value = 0.002

**Equivalency**

- Frequency
  - D
  - p.value = 0.02797

*niche overlap: D = 0.739*
**Terebra dislocata: LIG → PI**

**Temp max – LIG**

![Graph showing density of occurrence for PC1 vs. Temperature Max for LIG]

**Temp max – PI**

![Graph showing density of occurrence for PC1 vs. Temperature Max for PI]

**Similarity PI → LIG**

- Frequency
- D
- p.value = 0.002

**Similarity LIG → PI**

- Frequency
- D
- p.value = 0.02198

**Equivalency**

- Frequency
- D
- p.value = 0.002

**Niche overlap:**

- D = 0.526
Terebra dislocata: Pl→mPWP

**Temp max – PI**

![Graph](image1)

**Temp max – mPWP**

![Graph](image2)

**Similarity mPWP→Pl**

![Graph](image3)

**Similarity Pl→mPWP**

![Graph](image4)

**Equivalency**

![Graph](image5)

- **niches overlap:** $D = 0.344$
- **p.value:** 0.01588

---

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Appendix S2.3f. Minimum temperature comparisons

Results from comparison of minimum temperature tolerances using script of Broennimann et al. (2012). The right histogram is the simulated similarity values (D) and observed similarity value (red bar) for the niche equivalency test. The left two histograms are the simulated and observed (red bar) similarity values for niche similarity tests. Observed values falling within the null distribution do not allow for discrimination of similarity or differences based on the environment available to the entities in question. If the observed value falls to the right of the histogram, niches are statistically more similar than expected given the environmental background, whereas if the observed value falls to the left of the histogram, niches are statistically more different than expected given the environmental background.
Anomia simplex: LIG—mPWP

Min temp – LIG

Min temp – mPWP

Similarity mPWP→LIG

Similarity LIG→mPWP

Equivalency

density of occurrence

PC1

PC1

D
p.value = 0.20579

D
p.value = 0.002

D
p.value = 0.002

niche overlap: D = 0.507
**Anomia simplex: LIG → PI**

**Min temp – LIG**

**Min temp – PI**

---

**Similarity PI → LIG**

**Similarity LIG → PI**

**Equivalency**

<table>
<thead>
<tr>
<th>Frequency</th>
<th>D</th>
<th>p.value</th>
</tr>
</thead>
<tbody>
<tr>
<td>0-0.3</td>
<td></td>
<td></td>
</tr>
<tr>
<td>0.4-0.7</td>
<td></td>
<td></td>
</tr>
<tr>
<td>0.8-1.0</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Frequency</th>
<th>D</th>
<th>p.value</th>
</tr>
</thead>
<tbody>
<tr>
<td>0-0.3</td>
<td></td>
<td></td>
</tr>
<tr>
<td>0.4-0.7</td>
<td></td>
<td></td>
</tr>
<tr>
<td>0.8-1.0</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

- **Equivalency**
  - niche overlap: $D = 0.808$
  - D
  - p.value = 0.01798
Anomia simplex: PI—mPWP

Min temp – PI

Min temp – mPWP

Similarity mPWP→PI

Similarity PI→mPWP

Equivalency

nich overlap: D= 0.669

p.value = 0.002

D

p.value = 0.002

D

p.value = 0.00799

Frequency

Frequency

Frequency

0 300 700

0 200

0 300

0 0.2 0.4 0.6

0.0 0.4

0.0 0.6

0.0 0.8 1.0

0.0 0.2 0.4 0.6

0.0 0.2 0.4 0.6
**Bulla occidentalis: LIG−mPWP**

**Temp min – LIG**

**Temp min – mPWP**

**Similarity mPWP→LIG**

**Similarity LIG→mPWP**

**Equivalency**

---

nich overlap: 
D= 0.423

---

D  
p.value = 0.66134

D  
p.value = 0.004

D  
p.value = 0.002
**Bulla occidentalis: LIG—PI**

**Temp min – LIG**

**Temp min – PI**

**Similarity PI→LIG**

**Similarity LIG→PI**

**Equivalency**

nch overlap:

\[ D = 0.759 \]

\[ D = 0.002 \]

\[ D = 0.09191 \]

\[ D = 0.0999 \]

\[ p. value = 0.09191 \]

\[ p. value = 0.0999 \]

\[ p. value = 0.002 \]
Crassostrea virginica: LIG—mPWP

Temp min – LIG

Temp min – mPWP

Similarity mPWP→LIG

Similarity LIG→mPWP

Equivalency

n niche overlap:

D = 0.465

D

p.value = 0.90709

D

p.value = 0.04995

D

p.value = 0.002

p.value = 0.90709
Crassostrea virginica: LIG→PI

**Temp min – LIG**

**Temp min – PI**

**Similarity PI→LIG**

**Similarity LIG→PI**

**Equivalency**

nich overlap: D= 0.596

D  p.value = 0.002

D  p.value = 0.03397

D  p.value = 0.002
Crasostrea virginica: PI—mPWP

Temp min – PI

Temp min – mPWP

Similarity mPWP→PI

Similarity PI→mPWP

Equivalency

niche overlap: 
D = 0.66

D
p.value = 0.00999

D
p.value = 0.002

D
p.value = 0.00799
Crepidula fornicata: LIG→mPWP

Similarity mPWP→LIG
Frequency 0 300

D
p.value = 0.16583

Similarity LIG→mPWP
Frequency 0 300

D
p.value = 0.002

Equivalency
Frequency 0 150

D
p.value = 0.002

niche overlap: D= 0.454
Crepidula fornicata: LIG → PI

**Temp min – LIG**

**Temp min – PI**

**Similarity PI → LIG**

**Similarity LIG → PI**

**Equivalency**

- **nich overlap:**
  - $D = 0.602$
  - $p\text{.value} = 0.002$

- **D**  
  - $p\text{.value} = 0.00599$
  - $p\text{.value} = 0.002$

- **D**  
  - $p\text{.value} = 0.002$
**Crepidula fornicata: PI—mPWP**

**Temp min – PI**

![Graph showing density of occurrence for PC1]

**Temp min – mPWP**

![Graph showing density of occurrence for PC1]

**Similarity mPWP→PI**

- Frequency distribution
- **D**
- p.value = 0.44156

**Similarity PI→mPWP**

- Frequency distribution
- **D**
- p.value = 0.004

**Equivalency**

- Frequency distribution
- **D**
- p.value = 0.002

nich overlap: D= 0.524
**Dinocardium robustum: LIG—mPWP**

**Temp min – LIG**

**Temp min – mPWP**

**Similarity mPWP→LIG**

**Similarity LIG→mPWP**

**Equivalency**

- **Frequency**
  - **D**
  - **p.value = 0.10789**
  - **D**
  - **p.value = 0.004**
  - **nich overlap:**
  - **D = 0.55**
  - **D**
  - **p.value = 0.002**
**Dinocardium robustum: PI—mPWP**

**Temp min – PI**

**Temp min – mPWP**

**Similarity mPWP→PI**

**Similarity PI→mPWP**

**Equivalency**

- **nich overlap:** 
  - D = 0.706
  - p.value = 0.002
Lucina pensylvanica: LIG—mPWP

Temp min – LIG

Temp min – mPWP

Similarity mPWP→LIG

Similarity LIG→mPWP

Equivalency

nich overlap: 
D= 0.512

D
p.value = 0.67732

D
p.value = 0.004

D
p.value = 0.002
Lucina pensylvanica: \textbf{LIG—PI}

**Temp min – LIG**

![Histogram of PC1 density of occurrence for LIG](image1)

**Temp min – PI**

![Histogram of PC1 density of occurrence for PI](image2)

**Similarity PI→LIG**

- Frequency
  - D
    - p.value = 0.002

**Similarity LIG→PI**

- Frequency
  - D
    - p.value = 0.002

**Equivalency**

- Frequency
  - D
    - p.value = 0.002

niche overlap: D = 0.8
**Lucina pensylvanica: PI—mPWP**

**Temp min – PI**

**Temp min – mPWP**

**Similarity mPWP→PI**

**Similarity PI→mPWP**

**Equivalency**

**Frequency**

- **Similarity mPWP→PI**
  - Frequency: 0 to 150
  - D
  - p.value = 0.77323

- **Similarity PI→mPWP**
  - Frequency: 0 to 200
  - D
  - p.value = 0.22178

**nich overlap:**

D = 0.494

**Frequency**

- **Equivalency**
  - Frequency: 0 to 150
  - D
  - p.value = 0.002
Mercenaria campechiensis: LIG—mPWP

Temp min – LIG

Temp min – mPWP

Similarity mPWP→LIG

Similarity LIG→mPWP

Equivalency

Frequency

Frequency

Frequency

D

D

D

p.value = 0.81918

p.value = 0.002

p.value = 0.002

niche overlap: D = 0.65

325
Mercenaria campechiensis: LIG—PI

Temp min – LIG

Temp min – PI

Similarity PI→LIG

Similarity LIG→PI

Equivalency

nich overlap: D= 0.707

d p.value = 0.002

d p.value = 0.002

d p.value = 0.002
Mercenaria campechiensis: PI—mPWP

Temp min – PI

Temp min – mPWP

Similarity mPWP→PI  Similarity PI→mPWP

Equivalency

nich overlap:

D = 0.648

D

p.value = 0.00799

D

p.value = 0.004

D

p.value = 0.002
Neverita duplicata: LIG—mPWP

**Temp min – LIG**

**Temp min – mPWP**

**Similarity mPWP→LIG**

**Similarity LIG→mPWP**

**Equivalency**

- **nich overlap:** D = 0.507
- **Frequency**
  - **D**
  - **p.value = 0.5035**
- **Frequency**
  - **D**
  - **p.value = 0.002**
- **Frequency**
  - **D**
  - **p.value = 0.002**
**Neverita duplicata: LIG—PI**

**Temp min – LIG**

**Temp min – PI**

- **Similarity PI→LIG**
  - Frequency
  - D
  - p.value = 0.05195

- **Similarity LIG→PI**
  - Frequency
  - D
  - p.value = 0.002

- **Equivalency**
  - Frequency
  - D
  - p.value = 0.002

niche overlap:
D = 0.653
**Neverita duplicata: PL—mPWP**

**Temp min – PI**

**Temp min – mPWP**

**Similarity mPWP→PI**

Similarity PI→mPWP

**Equivalency**

Niche overlap: 
\[ D = 0.663 \]

Frequency

- **D**
  - p.value = 0.004

- **D**
  - p.value = 0.002

- **D**
  - p.value = 0.002
Oliva sayana: LIG—mPWP

Temp min – LIG

Similarity mPWP→LIG

Frequency

0 0.2 0.4 0.6 0.8

0 300

D
p.value = 0.06993

Similarity LIG→mPWP

Frequency

0 0.2 0.4

0 150

D
p.value = 0.002

Equivalency

Frequency

0 0.5 0.7 0.9

0 300

D
p.value = 0.002

niche overlap: D= 0.478
Oliva sayana: LIG—PI

Temp min – LIG

Temp min – PI

Similarity PI→LIG

Similarity LIG→PI

Equivalency

nich overlap: D= 0.546

D p.value = 0.03197

D p.value = 0.002

D p.value = 0.002
Oliva sayana: PI—mPWP

Temp min – PI

Temp min – mPWP

Similarity mPWP→PI

Similarity PI→mPWP

Equivalency

nich overlap: $D = 0.432$

$D$
p.value = 0.29171

$D$
p.value = 0.002

$D$
p.value = 0.002
*Terebra dislocata: LIG—mPWP*

**Temp min – LIG**

**Temp min – mPWP**

**Similarity mPWP→LIG**

**Similarity LIG→mPWP**

**Equivalency**

*niche overlap: D= 0.419*

D  
*p.value = 0.17782*

D  
*p.value = 0.002*

D  
*p.value = 0.002*
**Terebra dislocata: LIG—PI**

**Temp min – LIG**

![Graph](image1)

**Temp min – PI**

![Graph](image2)

**Similarity PI→LIG**

![Graph](image3)

**Similarity LIG→PI**

![Graph](image4)

**Equivalency**

![Graph](image5)

- **nich overlap:** $D = 0.67$
- $p$-value $= 0.002$

---

**Terebra dislocata: LIG—PI**

**Temp min – LIG**

![Graph](image1)

**Temp min – PI**

![Graph](image2)

**Similarity PI→LIG**

![Graph](image3)

**Similarity LIG→PI**

![Graph](image4)

**Equivalency**

![Graph](image5)

- **nich overlap:** $D = 0.67$
- $p$-value $= 0.002$
**Terebra dislocata: PI—mPWP**

**Temp min – PI**

---

**Temp min – mPWP**

---

**Similarity mPWP→PI**

- Frequency
- D
- p.value = 0.04995

**Similarity PI→mPWP**

- Frequency
- D
- p.value = 0.002

**Equivalency**

- Frequency
- D
- p.value = 0.002

*niche overlap: D= 0.616*