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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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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Dedication

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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.

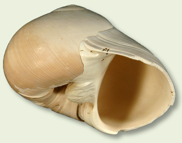
Species			Author	Details	Climatic Zone	Larval Strategy
Bivalvia		*Anomia simplex*	d'Orbigny, 1853	Referred to as the common jingle shell	Temperate—Tropical	Planktonic
		*Crassostrea virginica*	Gmelin, 1791	The eastern oyster -- of economic value.	Temperate—Tropical	Planktonic
		*Dinocardium robustum*	Lightfoot, 1786	The Atlantic giant cockle -- also used for food	Subtropical—Tropical	Planktonic
		*Lucina pensylvanica*	Linnaeus, 1758	Also referred to as the Pennsylvania lucine	Tropical	Benthic
		*Mercenaria campechiensis*	Gmelin, 1791	Referred to as the southern quahog. Commercially harvested.	Subtropical—Tropical	Planktonic
Gastropoda		*Bulla occidentalis*	Adams, 1850	Referred to as buble snails or shells. Hermaphroditic.	Tropical	Planktonic
		*Crepidula fornicata*	Linnaeus, 1758	Referred to as the common slipper shell. This species is considered invasive in Europe.	Temperate—Tropical	Planktonic
		*Neverita duplicata*	Say, 1822	Commonly referred to as the 'shark eye' or moon snails. This is a predatory gastropod species.	Temperate—Tropical	Planktonic
		*Oliva sayana*	Ravenel, 1834	Referred to as the lettered olive. This is a large predatory species.	Tropical	Planktonic
		*Terebra dislocata*	Say, 1822	Referred to as the eastern auger.	Subtropical—Tropical	Benthic

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

Allmon, W.D., Rosenberg, G. & Portell, R.W. (1993) Diversity of Atlantic Coastal Plain mollusks since the Pliocene. *Science* **260**, 1626–1629.

Araújo, M.B. & Rahbek, C. (2006) How does climate change affect biodiversity? *Science*, **313**, 1396–1397.

Boulangeat, I., Lavergne, S., Van Es, J., Garraud, L. & Thuiller, W. (2012) Niche breadth, rarity and ecological characteristics within a regional flora spanning large environmental gradients. *Journal of Biogeography*, **39**, 204–214.

Burrows, M.T., Schoeman, D.S., Buckley, L.B., Moore, P., Poloczanska, E.S., Brander, K.M., Brown, C., Bruno, J.F., Duarte, C.M., Halpern, B.S., Holding, J., Kappel, C.V., Kiessling, W., O'Connor, M.I., Pandolfi, J.M., Parmesan, C., Schwing, F.B., Sydeman, W.J. & Richardson, A.J. (1991) The pace of shifting climate in marine and terrestrial ecosystems. *Science*, **334**, 652–655.

Campbell, L.D. (1993) Pliocene mollusks from the Yorktown and Chowan River Formations in Virginia. *Virginica Division of Mineral Resources Publication*, **127**, 259 pp.

Colles, A., Liow, L.H. & Prinzing, A. (2009) Are specialists at risk under environmental change? Neoecological, paleoecological and phylogenetic approaches. *Ecology Letters*, **12**, 849–863.

Cronin, T.M. & Dowsett, H.F. (1996) Biotic and Oceanographic response to the Pliocene closing of the Central American Isthmus. *Evolution and Environment in Tropical*

America (ed. by J.B.C. Jackson, A.F. Budd and A.G. Coates), pp. 76–104. The University of Chicago Press, Chicago.

Devictor, V., Julliard, R., Clavel, J., Jiguet, F., Lee, A. & Couvet, D. (2008) Functional biotic homogenization of bird communities in disturbed landscapes. *Global Ecology and Biogeography*, **17**, 252–261.

Dietl, G.P. & Flessa, K.W. (2011) Conservation paleobiology: putting the dead to work. *Trends in Ecology and Evolution*, **26**, 30–37.

Dowsett, H.J. & Cronin, T.M. (1990) High eustatic sea level during the Middle Pliocene: evidence from the southeastern U.S. Atlantic coastal plain. *Geology*, **18**, 435–438.

Dowsett, H.J. & Wiggs, L.B. (1992) Planktonic foraminiferal assemblage of the Yorktown Formation, Virginia, USA. *Micropaleontology*, **38**, 75–86.

Eldredge, N. (1979) Alternative approaches to evolutionary theory. *Bulletin of the Carnegie Museum of Natural History*, **13**, 7–19.

Eldredge, N. & Gould, S.J. (1972) Punctuated equilibria: an alternative to phyletic gradualism. *Models in Paleobiology* (ed. by T.J.M. Schopf), pp. 82–115 Freeman Cooper, San Francisco.

Eldredge, N., Thompson, J.N., Brakefield, P.M., Gavrilets, S., Jablonski, D., Jackson, J.B.C., Lenski, R.E., Lieberman, B.S., McPeek, M.A. & Miller, W.I. (2005) The dynamics of evolutionary stasis. *Paleobiology*, **31**, 133–145.

Fritz, S.A., Bininda-Emonds, O.R.P. & Purvis, A. (2009) Geographical variation in predictors of mammalian extinction risk: big is bad, but only in the tropics. *Ecology Letters*, **12**, 538–549.

Fritz, S.A., Schnitzler, J., Eronen, J.T., Hof, C., Böhning-Gaese, K. & Graham, C.H. (2013) Diversity in time and space: wanted dead and alive. *Trends in Ecology and Evolution*, **28**, 509–516.

Gould, S.J. (2002) *The Structure of Evolutionary Theory*. The Belknap Press of Harvard University Press, Cambridge.

Harley, C.D.G., Hughes, A.R., Hultgren, K.M., Miner, B.G., Sorte, C.J.B., Thornber, C.S., Rodriguez, L.F., Tomanek, L. & Williams, S.L. (2006) The impacts of climate change in coastal marine systems. *Ecology Letters*, **9**, 228–241.

Harnik, P.G. (2011) Direct and indirect effects of biological factors on extinction risk in fossil bivalves. *Proceedings of the National Academy of Sciences USA* **108**, 13594–13599.

Hendricks, J.R. (2009) The genus *Conus* (Mollusca: Neogastropoda) in the Plio-Pleistocene of the southeastern United States. *Bulletin of American Paleontology*, **375**, 180 pp.

IPCC (2007) *Climate Change 2007: The Physical Science Basis*. Cambridge University Press, Cambridge.

Jablonski, D. (1991) Extinctions: a paleontological perspective. *Science*, **253**, 754–757.

Jablonski, D. & Hunt, G. (2006) Larval ecology, geographic range, and species survivorship in Cretaceous mollusks: organismic versus species-level explanations. *The American Naturalist*, **168**, 556–564.

Knowles, T., Taylor, P.D., Williams, M., Haywood, A.M. & Okamura, B. (2009) Pliocene seasonality across the North Atlantic inferred from cheilostome bryozoans. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **277**, 226–235.

Krantz, D.E. (1990) Mollusk-isotope records of Plio-Pleistocene marine paleoclimate, US Middle Atlantic Coastal plain. *Palaios*, **5**, 317–335.

Lieberman, B.S. & Vrba, E.S. (1995) Hierarchy theory, selection, and sorting. *Bioscience*, **45**, 394–399.

Mace, G.M., Collar, N.J., Gaston, K.J., Hilton-Taylor, C., Akçakaya, H.R., Leader-Williams, N., Milner-Gulland, E.J. & Stuart, S.N. (2008) Quantification of extinction risk:

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

McKinney, M.L. (1997) Extinction vulnerability and selectivity: combining ecological and paleontological views. *Annual Review of Ecology and Systematics*, **28**, 495–516.

Myers, C.E. & Saupe, E.E. (2013) A macroevolutionary expansion of the Modern Synthesis and the importance of extrinsic abiotic factors. *Palaeontology*, **56**, 1179–1198.

Parmesan, C. (2006) Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology, Evolution, and Systematics*, **37**, 637–669.

Patzkowsky, M.E. & Holland, S.M. (2012) *Stratigraphic Paleobiology: Understanding the Distribution of Fossil Taxa in Time and Space*. University of Chicago Press, Chicago.

Payne, J.L. & Finnegan, S. (2007) The effect of geographic range on extinction risk during background and mass extinction. *Proceedings of the National Academy of Sciences USA*, **104**, 10506–10511.

Peterson, A.T., Ortega-Huerta, M.A., Bartley, J., Sánchez-Cordero, V., Soberón, J., Buddemeier, R.H. & Stockwell, D.R.B. (2002) Future projections for Mexican faunas under global climate change scenarios. *Nature*, **416**, 62–629.

Robinson, M.M. & Dowsett, H.J. (2008) Pliocene role in assessing future climate impacts. *EOS, Transactions American Geophysical Union*, **89**, 501–502.

Ross, R.M. & Allmon, W.D. (eds.) (1990) *Causes of Evolution: a Paleontological Perspective*. University of Chicago Press, Chicago.

Roy, K., Valentine, J.W., Jablonski, D. & Kidwell, S.M. (1996) Scales of climatic variability and time averaging in Pleistocene biotas: implications for ecology and evolution. *Trends in Ecology and Evolution*, **11**, 458–463.

Saupe, E.E., Hendricks, J.R., Peterson, A.T. & Lieberman, B.S. (2014, in press) Climate change and marine mollusks of the western North Atlantic: future prospects and perils. *Journal of Biogeography.*

Saupe, E.E., Hendricks, J.R., Portell, R.W., Dowsett, H.J., Haywood, A., Hunter, S.J. & Lieberman, B.S. (in review) Macroevolutionary consequences of profound climate change on niche evolution in marine mollusks over the past three million years. *Proceedings of the National Academy of Sciences USA*.

Schwartz, M.W., Iverson, L.R., Prasad, A.M., Matthews, S.N. & O'Connor, R.J. (2006) Predicting extinction as a result of climate change. *Ecology*, **87**, 1611–1615.

Thuiller, W., Lavorel, S., Araújo, M.B., Sykes, M.T. & Prentice, I.C. (2005) Climate change threats to plant diversity in Europe. *Proceedings of the National Academy of Sciences USA*, **102**, 8245–8250.

Todd, J.A., Jackson, J.B.C., Johnson, K.G., Fortunato, H.M., Heitz, A., Alvarez, M. & Jung, P. (2002) The ecology of extinction: molluscan feeding and faunal turnover in the Caribbean Neogene. *Proceedings of the Royal Society of London B*, **269**, 571–577.

Toscano, M.A. & York, L.L. (1992) Quaternary stratigraphy and sea-level history of the US Middle Atlantic Coastal Plain. *Quaternary Science Reviews*, **11**, 301–328.

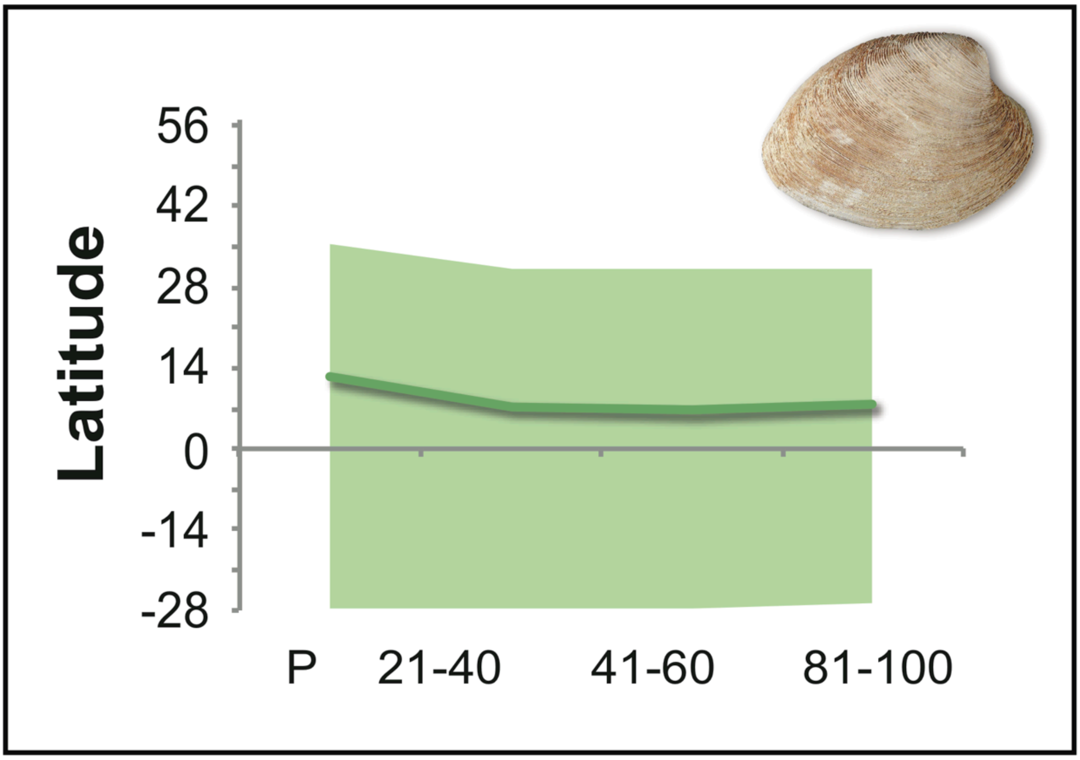
Vermeij, G.J. (2005) One-way traffic in the western Atlantic: causes and consequences of Miocene to early Pleistocene molluscan invasions in Florida and the Caribbean. *Paleobiology*, **31**, 624–642.

Vrba, E.S. (1980) Evolution, species and fossils: how does life evolve? *South African Journal of Science*, **76**, 61–84.

Wiley, E.O. & Lieberman, B.S. (2011) *The Theory and Practice of Phylogenetic Systematics, Second Edition*. Wiley-Blackwell, Hoboken, New Jersey.

Williams, M., Haywood, A.M., Harper, E.M., Johnson, A.L.A., Knowles, T., Leng, M.J., Lunt, D.J., Okamura, B., Taylor, P.D. & Zalasiewicz, J. (2009) Pliocene climate and seasonality in North Atlantic shelf seas. *Philosophical Transactions of the Royal Society A*, **367**, 85–108.

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



By: Erin E. Saupe, Jonathan R. Hendricks, A. Townsend Peterson and Bruce S. Lieberman. (2014, in press). Climate change and marine mollusks of the western North Atlantic: future prospects and perils. *Journal of Biogeography*.

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

record.

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 S1.1.1 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).

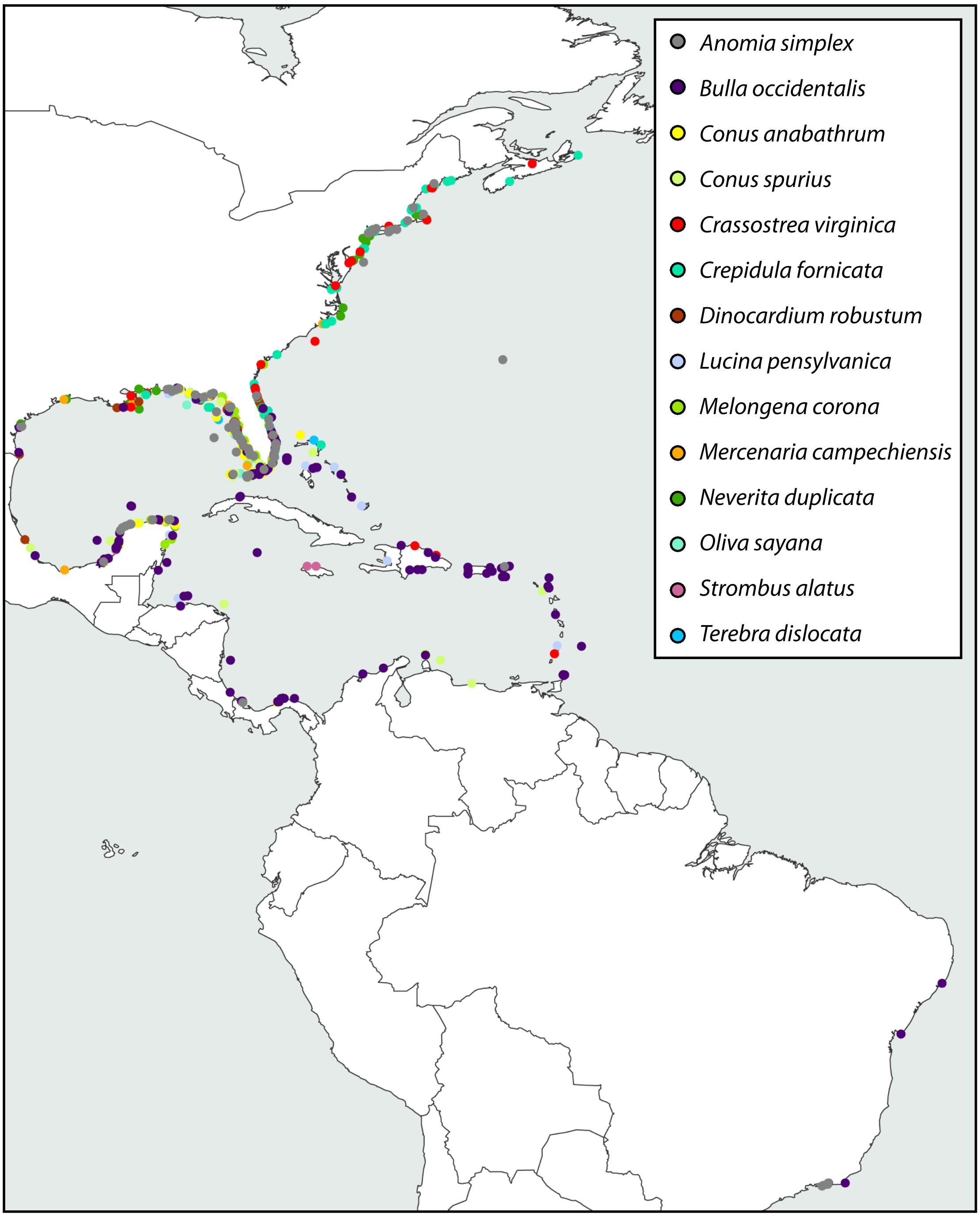


Figure 1.1 Distributional data for all 14 marine mollusk species within the western North Atlantic. For individual maps, see Figs S1.1.1–1.1.4 in Appendix S1.1.

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.

		MAXENT			**GARP**		
Species	No. of spatially unique training points	*P*	AUC ratio	% pts omitted	*P*	AUC ratio	% pts omitted
Bivalvia							
Anomia simplex	24	0.0112	1.36	6.1%	0.0284	1.43	20.4%
Crassostrea virginica	22	0.0000	1.64	27.6%	0.0000	1.70	0.0%
Dinocardium robustum	21	0.0000	1.67	5.4%	0.0000	1.63	2.7%
Lucina pensylvanica	17	0.0000	1.44	7.5%	0.0641	1.24	20.0%
Mercenaria campechiensis	15	0.0000	1.72	28.6%	0.1196	1.13	34.3%
Gastropoda							
Bulla occidentalis	47	0.0000	1.59	3.1%	0.0000	1.54	3.1%
Conus anabathrum	17	0.0000	1.51	5.6%	0.0043	1.30	11.1%
Conus spurius	24	0.0000	1.56	6.5%	0.0000	1.51	8.7%
Crepidula fornicata	29	0.0000	1.48	11.5%	0.0096	1.45	7.7%
Melongena corona	19	0.0478	1.32	14.7%	0.0161	1.48	12.0%
Neverita duplicata	23	0.0222	1.63	9.1%	0.0066	1.57	13.6%
Oliva sayana	19	0.0000	1.85	32.5%	0.0000	1.70	5.0%
Strombus alatus	19	0.0001	1.64	5.0%	0.0054	1.58	7.5%
Terebra dislocata	18	0.0002	1.61	6.7%	0.0473	1.46	8.9%

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).

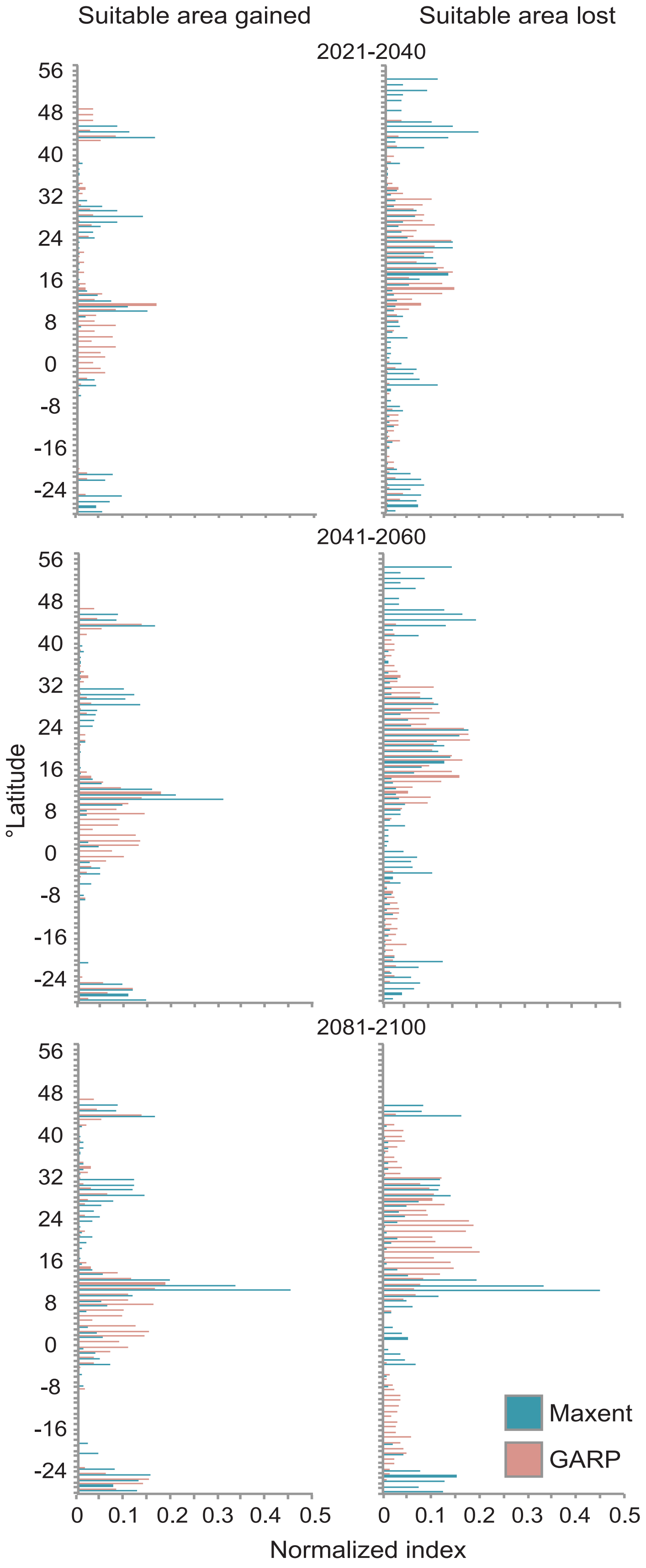


Figure 1.2 Cumulative suitable area lost/gained for all 14 marine mollusk species in the western North Atlantic for Representative Concentration Pathways (RCP) 2.6 emission scenario, tabulated across latitudes and standardized for the available area per latitude.

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.

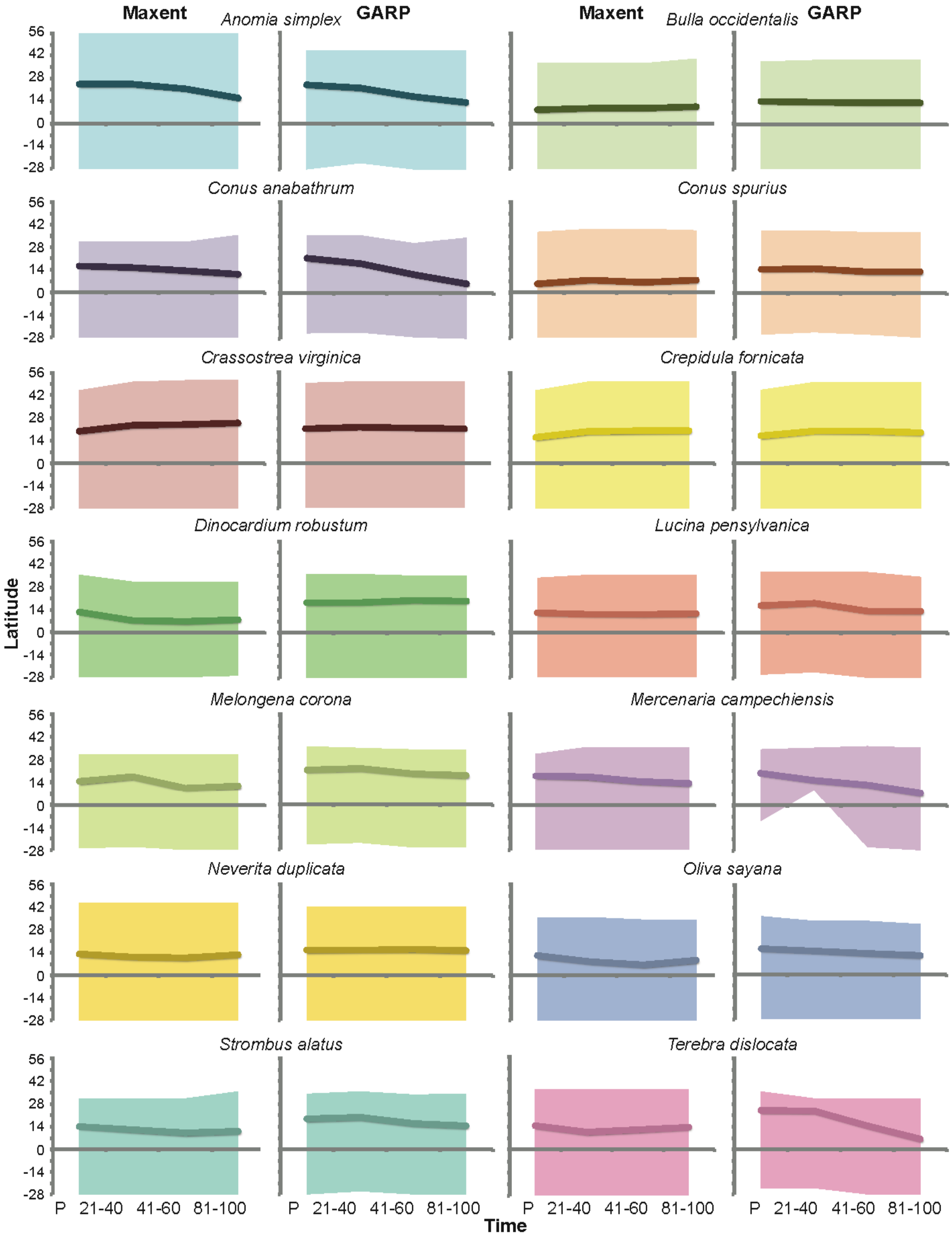
RCP scenario	**MAXENT**	**GARP**
2.6	−1.43	−5.14
4.5	−3.46	−4.14
8.5	−4.37	−3.70
Mean	−3.09	−4.33

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.



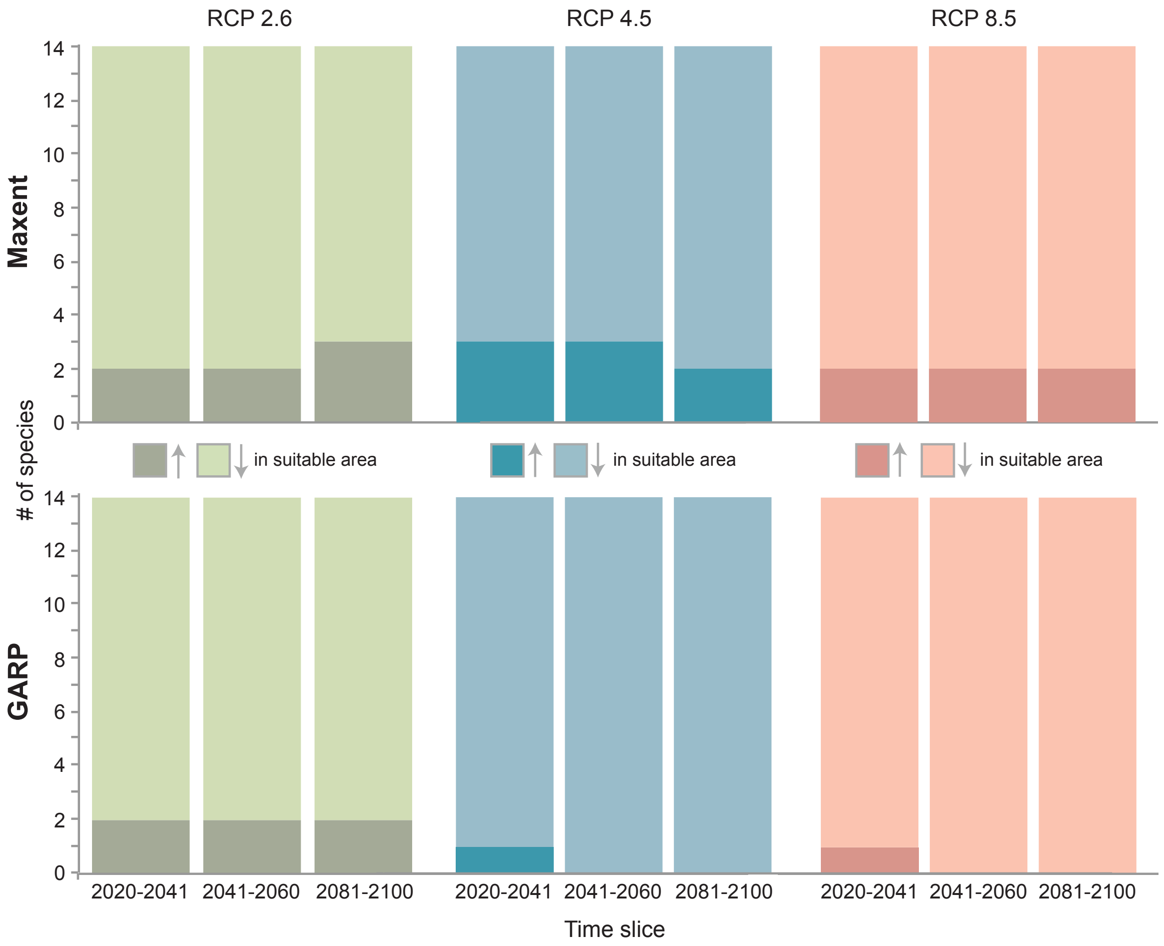


Figure 1.4 Histograms depicting the number of marine mollusk species that gained or lost suitable area in the western North Atlantic per time slice, algorithm and RCP emission scenario compared to present-day models. Darker colours indicate gains in suitable area, whereas lighter colours indicate loss 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.

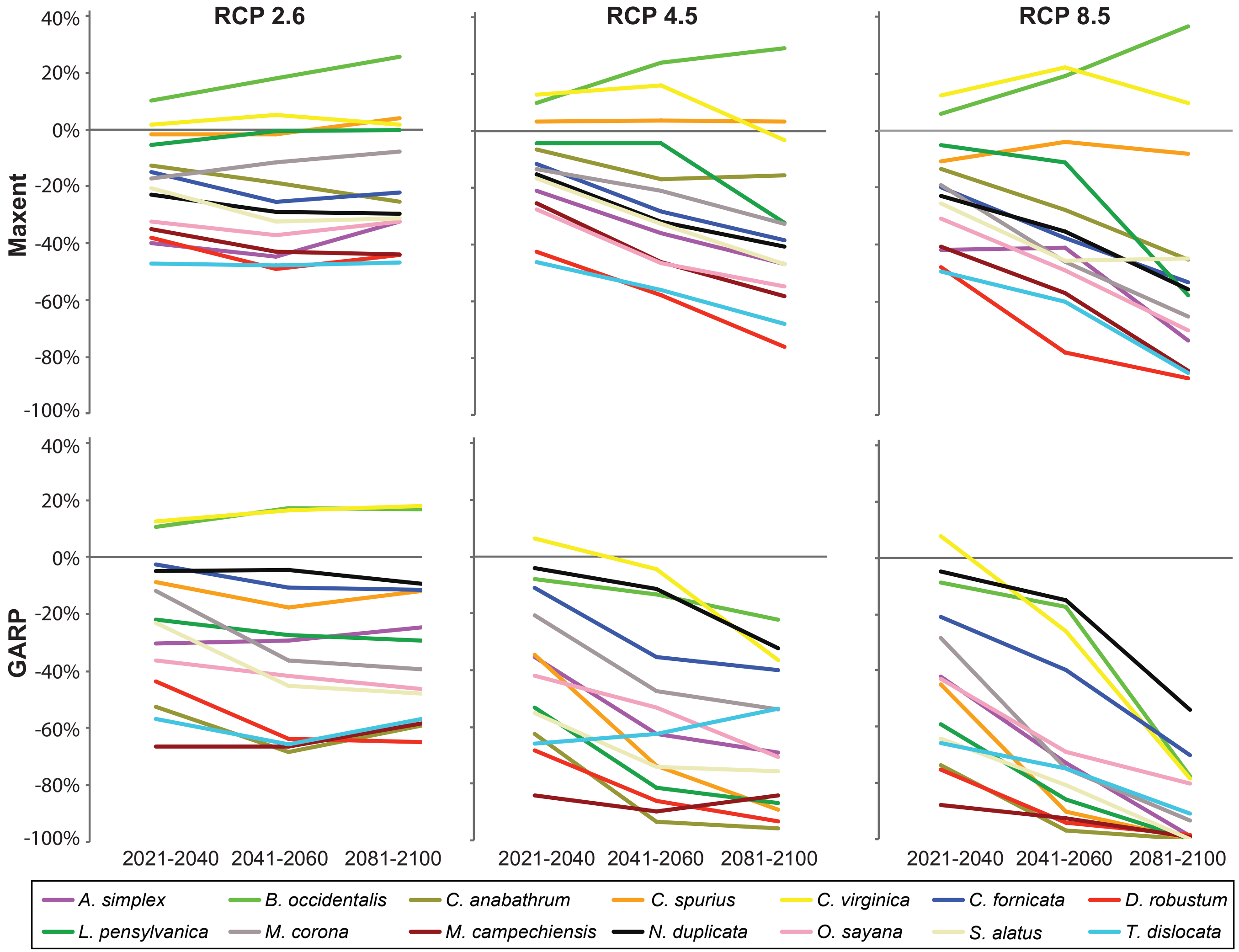


Figure 1.5 Percentage change in suitable area in the western North Atlantic for each of the 14 marine mollusk species from the present day to three future time slices (2021–2040, 2041–2060 and 2081–2100) for all (RCP) emission scenarios. See Table 1.1 for full species names.

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.

Species	**RCP**	**MAXENT**					**GARP**				
		2021–2040	2041–2060	2081–2100	All suitable	Present	2021–2040	2041–2060	2081–2100	All suitable	Present
Bivalvia											
Anomia simplex	2.6	55.1	52.3	52.7	46.5	5.7	37.1	50.6	51.2	43.2	4.3
	4.5	55.9	52.0	52.0	37.5		53.6	51.8	51.2	7.4	
	8.5	55.9	52.0	52.3	20.7		53.6	51.8	51.8	0.0	
Crassostrea virginica	2.6	95.9	95.6	96.9	74.2	4.6	62.8	61.5	52.6	87.3	7.4
	4.5	95.6	96.3	95.9	70.4		64.1	62.8	53.2	38.0	
	8.5	95.6	96.3	96.3	60.8		64.1	62.8	53.8	11.0	
Dinocardium robustum	2.6	60.5	46.7	50.0	44.7	4.0	65.1	49.1	46.7	29.1	3.6
	4.5	57.9	46.7	50.7	19.7		63.9	46.2	49.7	6.4	
	8.5	57.9	46.7	50.7	0.7		63.9	46.2	49.7	1.4	
Lucina pensylvanica	2.6	90.1	87.8	86.4	85.8	9.0	79.3	72.6	67.7	50.2	6.1
	4.5	90.6	87.2	85.8	58.8		79.3	73.8	72.6	5.4	
	8.5	90.6	87.2	86.6	31.0		79.3	72.0	71.3	0.0	
Mercenaria campechiensis	2.6	60.7	53.6	44.0	41.7	2.2	22.4	16.0	18.6	12.9	3.6
	4.5	58.3	48.8	42.9	38.1		22.4	16.3	18.6	3.6	
	8.5	58.3	48.8	42.9	11.9		22.4	16.3	18.6	0.0	
Gastropoda											
Bulla occidentalis	2.6	95.1	93.9	95.0	91.4	16.1	91.8	89.6	85.6	95.9	13.6
	4.5	95.1	94.1	93.9	92.2		91.8	88.6	87.5	71.0	
	8.5	95.1	94.1	94.0	87.8		91.8	88.9	87.7	20.0	
Conus anabathrum	2.6	80.8	67.8	56.3	55.1	6.3	25.6	19.5	11.3	14.3	4.1
	4.5	80.4	66.9	57.1	67.8		24.8	18.8	15.0	0.0	
	8.5	80.4	66.9	57.1	29.4		24.8	18.8	15.0	0.0	
Conus spurius	2.6	86.5	84.6	85.9	81.0	12.1	97.3	95.0	92.1	63.8	10.1
	4.5	85.3	84.4	85.7	81.6		97.1	94.4	93.7	5.8	
	8.5	85.3	84.4	85.7	69.4		97.1	94.6	93.7	0.0	
Crepidula fornicata	2.6	77.3	66.7	69.7	63.9	8.4	89.4	84.9	74.3	73.6	8.7
	4.5	73.9	67.9	67.9	49.7		88.6	82.9	80.8	44.5	
	8.5	73.9	67.9	69.1	38.8		88.6	83.3	80.8	17.8	
Melongena corona	2.6	72.9	68.8	56.3	50.0	1.3	43.5	27.5	24.6	33.3	2.2
	4.5	72.9	64.6	56.3	47.9		42.0	27.5	26.1	19.5	
	8.5	72.9	64.6	56.3	16.7		42.0	27.5	26.1	3.4	
Neverita duplicata	2.6	79.5	73.4	72.7	66.9	5.0	84.0	68.6	59.4	83.4	6.7
	4.5	80.9	73.4	73.0	57.0		73.0	67.6	64.2	60.5	
	8.5	80.9	73.4	74.1	43.7		73.0	67.6	64.2	41.0	
Oliva sayana	2.6	87.9	79.3	58.6	58.4	3.6	73.7	62.3	44.9	43.7	4.3
	4.5	86.2	79.3	62.1	38.7		74.3	61.1	55.1	19.8	
	8.5	86.2	79.3	62.1	27.0		74.3	61.7	55.1	13.8	
Strombus alatus	2.6	75.5	52.9	51.5	57.7	6.6	47.6	18.4	10.9	34.7	4.4
	4.5	64.5	52.9	51.9	42.3		25.6	18.1	15.0	10.6	
	8.5	64.5	52.9	51.9	26.1		25.6	18.4	15.0	0.0	
Terebra dislocata	2.6	53.8	30.7	29.7	48.6	4.5	27.7	9.6	10.2	20.0	2.1
	4.5	31.4	30.7	29.0	30.6		10.9	9.6	11.3	15.3	
	8.5	31.4	30.7	29.0	14.5		10.9	8.9	10.9	3.5	

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 interspecfic 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

Albouy, C., Guilhaumon, F., Leprieur, F., Lasram, F.B.R., Somot, S., Aznar, R., Velez, L., Le Loc'h, F. & Mouillot, D. (2013) Projected climate change and the changing biogeography of coastal Mediterranean fishes. *Journal of Biogeography*, **40**, 534–547.

Alonso, D., Khalil, Z., Satkunanthan, N. & Livett, B.G. (2003) Drugs from the sea: conotoxins as drug leads for neuropathic pain and other neurological conditions. *Mini-Reviews in Medicinal Chemistry*, **3**, 785–787.

Amante, C. & Eakins, B.W. (2009) *ETOPO1 1 arc-minute global relief model: procedures, data sources and analysis*. NOAA Technical Memorandum NESDIS NGDC-24. National Geophysical Data Center, Boulder, CO.

Anderson, R.P., Lew, D. & Peterson, A.T. (2003) Evaluating predictive models of species distributions: criteria for selecting optimal models. *Ecological Modeling*, **162**, 211–232.

Anderson, B.J., Akçakaya, H.R., Araújo, M.B., Fordham, D.A., Martinez-Meyer, E., Thuiller, W. & Brook, B.W. (2009) Dynamics of range margins for metapopulations under climate change. *Proceedings of the Royal Society B: Biological Sciences*, **276**, 1415–1420.

Aranda, S.C. & Lobo, J.M. (2011) How well does presence-only-based species distribution modeling predict assemblage diversity? A case study of the Tenerife flora. *Ecography*, **34**, 31–38.

Araújo, M.B. & Guisan, A. (2006) Five (or so) challenges for distribution modeling. *Journal of Biogeography*, **33**, 1677–1688.

Araújo, M.B., Ferri-Yáñez, F., Bozinovic, F., Marquet, P.A., Valladares, F., Chown, S.L. (2013) Heat freezes niche evolution. *Ecology Letters*, **16**, 1206–1219.

Barve, N., Barve, V., Jiménez-Valverde, A., Lira-Noriega, A., Maher, S.P., Peterson, A.T., Soberón, J. & Villalobos, F. (2011) The crucial role of the accessible area in ecological niche modeling and species distribution modeling. *Ecological Modeling*, **222**, 1810–1819.

Bentlage, B., Peterson, A.T., Barve, N., Cartwright, P. (2013) Plumbing the depths: extending ecological niche modeling and species distribution modeling in three dimensions. *Global Ecology and Biogeography*, **22**, 952–961.

Bivand, R. & Rundel, C. (2011) *rgeos: interface to Geometry Engine – Open Source (GEOS)*. R package version 0.1-8. Available at: http://cran.r-project.org/web/packages/rgeos/.

Buckley, L.B., Hurlbert, A.H. & Jetz, W. (2012) Broad-scale ecological implications of ectothermy and endothermy in changing environments. *Global Ecology and Biogeography*, **9**, 873–885.

Burrows, M.T., Schoeman, D.S., Buckley, L.B., Moore, P., Poloczanska, E.S., Brander, K.M., Brown, C., Bruno, J.F., Duarte, C.M., Halpern, B.S., Holding, J., Kappel, C.V., Kiessling, W., O'Connor, M.I., Pandolfi, J.M., Parmesan, C., Schwing, F.B., Sydeman, W.J. & Richardson, A.J. (1991) The pace of shifting climate in marine and terrestrial ecosystems. *Science*, **334**, 652–655.

Chapman, A.D. & Wieczorek, J. (eds.) (2006) *Guide to best practices for georeferencing*. Global Biodiversity Information Facility, Copenhagen.

Chen, I-C., Hill, J.K., Ohlemüller, R., Roy, D.B. & Thomas, C.D. (2011) Rapid range shifts of species associated with high levels of climate warming. *Science*, **333**, 1024–1026.

Cheung, W.W.L., Lam, V.W.Y., Sarmiento, J.L., Kearney, K., Watson, R. & Pauly, D. (2009) Projecting global marine biodiversity impacts under climate change scenarios. *Fish and Fisheries*, **10**, 235–251.

Clark, R.A., Fox, C.J., Viner, D. & Livermore, M. (2003) North Sea cod and climate change – modeling the effects of temperature on population dynamics. *Global Change Biology*, **9**, 1669–1680.

Collins, W.J., Bellouin, N., Doutriaux-Boucher, M., Gedney, N., Halloran, P., Hinton, T., Hughes, J., Jones, C.D., Joshi, M., Liddicoat, S., Martin, G., O'Connor, F., Rae, J., Senior, C., Sitch, S., Totterdell, I., Wiltshire, A. & Woodward, S. (2011) Development and evaluation of an Earth-system model – HadGEM2. *Geoscientific*

Model Development Discussions, **4**, 997–1062.

Compton, T.J., Rijkenberg, M.J.A., Drent, J. & Piersma, T. (2007) Thermal tolerance ranges and climate variability: a comparison between bivalves from differing climates. *Journal of Experimental Marine Ecology*, **352**, 200–211.

Dambach, J. & Rödder, D. (2011) Applications and future challenges in marine species distribution modeling. *Aquatic Conservation: Marine and Freshwater Ecosystems*, **21**, 92–100.

Davis, A.J., Jenkinson, L.S., Lawton, J.H., Shorrocks, B. & Wood, S. (1998) Making mistakes when predicting shifts in species range in response to global warming. *Nature*, **391**, 783–786.

Drinkwater, K.F., Beaugrand, G., Kaeriyama, M., Kim, S., Ottersen, G., Perry, R.I., Pörtner, H.-O., Polovina, J.J. & Takasuka, A. (2010) On the processes linking climate to ecosystem changes. *Journal of Marine Systems*, **79**, 374–388.

Edwards, M. & Richardson, A.J. (2004) Impact of climate change on marine pelagic phenology and trophic mismatch. *Nature*, **430**, 881–884.

Elith, J., Phillips, S.J., Hastie, T., Dudík, M., Chee, Y.E. & Yates, C.J. (2011) A statistical explanation of MaxEnt for ecologists. *Diversity and Distributions*, **17**, 43–57.

Fordham, D.A., Wigley, T.M.L., Watts, M.J. & Brook, B.W. (2012a) Strengthening forecasts of climate change impacts with multi-ensemble averaged projections using MAGICC/SCENGEN 5.3. *Ecography*, **35**, 4–8.

Fordham, D.A., Akçakaya, H.R., Araújo, M.B., Elith, J., Keith, D.A., Pearson, R., Auld, T.D., Mellin, C., Morgan, J.W., Regan, T.J., Tozer, M., Watts, M.J., White, M., Wintle, B.A., Yates, C. & Brook, B.W. (2012b). Plant extinction risk under climate change: are forecast range shifts alone a good indicator of species vulnerability to global warming? *Global Change Biology*, **18**, 1357–1371.

Fordham, D.A., Mellin, C., Russell, B.D., Akçakaya, R.H., Bradshaw, C.J.A., Aiello-Lammens, M.E., Caley, J.M., Connell, S.D., Mayfield, S., Shepherd, S.A. & Brook, B.W. (2013) Population dynamics can be more important than physiological limits for determining range shifts under climate change. *Global Change Biology*, **19**, 3224–3237.

Foster, D., Schoonmaker, P. & Pickett, S. (1990) Insights from paleoecology to community ecology. *Trends in Ecology & Evolution*, **5**, 119–122.

Gaines, S.D., Gaylord, B., Gerber, L.R., Hastings, A. & Kinlan, B.P. (2007) Connecting places: the ecological consequences of dispersal in the sea. *Oceanography*, **20**, 90–99.

Graham, C.H., Elith, J., Hijmans, R.J., Guisan, A., Peterson, A.T., Loiselle, B.A. & NCEAS Predicting Species Distributions Working Group (2008) The influence of spatial errors in species occurrence data used in distribution models. *Journal of Applied Ecology*, **45**, 239–247.

Guralnick, R.P., Wieczorek, J., Beaman, R., Hijmans, R.J. & BioGeomancer Working Group (2006) BioGeomancer: automated georeferencing to map the world's biodiversity data. *PLoS Biology*, **4**, e381.

Harley, C.D.G. (2011) Climate change, keystone predation, and biodiversity loss. *Science*, **334**, 1124–1127.

Harley, C.D.G., Hughes, A.R., Hultgren, K.M., Miner, B.G., Sorte, C.J.B., Thornber, C.S., Rodriguez, L.F., Tomanek, L. & Williams, S.L. (2006) The impacts of climate change in coastal marine systems. *Ecology Letters*, 9, 228–241.

Hiddink, J.G. (2003) Modeling the adaptive value of intertidal migration and nursery use in the bivalve *Macoma balthica*. *Marine Ecology Progress Series*, 252, 173–185.

Holt, J., Harle, J., Proctor, R., Michel, S., Ashworth, M., Bastone, C., Allen, I., Holmes, R., Smyth, T., Haines, K., Bretherton, D.A. & Smith, G. (2009) Modeling the global coastal ocean. *Philosophical Transactions of the Royal Society A: Mathematical,* *Physical and Engineering Sciences*, **367**, 939–951.

IPCC (2007) *Climate change 2007: the physical science basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change* (ed. by S. Solomon, D. Qin, M. Manning, Z. Chen, M. Marquis, K.B. Averyt, M. Tignor and H.L. Milller). Cambridge University Press, Cambridge, UK.

Jones, C.D., Hughes, J.K., Bellouin, N. *et al.* (2011) The HadGEM2-ES implementation of CMIP5 centennial simulations. *Geoscience Model Development Discussions*, **4**, 689–763.

Jones, M.C., Dye, S.R., Fernandes, J.A., Frölicher, T.L., Pinnegar, J.K., Warren, R. & Cheung, W.W.L. (2013) Predicting the impact of climate change on threatened species in UK waters. *PLoS ONE*, **8**, e54216.

Jones, S.J., Mieszkowska, N. & Wethey, D.S. (2009) Linking thermal tolerances and biogeography: *Mytilus edulis* (L.) at its southern limit on the east coast of the United States. *Biological Bulletin*, **217**, 73–85.

Jones, S.J., Lima, F.P. & Wethey, D.S. (2010) Rising environmental temperatures and biogeography: poleward range contraction of the blue mussel, *Mytilus edulis* L., in the western Atlantic. *Journal of Biogeography*, **37**, 2243–2259.

Korty, R.L., Emanuel, K.A. & Scott, J.R. (2008) Tropical cyclone-induced upper-ocean mixing and climate: application to equable climates. *Journal of Climate*, **21**, 638–654.

Lenoir, S., Beaugrand, G. & Lecuyer, É. (2011) Modeled spatial distribution of marine fish and projected modifications in the North Atlantic Ocean. *Global Change Biology*, **17**, 115–129.

Lima, F.P., Ribeiro, P.A., Queiroz, N., Xavier, R., Tarroso, P., Hawkins, S.J. & Santos, A.M. (2007) Modeling past and present geographical distribution of the marine gastropod *Patella rustica* as a tool for exploring responses to environmental change. *Global Change Biology*, **13**, 2065–2077.

Liu, C., Berry, P.M., Dawson, T.P. & Pearson, R.G. (2005) Selecting thresholds of occurrence in the prediction of species distributions. *Ecography*, **28**, 385–393.

Martin, G.M., Bellouin, N., Collins, W.J. *et al.* (2011) The HadGEM2 family of Met Office Unified Model climate configurations. *Geoscientific Model Development Discussions*, **4**, 765–841.

Mellin, C., Russell, B.D., Connell, S.D., Brook, B.W. & Fordham, D.A. (2012) Geographic range determinants of two commercially important marine mollusks. *Diversity and Distributions*, **18**, 133–146.

Moss, R.H., Edmonds, J.A., Hibbard, K.A., Manning, M.R., Rose, S.K., van Vuuren, D.P., Carter, T.R., Emori, S., Kainuma, M., Kram, T., Meehl, G.A., Mitchell, J.F.B., Nakicenovic, N., Riahi, K., Smith, S.J., Stouffer, R.J., Thomson, A.M., Weyant, J.P. & Wilbanks, T.J. (2010) The next generation of scenarios for climate change research and assessment. *Nature*, **463**, 747–756.

Nenzen, H.K. & Araújo, M.B. (2011) Choice of threshold alters projections of species range shifts under climate change. *Ecological Modeling*, **222**, 3346–3354.

Noble, M.A. (2001) Current patterns over the continental shelf and slope. *Beyond the Golden Gate—oceanography, geology, biology, and environmental issues in the Gulf of the Farallones* (ed. by H.A. Karl, J.L. Chin, E. Ueber, P.H. Stauffer & J.W. Hendley II), pp. 67–89. USGS Circular 1198, United States Geological Survey, Reston, VA.

Owens, H.L., Campbell, L.P., Dornak, L., Saupe, E.E., Barve, N., Soberón, J., Ingenloff, K., Lira-Noriega, A., Hensz, C.M., Myers, C.E. & Peterson, A.T. (2013) Constraints on interpretation of ecological niche models by limited environmental ranges on calibration areas. *Ecological Modeling*, **263**, 10–18.

Pauly, K., Jupp, B.P. & De Clerck, O. (2011) Modeling the distribution and ecology of *Trichosolen* blooms on coral reefs worldwide. *Marine Biology*, **158**, 2239–2256.

Pearman, P.B., Guisan, A., Broennimann, O. & Randin, C.F. (2008) Niche dynamics in space and time. *Trends in Ecology and Evolution*, **23**, 149–158.

Pereira, H.M., Leadley, P.W., Proença, V., Alkemade, R., Scharlemann, J.P.W., Fernandez-Manjarrés, J.F., Araújo, M.B., Balvanera, P., Biggs, R., Cheung, W.W.L., Chini, L., Cooper, H.D., Gilman, E.L., Guénette, S., Hurtt, G.C., Huntington, H.P., Mace, G.M., Oberdorff, T., Revenga, C., Rodrigues, P., Scholes, R.J., Sumaila, U.R. & Walpole, M. (2010) Scenarios for global biodiversity in the 21st Century. *Science*, **330**, 1496–1501.

Peterson, A.T. (2011) Ecological niche conservatism: a time-structured review of evidence. *Journal of Biogeography*, **38**, 817–827.

Peterson, A.T., Stewart, A., Mohamed, K.I. & Araújo, M.B. (2008a) Shifting global invasive potential of European plants with climate change. *PLoS ONE*, **3**, e2441.

Peterson, A.T., Papes, M. & Soberón, J. (2008b) Rethinking receiver operating characteristic analysis. *Ecological Modeling*, **213**, 63–72.

Peterson, A.T., Soberón, J., Pearson, R.G., Anderson, R.P., Martínez-Meyer, E., Nakamura, M. & Araújo, M.B. (2011) *Ecological niches and geographic distributions.* Princeton University Press, Princeton, NJ.

Phillips, S.J., Dudík, M., Elith, J., Graham, C.H., Lehmann, A., Leathwick, J. & Ferrier, S. (2009) Sample selection bias and presence-only distribution models: implications for background and pseudo-absence data. *Ecological Applications*, **19**, 181–197.

Pörtner, H.O. & Knust, R. (2007) Climate change affects marine fishes through the oxygen limitation of thermal tolerance. *Science*, **315**, 95–97.

R Core Team (2012) *R: a language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria.

Reiss, H., Cunze, S., König, K., Neumann, H. & Kröncke, I. (2011) Species distribution modeling of marine benthos: a North Sea case study. *Marine Ecology Progress Series*, 442, 71–86.

Richardson, A.J. & Poloczanska, E.S. (2008) Under-resourced, under threat. *Science*, 320, 1294–1295.

Robinson, L.M., Elith, J., Hobday, A.J., Pearson, R.G., Kendall, B.E., Possingham, H.P. & Richardson, A.J. (2011) Pushing the limits in marine species distribution modeling: lessons from the land present challenges and opportunities. *Global Ecology and Biogeography*, **20**, 789–802.

Royle, J.A., Chandler, R.B., Yackulic, C. & Nichols, J.D. (2012) Likelihood analysis of species occurrence probability from presence-only data for modeling species distributions. *Methods in Ecology and Evolution*, **3**, 545–554.

Russell, B.D., Connell, S.D., Mellin, C., Brook, B.W., Burnell, O.W. & Fordham, D.A. (2012) Predicting the distribution of commercially important invertebrate stocks under future climate. *PLoS ONE*, **7**, e46554.

Sibson, R. (1981) A brief description of natural neighbor interpolation. *Interpolating multivariate data* (ed. by V. Barnett), pp. 21–36. John Wiley & Sons, NY.

Somero, G.N. (2002) Thermal physiology and vertical zonation of intertidal animals: optima, limits, and costs of living. *Integrative and Comparative Biology*, **42**, 780–789.

Sorte, C.J.B., Williams, S.L. & Carlton, J.T. (2010) Marine range shifts and species introductions: comparative spread rates and community impacts. *Global Ecology and Biogeography*, **19**, 303–316.

Stockwell, D.R.B. & Peters, D.P. (1999) The GARP modeling system: problems and solutions to automated spatial prediction. *International Journal of Geographical Information Science*, **13**, 143–158.

Sunday, J.M., Bates, A.E. & Dulvy, N.K. (2012) Thermal tolerance and the global redistribution of animals. *Nature Climate Change*, **2**, 686–690.

Talmage, S.C. & Gobler, C.J. (2009) The effects of elevated carbon dioxide concentrations on the metamorphosis, size, and survival of larval hard clams (*Mercenaria mercenaria*), bay scallops (*Argopecten irradians*) and Eastern oysters (*Crassostrea virginica*). *Limnology and Oceanography*, **54**, 2072–2080.

Tewksbury, J.J., Huey, R.B. & Deutsch, C.A. (2008) Putting the heat on tropical animals. *Science*, 320, 1296–1297.

Thomas, C.D., Cameron, A., Green, R.E., Bakkenes, M., Beaumont, L.J., Collingham, Y.C., Erasmus, B.F.N., Ferreira de Siqueira, M., Grainger, A., Hannah, L., Hughes, L., Huntley, B., van Jaarsveld, A.S., Midgley, G.F., Miles, L., Ortega-Huerta, M.A., Peterson, A.T., Phillips, O.L. & Williams, S.E. (2004) Extinction risk from climate change. *Nature*, **427**, 145–148.

Thuiller, W., Lavorel, S., Araújo, M.B., Sykes, M.T. & Prentice, I.C. (2005) Climate change threats to plant diversity in Europe. *Proceedings of the National Academy of Sciences USA*, **102**, 8245–8250.

Tomašových, A. & Kidwell, S.M. (2009) Preservation of spatial and environmental gradients by death assemblages. *Paleobiology*, **35**, 119–145.

Tunnell, J.W., Andrews, J., Barrera, N.C. & Moretzsohn, F. (2010) *Encyclopedia of Texas seashells*: *identification, ecology, distribution, and history.* Texas A&M University Press, College Station, TX.

Tyberghein, L., Verbruggen, H., Pauly, K., Troupin, C., Mineur, F. & De Clerck, O. (2012) Bio-ORACLE: a global environmental dataset for marine species distribution modeling. *Global Ecology and Biogeography*, **21**, 272–281.

Urban, M.C., Tewksbury, J.J. & Sheldon, K.S. (2012) On a collision course: competition and dispersal differences create no-analogue communities and cause extinctions during climate change. *Proceedings of the Royal Society B: Biological Sciences*, **279**, 2072–2080.

VanDerWal, J., Shoo, L.P., Graham, C. & Williams, S.E. (2009) Selecting pseudo-absence data for presence-only distribution modeling: how far should you stray from what you know? *Ecological Modeling*, **220**, 589–594.

VanDerWal, J., Murphy, H.T., Kutt, A.S., Perkins, G.C., Bateman, B.L., Perry, J.J. & Reside, A.E. (2013) Focus on poleward shifts in species' distribution underestimates the fingerprint of climate change. *Nature Climate Change*, **3**, 239–243.

Visconti, P., Pressey, R.L., Giorgini, D., Maiorano, L., Bakkenes, M., Boitani, L., Alkemade, R., Falcucci, A., Chiozza, F. & Rondinini, C. (2011) Future hotspots of terrestrial mammal loss. *Philosophical Transactions of the Royal Society B*, **366**, 2693–1701.

Wieczorek, J., Guo, Q., Boureau, C. & Wieczorek, C. (2001) *Georeferencing calculator*. University of California, Berkeley, CA. Available at: http://manisnet.org/gci2.html (accessed January 2013).

Wieczorek, J., Guo, Q. & Hijmans, R.J. (2004) The point-radius method for georeferencing locality descriptions and calculating associated uncertainty. *International Journal of Geographical Information Science*, **18**, 745–767.

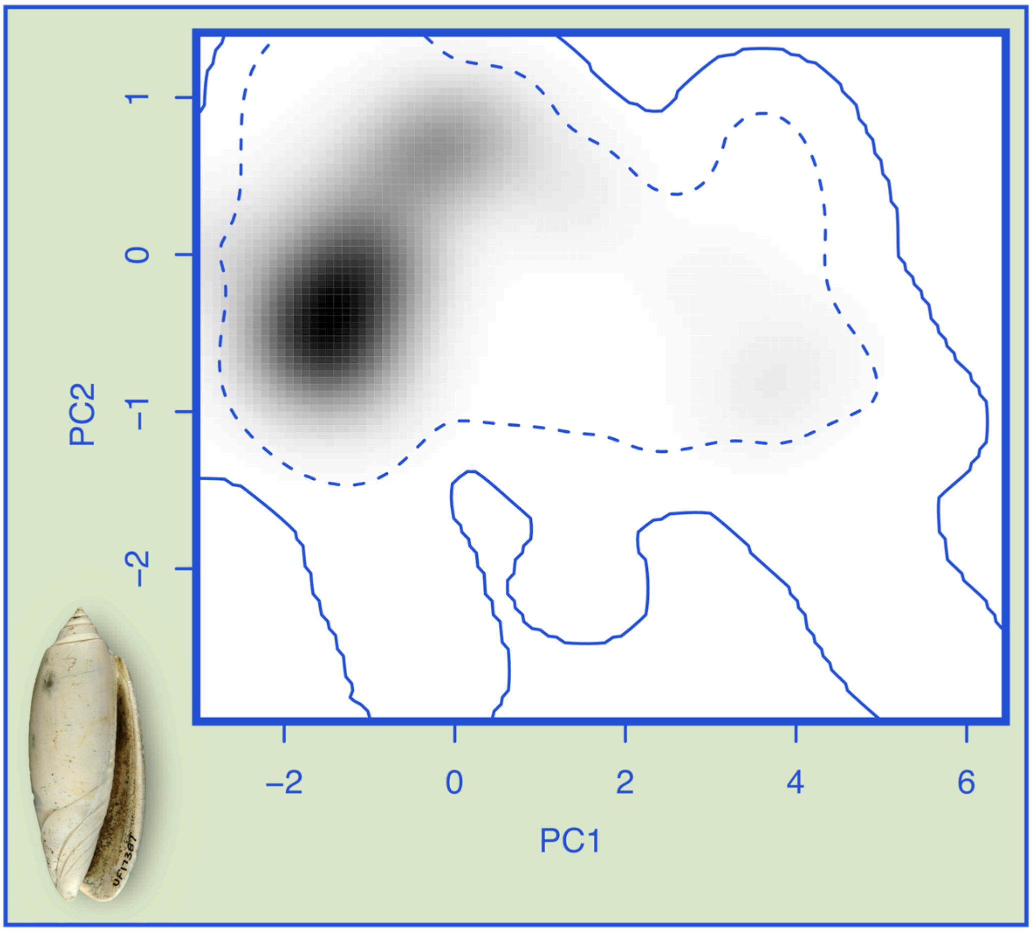
Worm, B., Barbier, E.B., Beaumont, N., Duffy, J.E., Folke, C., Halpern, B.S., Jackson, J.B.C., Lotze, H.K., Micheli, F., Palumbi, S., Sala, E., Selkoe, K.A., Stachowicz, J.J. & Watson, R. (2006) Impacts of biodiversity loss on ocean ecosystem services. *Science*, **314**, 787–790.

Yackulic, C.B., Chandler, R., Zipkin, E.F., Royle, J.A., Nichols, J.D., Campbell Grant, E.H. & Veran, S. (2013) Presence-only modeling using MAXENT: when can we trust the inferences? *Methods in Ecology and Evolution*, **4**, 236–243.

Yesson, C., Taylor, M.L., Tittensor, D.P., Davies, A.J., Guinotte, J., Baco, A., Black, J., Hall-Spencer, J.M. & Rogers, A.D. (2012) Global habitat suitability of cold-water octocorals. *Journal of Biogeography*, **39**, 1278–1292.

Zurrell, D., Elith, J. & Schröder, B. (2012) Predicting to new environments: tools for visualizing model behaviour and impacts on mapped distributions. *Diversity and Distributions*, **18**, 628–634.

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

(Appendix S2.2). 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 overoptimistic 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

Species/Comparison		mPWP—LIG	LIG—mPWP	PI—LIG	LIG—PI	mPWP—PI	PI—mPWP
Environmental comparison: p-values for tests using PCA on all 6 variables							
Bivalvia	*Anomia simplex*	**0.06**	0.00	0.00	0.00	0.04	0.00
	Crassostrea virginica	0.05	0.01	0.00	0.00	0.03	0.00
	Dinocardium robustum	**0.32**	0.00	0.00	0.00	0.01	0.00
	Lucina pensylvanica	**0.16**	0.00	**0.09**	0.00	**0.14**	0.00
	Mercenaria campechiensis	**0.15**	0.00	0.00	0.00	**0.06**	0.00
Gastropoda	*Bulla occidentalis*	**0.11**	0.00	0.00	0.00	**0.16**	0.00
	Crepidula fornicata	**0.11**	0.00	0.01	0.00	0.01	0.01
	Neverita duplicata	**0.09**	0.00	0.00	0.00	**0.05**	0.00
	Oliva sayana	**0.12**	0.00	0.00	0.00	0.03	0.00
	Terebra dislocata	**0.06**	0.01	0.00	0.00	0.01	0.00
Environmental comparison: p-values for tests using PCA on 3 most important variables							
Bivalvia	*Anomia simplex*	0.01	0.00	0.00	0.00	0.01	0.00
	Crassostrea virginica	0.04	0.00	0.03	0.00	0.00	0.00
	Dinocardium robustum	0.01	0.00	0.00	0.02	**0.09**	0.00
	Lucina pensylvanica	**0.25**	0.01	0.00	0.00	0.03	0.03
	Mercenaria campechiensis	0.01	0.00	0.00	0.02	0.00	0.00
Gastropoda	*Bulla occidentalis*	**0.34**	**0.54**	**0.10**	**0.29**	**0.31**	**0.20**
	Crepidula fornicata	0.03	0.00	0.02	0.00	**0.29**	**0.58**
	Neverita duplicata	0.08	0.00	0.01	**0.44**	0.01	0.00
	Oliva sayana	0.02	0.00	0.00	0.00	0.00	0.00
	Terebra dislocata	0.02	0.00	0.00	0.01	0.00	0.00
Environmental comparison: p-values for tests using raw temperature variables							
Bivalvia	*Anomia simplex*	<0.05	<0.05	<0.05	<0.05	<0.05	<0.05
	Crassostrea virginica	<0.05	**NS**	<0.05	<0.05	<0.05	**NS**
	Dinocardium robustum	<0.05	<0.05	<0.05	<0.05	<0.05	<0.05
	Lucina pensylvanica	<0.05	<0.05	<0.05	<0.05	<0.05	<0.05
	Mercenaria campechiensis	<0.05	<0.05	<0.05	<0.05	<0.05	<0.05
Gastropoda	*Bulla occidentalis*	**NS**	**NS**	<0.05	<0.05	<0.05	**NS**
	Crepidula fornicata	<0.05	<0.05	<0.05	<0.05	<0.05	<0.05
	Neverita duplicata	<0.05	<0.05	<0.05	<0.05	<0.05	<0.05
	Oliva sayana	<0.05	<0.05	<0.05	<0.05	<0.05	**NS**
	Terebra dislocata	<0.05	<0.05	<0.05	<0.05	<0.05	<0.05
Geographic comparison: p-values for tests using ecological niche models							
Bivalvia	*Anomia simplex*	<0.05	<0.05	<0.05	<0.05	<0.05	<0.05
	Crassostrea virginica	**NS**	<0.05	<0.05	<0.05	<0.05	<0.05
	Dinocardium robustum	<0.05	<0.05	<0.05	<0.05	<0.05	<0.05
	Lucina pensylvanica	<0.05	<0.05	<0.05	<0.05	<0.05	**NS**
	Mercenaria campechiensis	<0.05	<0.05	<0.05	<0.05	<0.05	<0.05
Gastropoda	*Bulla occidentalis*	<0.05*	<0.05	<0.05	<0.05	<0.05	**NS**
	Crepidula fornicata	<0.05	<0.05	<0.05	<0.05	<0.05	<0.05
	Neverita duplicata	<0.05	<0.05	<0.05	<0.05	<0.05	<0.05
	Oliva sayana	<0.05	<0.05	<0.05	<0.05	<0.05	<0.05
	Terebra dislocata	<0.05	<0.05	<0.05	<0.05	<0.05	<0.05

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.

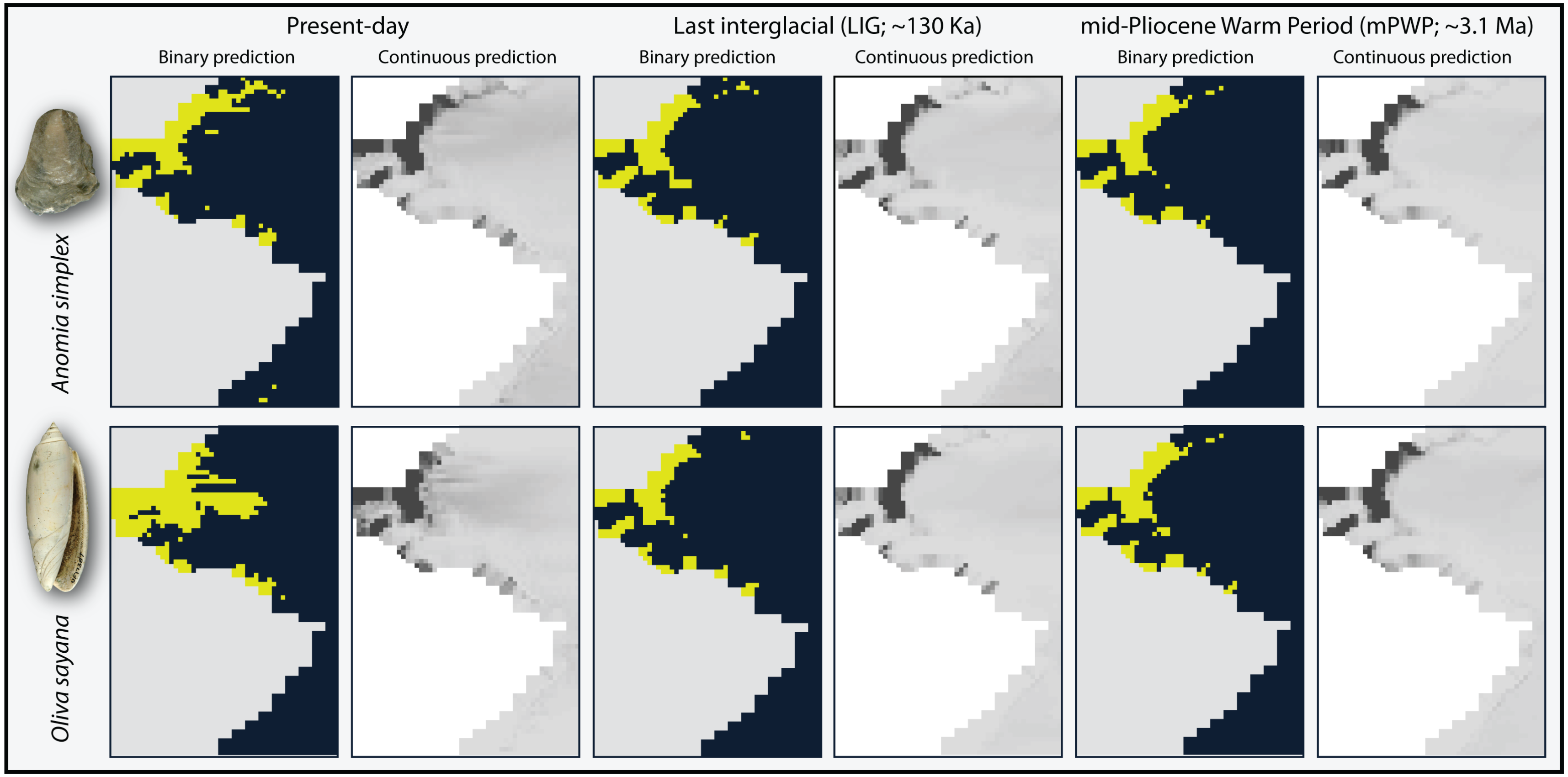


Figure 2.1 Representative ecological niche models for the present, LIG, and mPWP time slices for two species: *Anomia simplex* and *Oliva sayana*. Binary and continuous predictions are presented, with binary predictions thresholded using the mean suitability value from the continuous output. For the 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.

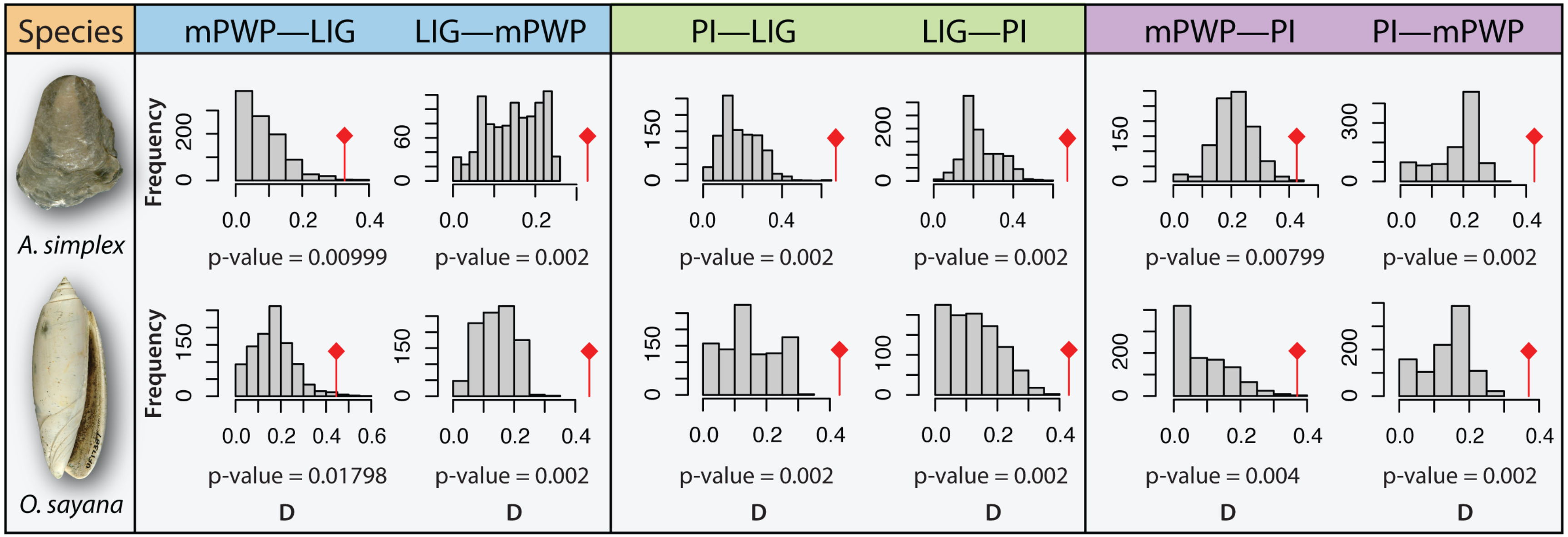


Figure 2.2 Representative results from the analyses using a PCA on the three most important environmental variables (maximum and minimum surface temperature, and maximum surface salinity) for *Anomia simplex* and *Oliva sayana*. Comparisons are shown for the Last Interglacial (LIG, ~130 Ka), mid-Pliocene 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.

Species/Comparison		mPWP—LIG	LIG—mPWP	PI—LIG	LIG—PI	mPWP—PI	PI—mPWP
Environmental comparison: maximum surface temperature							
Bivalvia	*Anomia simplex*	0.04	0.00	0.00	0.00	0.00	0.00
	Crassostrea virginica	0.00	0.00	0.00	0.02	0.01	0.00
	Dinocardium robustum	0.03	0.00	0.00	0.00	**0.09**	0.00
	Lucina pensylvanica	0.00	0.00	0.00	0.00	**0.81**	**0.42**
	Mercenaria campechiensis	0.01	0.00	0.00	0.03	0.00	0.00
Gastropoda	*Bulla occidentalis*	0.00	0.00	0.02	**0.60**	**0.96**	0.02
	Crepidula fornicata	0.00	0.00	0.00	0.00	0.01	0.00
	Neverita duplicata	0.01	0.00	0.00	**0.06**	0.00	0.00
	Oliva sayana	0.00	0.00	0.01	**0.15**	**0.54**	0.00
	Terebra dislocata	0.03	0.00	0.00	0.02	**0.43**	0.02
Environmental comparison: minimum surface temperature							
Bivalvia	*Anomia simplex*	**0.21**	0.00	0.00	0.00	0.00	0.00
	Crassostrea virginica	**0.91**	0.05	0.00	0.03	0.01	0.00
	Dinocardium robustum	**0.11**	0.00	0.00	0.00	0.00	0.00
	Lucina pensylvanica	**0.68**	0.00	0.00	0.00	**0.77**	**0.22**
	Mercenaria campechiensis	**0.82**	0.00	0.00	0.00	0.01	0.00
Gastropoda	*Bulla occidentalis*	**0.66**	0.00	**0.09**	0.10	**0.85**	**0.10**
	Crepidula fornicata	**0.17**	0.00	0.01	0.00	**0.44**	0.00
	Neverita duplicata	0.50	0.00	**0.05**	0.00	0.00	0.00
	Oliva sayana	**0.07**	0.00	0.03	0.00	**0.29**	0.00
	Terebra dislocata	**0.18**	0.00	0.00	0.00	0.05	0.00

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* *al.*, 2011). 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.*, 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

Allmon, W.D. (2001) Nutrients, temperature, disturbance, and evolution: a model for the late Cenozoic marine record of the western Atlantic. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **166**, 9–26.

Allmon, W.D., Rosenberg, G., Portell, R.W. & Schindler, K. (1993) Diversity of Pliocene to Recent Atlantic coastal plain mollusks. *Science*, **260**, 1626–1628.

Angilletta, M. (2009) *Thermal Adaptation: A Theoretical and Empirical Synthesis*. Oxford University Press, Oxford.

Araújo, M.B. & Peterson, A.T. (2012) Uses and misuses of bioclimatic envelope modeling. *Ecology*, **93**, 1527–1539.

Araújo, M.B., Ferri-Yanez, F., Bozinovic, F., Marquet, P.A., Valladares, F. & Chown, S.L. (2013) Heat freezes niche evolution. *Ecology Letters*, **16**, 1206–1219.

Austin, M.P. (1985) Continuum concept, ordination methods and niche theory. *Annual Review of Ecology and Systematics*, **16**, 39–61.

Austin, M.P., Nicholls, A.O., Doherty, M.D. & Meyers, J.A. (1994) Determining species response functions to an environmental gradient by means of a beta-function. *Journal of Vegetation Science*, **5**, 215–228.

Balanyá, J., Oller, J.M., Huey, R.B., Gilchrist, G.W. & Serra, L. (2006) Global genetic change tracks global warming in *Drosophila subobscura*. *Science*, **313**, 1773–1775.

Berger, A. & Loutre, M.F. (1991) Insolation values for the climate of the last 10 million years. *Quaternary Science Reviews*, **10**, 297–317.

Bijma, J., Pörtner, H.-O., Yesson, C. & Rogers, A.D. (2013) Climate change and the oceans – what does the future hold? *Marine Pollution Bulletin*, **74**, 495–505.

Braconnot, P., Otto-Bliesner, B., Harrison, S., Joussaume, S., Peterchmitt, J.-Y., Abe-Ouchi, A., Crucifix, M., Driesschaert, E., Fichefet, T., Hewitt, C.D., Kageyama, M., Kitoh, A., Laîné, A., Loutre, M.-F., Marti, O., Merkel, U., Ramstein, G., Valdes, P., Weber, S.L., Yu, Y. & Zhao, Y. (2007) Results of PMIP2 coupled simulations of the Mid-Holocene and Last Glacial Maximum – Part 1: experiments and large-scale features. *Climate of the Past*, **3**, 261–277.

Broennimann, O., Treier, U.A., Müller-Schärer, H., Thuiller, W., Peterson, A.T. & Guisan, A. (2007) Evidence of climatic niche shift during biological invasion. *Ecology Letters*, **10**, 701–709.

Broennimann, O., Fitzpatrick, M.C., Pearman, P.B., Petitpierre, B., Pellissier, L., Yoccoz, N.G., Thuiller, W., Fortin, M.-J., Randin, C., Zimmermann, N.E., Graham, C.H. & Guisan, A. (2012) Measuring ecological niche overlap from occurrence and spatial environmental data. *Global Ecology and Biogeography*, **21**, 481–497.

Buckley, L.B., Hurlbert, A.H. & Jetz, W. (2012) Broad-scale ecological implications of ectothermy and endothermy in changing environments. *Global Ecology and Biogeography*, **9**, 873–885.

Chapman, A.D. & Wieczorek, J. (ed.^eds) (2006) *Guide to best practices for georeferencing*. Global Biodiversity Information Facility, Copenhagen.

Cheddadi, R., Vendramin, G.G., Litt, T., François, L., Kageyama, M., Lorentz, S., Laurent, J.-M., de Beaulieu, J.-L., Sadori, L., Jost, A. & Lunt, D. (2006) Imprints of glacial refugia in the modern genetic diversity of *Pinus sylvestris*. *Global Ecology and Biogeography*, **15**, 271–282.

Chen, I.-C., Hill, J.K., Ohlemüller, R., Roy, D.B. & Thomas, C.D. (2011) Rapid range shifts of species associated with high levels of climate warming. *Science*, **333**, 1024–1026.

Cronin, T.M. (1988) Evolution of marine climates of the U.S. Atlantic Coast during the past four million years. *Philosophical Transactions of the Royal Society B*, **318**, 661–678.

Davis, A.J., Jenkinson, L.S., Lawton, J.H., Shorrocks, B. & Wood, S. (1998) Making mistakes when predicting shifts in species range in response to global warming. *Science*, **391**, 783–786.

Dawson, T.P., Jackson, S.T., House, J.I., Prentice, I.C. & Mace, G.M. (2011) Beyond predictions: biodiversity conservation in a changing climate. *Science*, **332**, 53–58.

Dietl, G.P. & Flessa, K.W. (2011) Conservation paleobiology: putting the dead to work. *Trends in Ecology and Evolution*, **26**, 30–37.

Dowsett, H.J., Chandler, M.A. & Robinson, M.M. (2009) Surface temperatures of the Mid-Pliocene North Atlantic Ocean: implications for future climate. *Philosophical Transactions of the Royal Society A*, **367**, 69–84.

Dudík, M., Schapire, R.E. & Phillips, S.J. (2005) Correcting sample selection bias in maximum entropy density estimation. *Advances in Neural Information Processing Systems*, pp. 323–330. The MIT Press.

Eldredge, N., Thompson, J.N., Brakefield, P.M., Gavrilets, S., Jablonski, D., Jackson, J.B.C., Lenski, R.E., Lieberman, B.S., McPeek, M.A. & Miller, W.I. (2005) The dynamics of evolutionary stasis. *Paleobiology*, **31**, 133–145.

Elith, J., Phillips, S.J., Hastie, T., Dudik, M., Chee, Y.E. & Yates, C.J. (2011) A statistical explanation of MaxEnt for ecologists. *Diversity and Distributions*, **17**, 43–57.

Fordham, D.A., Wigley, T.M.L., Watts, M.J. & Brook, B.W. (2012) Strengthening forecasts of climate change impacts with multi-ensemble averaged projections using MAGICC/SCENGEN 5.3. . *Ecography*, **45**, 4–8.

Fordham, D.A., Mellin, C., Russell, B.D., Akçakaya, R.H., Bradshaw, C.J.A., Aiello-Lammens, M.E., Caley, J.M., Connell, S.D., Mayfield, S., Shepherd, S.A. & Brook, B.W. (2013) Population dynamics can be more important than physiological limits for determining range shifts under climate change *Global Change Biology*, **19**, 3224–3237.

Foster, D., Schoonmaker, P. & Pickett, S. (1990) Insights from paleoecology to community ecology. *Trends in Ecology & Evolution*, **5**, 119–122.

Freeman, E.A. & Moisen, G.G. (2008) A comparison of the performance of threshold criteria for binary classification in terms of predicted prevalence and kappa. *Ecological Modeling*, **217**, 48–58.

Fritz, S.A., Schnitzler, J., Eronen, J.T., Hof, C., Böhning-Gaese, K. & Graham, C.H. (2013) Diversity in time and space: wanted dead and alive. *Trends in Ecology and Evolution*, **28**, 509–516.

Gordon, C., Cooper, C., Senior, C.A., Banks, H., Gregory, J.M., Johns, T.C., Mitchell, J.F.B. & Wood, R.A. (2000) The simulation of SST, sea ice extents and ocean heat transports in a version of the Hadley Centre coupled model without flux adjustments. *Climate Dynamics*, **16**, 147–168.

Graham, C.H., Moritz, C. & Williams, S.E. (2006) Habitat history improves prediction of biodiversity in rainforest fauna. *Proceedings of the National Academy of Sciences*, **103**, 632–636.

Graham, C.H., Elith, J., Hijmans, R.J., Guisan, A., Peterson, A.T., Loiselle, B.A. & Group, T.N.P.S.D.W. (2008) The influence of spatial errors in species occurrence data used in distribution models. *Journal of Applied Ecology*, **45**, 239–247.

Haug, G.H. & Tiedemann, R. (1998) Effect of the formation of the Isthmus of Panama on the Atlantic Ocean thermohaline circulation. *Nature*, **393**, 673–676.

Haywood, A.M., Dowsett, H.J., Robinson, M.M., Stoll, D.K., Dolan, A.M., Lunt, D.J., Otto-Bliesner, B. & Chandler, M.A. (2011) Pliocene Model Intercomparison Project (PlioMIP): experimental design and boundary conditions (Experiment 2). *Geoscientific Model Development*, **4**, 571–577.

Hernandez, P.A., Graham, C.H., Master, L.L. & Albert, D.L. (2006) The effect of sample size and species characteristics on performance of different distribution modeling methods. *Ecography*, **29**, 773–785.

Hickling, R., Roy, D.B., Hill, J.K., Fox, R. & Thomas, C.D. (2006) The distributions of a wide range of taxonomic groups are expanding polewards. *Global Change Biology*, **12**, 450–455.

Hof, C., Rahbek, C. & Araújo, M.B. (2010) Phylogenetic signals in the climatic niches of the world's amphibians. *Ecography*, **33**, 242–250.

Hof, C., Levinsky, I., Araújo, M.B. & Rahbek, C. (2011) Rethinking species' ability to cope with rapid climate change. *Global Change Biology*, **17**, 2987–2990.

Hoffmann, A.A. & Sgrò, C.M. (2011) Climate change and evolutionary adaptation. *Nature* **470**, 479–485.

Holt, R.D. (1996) Adaptive evolution in source-sink environments: direct and indirect effects of density-dependence on niche evolution. *Oikos*, **75**, 182–192.

Hooper, H.L., Connon, R., Callaghan, A., Fryer, G., Yarwood-Buchanan, S., Biggs, J., Maund, S.J., Hutchinson, T.H. & Sibly, R.M. (2008) The ecological niche of Daphnia magna characterized using population growth rate. *Ecology*, **89**, 1015–1022.

IPCC (2013) *Climate Change 2013: The Physical Science Basis.* Intergovernmental Panel on Climate Change Secretariat, Geneva.

Jablonski, D., Belanger, C.L., Berke, S.K., Huang, S., Krug, A.Z., Roy, K., Tomasovych, A. & Valentine, J.W. (2013) Out of the tropics, but how? Fossils, bridge species, and thermal ranges in the dynamics of the marine latitudinal diversity gradient. *Proceedings of the National Academy of Sciences*, **110**, 10487–10494.

Jackson, S.T. & Overpeck, J.T. (2000) Responses of plant populations and communities to environmental changes of the late Quaternary. *Paleobiology*, **26**, 194–220.

Jones, S.J., Mieszkowska, N. & Wethey, D.S. (2009) Linking thermal tolerances and biogeography: *Mytilus edulis* (L.) at its southern limit on the east coast of the United States. *Biological Bulletin*, **217**, 73–85.

Kawecki, T.J. (1995) Demography of source-sink populations and the evolution of ecological niches. *Evolutionary Ecology* **9**, 38–44.

Kearney, M., Shine, R. & Porter, W.P. (2009) The potential for behavioral thermoregulation to buffer "cold-blooded" animals against climate warming. *Proceedings of the National Academy of Sciences*, **106**, 3835–3840.

Kearney, M.R., Wintle, B.A. & Porter, W.P. (2010) Correlative and mechanistic models of species distribution provide congruent forecasts under climate change. *Conservation Letters*, **3**, 203–213.

Kearney, M.R., Simpson, S.J., Raubenheimer, D. & Kooijman, S.A.L.M. (2013) Balancing heat, water and nutrients under environmental change: a thermodynamic framework. *Functional Ecology*, **27**, 950–966.

Kidwell, S.M. & Holland, S.M. (2002) The quality of the fossil record: implications for evolutionary analyses. *Annual Review of Ecology and Systematics*, **33**, 561–588.

Klaus, J.S., Lutz, B.P., McNeill, D.F., Budd, A.F., Johnson, K.G. & Ishman, S.E. (2011) Rise and fall of Pliocene free-living corals in the Caribbean. *Geology*, **39**, 375–378.

Kozak, K.H. & Wiens, J.J. (2006) Does niche conservatism promote speciation? A case study in North American salamanders. *Evolution*, **60**, 2604–2621.

Lavergne, S., Mouquet, N., Thuiller, W. & Ronce, O. (2010) Biodiversity and climate change: integrating evolutionary and ecological responses of species and communities. *Annual Review of Ecology, Evolution, and Systematics* **41**, 321–350.

Liu, C., Berry, P.M., Dawson, T.P. & Pearson, R.G. (2005) Selecting thresholds of occurrence in the prediction of species distributions. *Ecography*, **28**, 385–393.

Loulergue, L., Schilt, A., Spahni, R., Masson-Delmotte, V., Blunier, T., Lemieux, B., Barnola, J.-M., Raynaud, D., Stocker, T.F. & Chappellaz, J. (2008) Orbital and millennial-scale features of atmospheric CH4 over the past 800,000 years. *Nature*, **453**, 383–386.

Maclean, I.M.D. & Wilson, R.J. (2011) Recent ecological responses to climate change support predictions of high extinction risk. *Proceedings of the National Academy of Sciences*, **108**, 12337–12342.

Malizia, R.W. & Stigall, A.L. (2011) Niche stability in Late Ordovician articulated brachiopod species before, during, and after the Richmondian invasion. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **311**, 154–170.

Martínez-Meyer, E. & Peterson, A.T. (2006) Conservatism of ecological niche characteristics in North American plant species over the Pleistocene-to-Recent transition. *Journal of Biogeography* **33**, 1779–1789.

Martínez-Meyer, E., Peterson, A.T. & Hargrove, W.W. (2004) Ecological niches as stable distributional constraints on mammal species, with implications for Pleistocene extinctions and climate change projections for biodiversity. *Global Ecology and Biogeography*, **13**, 305–314.

Moritz, C. & Agudo, R. (2013) The future of species under climate change: resilience or decline? . *Science*, **341**, 504–508.

Myers, C.E. & Saupe, E.E. (2013) A macroevolutionary expansion of the modern synthesis and the importance of extrinsic abiotic factors. *Palaeontology*, **56**, 1179–1198.

Owens, H.L., Campbell, L.P., Dornak, L.L., Saupe, E.E., Barve, N., Soberón, J., Ingenloff, K., Lira-Noriega, A., Hensz, C.M., Myers, C.E. & Peterson, A.T. (2013) Constraints on interpretation of ecological niche models by limited environmental ranges on calibration areas. *Ecological Modeling*, **263**, 10–18.

Pearman, P.B., Guisan, A., Broennimann, O. & Randin, C.F. (2008) Niche dynamics in space and time. *Trends in Ecology & Evolution*, **23**, 149–158.

Pearson, R.G., Raxworthy, C.J., Nakamura, M. & Peterson, A.T. (2007) Predicting species distributions from small numbers of occurrence records: a test case using cryptic geckos in Madagascar. *Journal of Biogeography*, **34**, 102–117.

Pereira, H.M., Leadley, P.W., Proença, V., Alkemade, R., Scharlemann, J.P.W., Fernandez-Manjarrés, J.F., Araújo, M.B., Balvanera, P., Biggs, R., Cheung, W.W.L., Chini, L., Cooper, H.D., Gilman, E.L., Guénette, S., Hurtt, G.C., Huntington, H.P., Mace, G.M., Oberdorff, T., Revenga, C., Rodrigues, P., Scholes, R.J., Sumaila, U.R. & Walpole, M. (2010) Scenarios for global biodiversity in the 21st Century. *Science*, **330**, 1496–1501.

Perneger, T.V. (1998) What's wrong with Bonferroni adjustments. *British Medical Journal*, **316**, 1236–1238.

Peterson, A.T. (2011) Ecological niche conservatism: a time-structured review of evidence. *Journal of Biogeography*, **38**, 817–827

Peterson, A.T., Soberón, J. & Sanchez-Cordero, V. (1999) Conservatism of ecological niches in evolutionary time. *Science*, **285**, 1265–1267.

Peterson, A.T., Papes, M. & Soberón, J. (2008) Rethinking receiver operating characteristic analysis. *Ecological Modeling*, **213**, 63–72.

Peterson, A.T., Soberón, J., Pearson, R.G., Anderson, R.P., Martínez-Meyer, E., Nakamura, M. & Araújo, M.B. (2011) *Ecological Niches and Geographic Distributions*. Princeton University Press, Princeton.

Petit, J.R., Jouzel, J., Raynaud, D., Barkov, N.I., Barnola, J.-M., Basile, I., Bender, M., Chappellaz, J., Davis, J., Delaygue, G., Delmotte, M., Kotlyakov, V.M., Legrand, M., Lipenkov, V., Lorius, C., Pepin, L., Ritz, C., Saltzman, E. & Stievenard, M. (1999) Climate and atmospheric history of the past 420,000 years from the Vostok Ice Core, Antarctica. *Nature*, **399**, 429–436.

Phillips, S.J., Anderson, R.P. & Schapire, R.E. (2006) Maximum entropy modeling of species geographic distributions. *Ecological Modeling*, **190**, 231–259.

Phillips, S.J., Dudík, M., Elith, J., Graham, C.H., Lehmann, A., Leathwick, J. & Ferrier, S. (2009) Sample selection bias and presence-only distribution models: implications for background and pseudo-absence data. *Ecological Applications*, **19**, 181–197.

Pope, V.D., Gallani, M.L., Rowntree, P.R. & Stratton, R.A. (2000) The impact of new physical parameterizations in the Hadley Centre Climate model: HadAM3. *Climate Dynamics*, **16**, 123–146.

Pörtner, H.O. & Knust, R. (2007) Climate change affects marine fishes through the oxygen limitation of thermal tolerance. *Science*, **315**, 95–97.

Robinson, M.M. & Dowsett, H.J. (2008) Pliocene role in assessing future climate impacts. *EOS, Transactions American Geophysical Union*, **89**, 501–502.

Rödder, D. & Lötters, S. (2009) Niche shift versus niche conservatism? Climatic characteristics of the native and invasive ranges of the Mediterranean house gecko (*Hemidactylus turcicus*). *Global Ecology and Biogeography*, **18**, 674–687.

Romdal, T., Araújo, M.B. & Rahbek, C. (2013) Life on a tropical planet: niche conservatism explains the global diversity gradient. *Global Ecology and Biogeography*, **22**, 344–350.

Roy, K., Valentine, J.W., Jablonski, D. & Kidwell, S.M. (1996) Scales of climatic variability and time averaging in Pleistocene biotas: implications for ecology and evolution. *Trends in Ecology & Evolution*, **11**, 458–463.

Roy, K., Hunt, G., Jablonski, D., Krug, A. & Valentine, J.W. (2009) A macroevolutionary perspective on species range limits. *Proceedings of the Royal Society B*, **276**, 1485–1493.

Royle, J.A., Chandler, R.B., Yackulic, C. & Nichols, J.D. (2012) Likelihood analysis of species occurrence probability from presence-only data for modeling species distributions. *Methods in Ecology and Evolution*, **3**, 545–554.

Saupe, E.E., Hendricks, J.R., Townsend, A.T. & Lieberman, B.S. (In Press) Climate change and marine mollusks of the western North Atlantic: future prospects and perils. *Journal of Biogeography*.

Schoener, T.W. (1968) *Anolis* lizards of Bimini: resource partitioning in a complex fauna. *Ecology*, **49**, 704–726.

Sinervo, B., Méndez-de-la-Cruz, F., Miles, D.B., Heulin, H., Bastiaans, E., Villagrán-Santa Cruz, M., Lara-Resendiz, R., Martínez-Méndez, N., Calderón-Espinosa, M.L., Meza-Lázaro, R.N., Gadsden, H., Avila, L.J., Morando, M., De la Riva, I.J., Sepulveda, P.V., Duarte Rocha, C.F., Ibargüengoytía, N., Puntriano, C.A., Massot, M., Lepetz, V., Oksanen, T.A., Chapple, D.G., Bauer, A.M., Branch, W.R., Clobert, J. & Sites, J.W.J. (2010) Erosion of lizard diversity by climate change and altered thermal niches. *Science*, **328**, 894–899.

Singarayer, J.S. & Valdes, P.J. (2010) High-latitude climate sensitivity to ice-sheet forcing over the last 120kyr. *Quaternary Science Reviews*, **29**, 43–55.

Singarayer, J.S., Valdes, P.J., Friedlingstein, P., Nelson, S. & Beerling, D.J. (2011) Late Holocene methane rise caused by orbitally controlled increase in tropical sources. *Nature*, **470**, 82–85.

Soberón, J. & Nakamura, M. (2009) Niches and distributional areas: concepts, methods, and assumptions. *Proceedings of the National Academy of Sciences*, **106**, 19644–19650.

Somero, G.N. (2002) Thermal physiology and vertical zonation of intertidal animals: optima, limits, and costs of living. *Integrative and Comparative Biology*, **42**, 780–789.

Sorte, C.J.B., Williams, S.L. & Carlton, J.T. (2010) Marine range shifts and species introductions: comparative spread rates and community impacts. *Global Ecology and Biogeography*, **19**, 303–316.

Spahni, R., Chappellaz, J., Stocker, T.F., Loulergue, L., Hausammann, G., Kawamura, K., Fluckiger, J., Schwander, J., Raynaud, D., Masson-Delmotte, V. & Jouzel, J. (2005) Variations of atmospheric methane and nitrous oxide during the last 650,000 years from Antarctic ice cores. *Science*, **310**, 1317–1321.

Stigall, A.L. (2012) Using ecological niche modeling to evaluate niche stability in deep time. *Journal of Biogeography*, **39**, 772–781.

Strubble, D., Broennimann, O., Chiron, F. & Matthysen, E. (2013) Niche conservatism in non-native birds in Europe: niche unfilling rather than niche expansion. *Global Ecology and Biogeography*, **22**, 962–970.

Sunday, J.M., Bates, A.E. & Dulvy, N.K. (2011) Global analysis of thermal tolerance and latitude in ectotherms. *Proceedings of the Royal Society B*, **278**, 1823–1830.

Sunday, J.M., Bates, A.E. & Dulvy, N.K. (2012) Thermal tolerance and the global redistribution of animals. *Nature Climate Change*, **2**, 686–690.

Svenning, J.-C., Fløjgaard, C., Marske, K.A., Nógues-Bravo, D. & Normand, S. (2011) Applications of species distribution modeling to paleobiology. *Quaternary Science Reviews*, **30**, 2930–2947.

Tewksbury, J.J., Huey, R.B. & Deutsch, C.A. (2008) Putting the heat on tropical animals. *Science*, **320**, 1296–1297.

Thuiller, W., Lavorel, S. & Araújo, M.B. (2005) Niche properties and geographical extent as predictors of species sensitivity to climate change. *Global Ecology and Biogeography*, **14**, 347–357.

Todd, J.A., Jackson, J.B.C., Johnson, K.G., Fortunato, H.M., Heitz, A., Alvarez, M. & Jung, P. (2002) The ecology of extinction: molluscan feeding and faunal turnover in the Caribbean Neogene. *Proceedings of the Royal Society of London B* **269**, 571–577.

Tomašových, A. & Kidwell, S.M. (2009) Preservation of spatial and environmental gradients by death assemblages. *Paleobiology*, **35**, 119–145.

Trakhtenbrot, A., Nathan, R., Perry, G. & Richardson, D.M. (2005) The importance of long-distance dispersal in biodiversity conservation. *Diversity and Distributions*, **11**, 173–181.

Tunnell, J.W., Andrews, J., Barrera, N.C. & Moretzsohn, F. (2010) *Encyclopedia of Texas Seashells: Identification, Ecology, Distribution & History*. Texas A&M University Press, College Station.

Umina, P.A., Weeks, A.R., Kearney, M.R., McKechnie, S.W. & Hoffmann, A.A. (2005) A rapid shift in a classic clinal pattern in *Drosophila* reflecting climate change. *Science*, **308**, 691–693.

Valentine, J.W. & Moores, E.M. (1970) Plate tectonic regulation of faunal diversity and sea level: a model. *Nature*, **228**, 657–659.

Valentine, J.W., Jablonski, D., Krug, A.Z. & Berke, S.K. (2012) The sampling and estimation of marine paleodiversity patterns: implications of a Pliocene model. *Paleobiology* **39**, 1–20.

van Dam, J.A., Aziz, H.A., Ángeles Álvarez Sierra, M., Hilgen, F.J., van den Hoek Ostende, L.W., Lourens, L.J., Mein, P., van der Meulen, A.J. & Palaez-Campomanes, P. (2006) Long-period astronomical forcing of mammal turnover. *Nature*, **443**, 687–691.

VanDerWal, J., Shoo, L.P., Graham, C. & Williams, S.E. (2009) Selecting pseudo-absence data for presence-only distribution modeling: how far should you stray from what you know? *Ecological Modeling*, **220**, 589–594.

Vermeij, G.J. (2005) One-way traffic in the western Atlantic: causes and consequences of Miocene to early Pleistocene molluscan invasions in Florida and the Caribbean. *Paleobiology*, **31**, 624–642.

Vrba, E.S. (1985) Environment and evolution: alternative causes of the temporal distribution of evolutionary events. *South African Journal of Science*, **81**, 229–236.

Warren, D.L., Glor, R.E. & Turelli, M. (2008) Environmental niche equivalency versus conservatism: Quantitative approaches to niche evolution. *Evolution*, **62**, 2868–2883.

Warren, D.L., Glor, R.E. & Turelli, M. (2010) ENMTools: a toolbox for comparative studies of environmental niche models. *Ecography*, **33**, 607–611.

Warren, R., VanDerWal, J., Price, J., Welbergen, J.A., Atkinson, I., Ramirez-Villegas, J., Osborn, T.J., Jarvis, A., Shoo, L.P., Williams, S.E. & Lowe, J. (2013) Quantifying the benefit of early climate change mitigation in avoiding biodiversity loss. *Nature Climate Change*, **3**, 678–682.

Wiens, J.J. & Graham, C.H. (2005) Niche conservatism: integrating evolution, ecology, and conservation biology. *Annual Review of Ecology, Evolution, and Systematics*, **36**, 519–539.

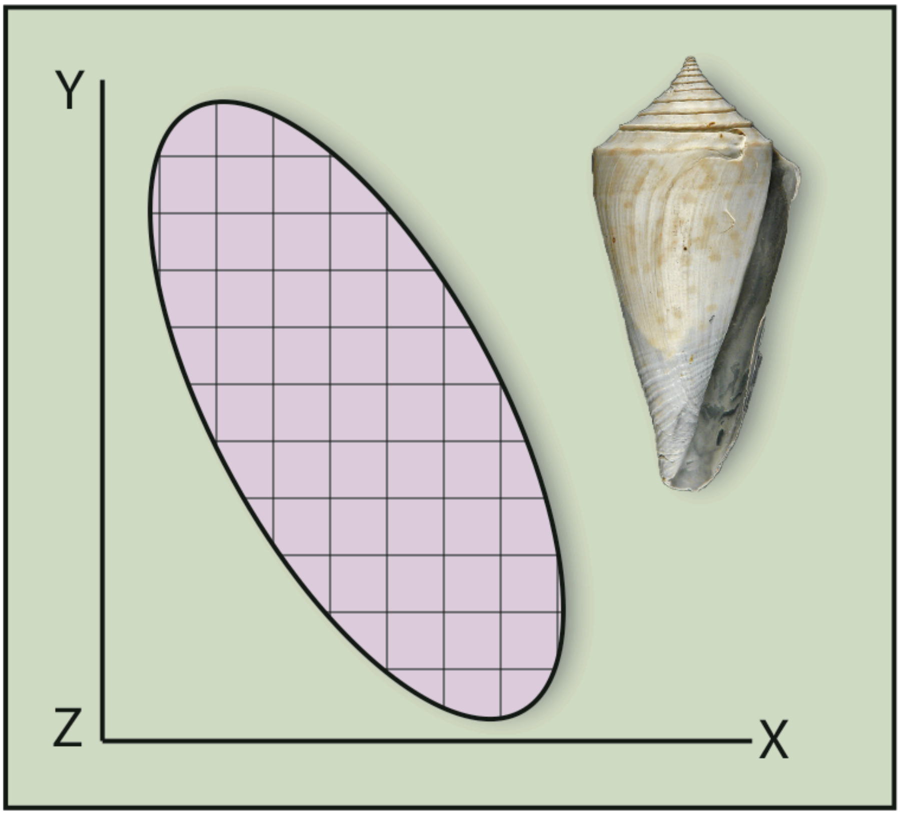
Williams, J.W. & Jackson, S.T. (2007) Novel climates, no-analog communities, and ecological surprises. *Frontiers in Ecology and the Environment*, **5**, 475–482.

Williams, J.W., Jackson, S.T. & Kutzbach, J.E. (2007) Projected distributions of novel and disappearing climates by 2100 AD. *Proceedings of the National Academy of Sciences*, **104**, 5738–5742.

Willis, K.J. & MacDonald, G.M. (2011) Long-term ecological records and their relevance to climate change predictions for a warmer world. *Annual Review of Ecology, Evolution, and Systematics*, **42**, 267–287.

Yackulic, C.B., Chandler, R., Zipkin, E.F., Royle, J.A., Nichols, J.D., Campbell Grant, E.H. & Veran, S. (2013) Presence-only modeling using MAXENT: when can we trust the inferences? *Methods in Ecology and Evolution*, **4**, 236–243.

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.*, 2013; Saupe *et al.*, 2014).

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, 2012). 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.

Table 3.1.1 Studied bivalve species, including 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 nspecies with two points, and in theses cases, models were deemed significant when they did not omit either point after thresholding.

Family	Genus	Species	Author	Extinction status	# of pts 2.5 arc-minute	# of pts 1.25°	P-value
Anomiidae	*Anomia*	*simplex*	d'Orbigny, 1853	Extant	48	12	<0.001
Arcidae	*Anadara*	*megarata*	Olsson & Harbison, 1953	Extinct	5	2	NA
Arcidae	*Anadara*	*notoflorida*	Vokes, 1969	Extinct	6	2	NA
Arcidae	*Anadara*	*idonea*	Conrad, 1832	Extinct	6	2	NA
Arcidae	*Arca*	*wagneriana*	Dall, 1898	Extinct	18	3	<0.001
Arcidae	*Barbatia*	*irregularis*	Dall, 1898	Extinct	5	2	NA
Arcidae	*Scapharca*	*scalarina*	Heilprin, 1886	Extinct	21	6	<0.001
Cardiidae	*Acrosterigma*	*dalli*	Heilprin, 1886	Extinct	4	2	NA
Cardiidae	*Dallocardia*	*muricata*	Linnaeus, 1758	Extinct	31	9	<0.001
Cardiidae	*Dinocardium*	*robustum*	Lightfoot, 1786	Extant	22	7	<0.001
Cardiidae	*Laevicardium*	*mortoni*	Conrad, 1831	Extant	110	19	<0.001
Cardiidae	*Papyridea*	*semisulcata*	Gray, 1825	Extant	4	3	0.025
Cardiidae	*Planicardium*	*virginianum*	Conrad, 1839	Extinct	6	3	0.033
Cardiidae	*Planicardium*	*acutilaqueatum*	Conrad, 1839	Extinct	13	6	<0.001
Cardiidae	*Trachycardium*	*egmontianum*	Shuttleworth, 1853	Extant	12	4	<0.001
Cardiidae	*Trachycardium*	*evergladeensis*	Mansfield, 1931	Extinct	7	3	0.026
Cardiidae	*Trachycardium*	*oedalium*	Dall, 1900	Extinct	11	5	<0.001
Cardiidae	*Trigoniocardia*	*willcoxi*	Dall, 1900	Extinct	13	3	<0.001
Carditidae	*Cardita*	*olga*	Mansfield, 1939	Extinct	7	2	NA
Carditidae	*Carditamera*	*tamiamiensis*	Mansfield, 1931	Extinct	5	3	<0.001
Carditidae	*Carditamera*	*dasytes*	Olsson, 1967	Extinct	8	3	<0.001
Carditidae	*Carditamera*	*floridana*	Conrad, 1838	Extant	4	4	<0.001
Carditidae	*Carditamera*	*arata*	Conrad, 1832	Extinct	29	11	<0.001
Carditidae	*Cyclocardia*	*granulata*	Say, 1824	Extinct	29	11	<0.001
Carditidae	*Pleuromeris*	*tridentata*	Say, 1826	Extant	22	9	<0.001
Carditidae	*Pteromeris*	*perplana*	Conrad, 1841	Extant	18	8	<0.001
Carditidae	*Pteromeris*	*abbreviata*	Conrad, 1841	Extinct	10	7	<0.001
Lucinidae	*Anodontia*	*schrammi*	Crosse, 1876	Extant	7	4	<0.001
Lucinidae	*Anodontia*	*alba*	Link, 1807	Extant	25	5	<0.001
Lucinidae	*Armimiltha*	*disciformis*	Heilprin, 1886	Extinct	15	3	<0.001
Lucinidae	*Callucina*	*keenae*	Chavan, 1971	Extant	24	11	<0.001
Lucinidae	*Cavilinga*	*blanda*	Dall, 1901	Extant	17	8	<0.001
Lucinidae	*Codakia*	*orbicularis*	Linnaeus, 1758	Extant	19	4	<0.001
Lucinidae	*Ctena*	*orbiculata*	Montagu, 1808	Extant	10	3	<0.001
Lucinidae	*Divalinga*	*quadrisulcata*	d'Orbigny, 1846	Extant	23	12	<0.001
Lucinidae	*Lucina*	*pensylvanica*	Linnaeus, 1758	Extant	37	6	<0.001
Lucinidae	*Luciniscа*	*nassula*	Conrad, 1846	Extant	16	7	<0.001
Lucinidae	*Miltha*	*caloosaensis*	Dall, 1898	Extinct	19	3	<0.001
Lucinidae	*Parvilucina*	*crenella*	Dall, 1901	Extant	11	5	<0.001
Lucinidae	*Pleurolucina*	*amabilis*	Dall, 1898	Extinct	7	3	<0.001
Lucinidae	*Stewartia*	*floridana*	Conrad, 1833	Extant	22	5	<0.001
Ostreidae	*Crassostrea*	*virginica*	Gmelin, 1791	Extant	21	7	<0.001
Tellinidae	*Arcopagia*	*fausta*	Pulteney, 1799	Extant	7	4	<0.001
Tellinidae	*Eurytellina*	*alternata*	Say, 1822	Extant	29	7	<0.001
Tellinidae	*Laciolina*	*magna*	Spengler, 1798	Extant	8	4	<0.001
Tellinidae	*Leporimetis*	*magnoliana*	Dall, 1900	Extinct	21	8	<0.001
Tellinidae	*Macoma*	*arctata*	Conrad, 1843	Extinct	5	4	0.0082
Tellinidae	*Merisca*	*aequistriata*	Say, 1824	Extant	16	8	<0.001
Tellinidae	*Tellidora*	*cristata*	Récluz, 1842	Extant	15	4	<0.001
Tellinidae	*Tellinella*	*listeri*	Röding, 1798	Extant	4	3	0.009
Veneridae	*Chione*	*erosa*	Dall, 1903	Extinct	36	7	<0.001
Veneridae	*Chionopsis*	*cribraria*	Conrad, 1843	Extinct	11	8	<0.001
Veneridae	*Dosinia*	*discus*	Reeve, 1850	Extant	8	2	NA
Veneridae	*Dosinia*	*elegans*	Conrad, 1843	Extant	21	7	<0.001
Veneridae	*Globivenus*	*rigida*	Dillwyn, 1817	Extant	4	2	NA
Veneridae	*Lirophora*	*latilirata*	Conrad, 1841	Extant	41	13	<0.001
Veneridae	*Macrocallista*	*nimbosa*	Lightfoot, 1786	Extant	32	4	<0.001
Veneridae	*Macrocallista*	*maculata*	Linnaeus, 1758	Extant	28	8	<0.001
Veneridae	*Mercenaria*	*campechiensis*	Gmelin, 1791	Extant	48	12	<0.001
Veneridae	*Panchione*	*ulocyma*	Dall, 1895	Extinct	19	6	<0.001
Veneridae	*Petricolaria*	*pholadiformis*	Lamarck, 1818	Extant	5	4	<0.001
Veneridae	*Timoclea*	*grus*	Holmes, 1858	Extant	13	6	<0.001

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 theses cases, models were deemed significant when they did not omit either point after thresholding.

Family	Genus	Species	Author	Extinction status	# of pts 2.5 arc-minute	# of pts 1.25°	P-value
Bullidae	*Bulla*	*occidentalis*	A. Adams, 1850	Extant	22	5	<0.001
Calyptraeidae	*Crepidula*	*fornicata*	Linnaeus, 1758	Extant	56	14	<0.001
Conidae	*Conus*	*delessertii*	Récluz, 1843	Extant	6	3	0.025
Conidae	*Conus*	*haytensis*	Sowerby II, 1850	Extinct	5	2	NA
Conidae	*Conus*	*yaquensis*	Gabb, 1873	Extinct	9	2	NA
Conidae	*Conus*	*bassi*	Petuch, 1991	Extinct	8	3	<0.001
Conidae	*Conus*	*miamiensis*	Petuch, 1986	Extinct	9	3	0.026
Conidae	*Conus*	*paranobilis*	Petuch, 1991	Extinct	4	3	<0.001
Conidae	*Conus*	*daucus*	Hwass, 1792	Extant	5	3	<0.001
Conidae	*Conus*	*marylandicus*	Green, 1830	Extinct	15	9	<0.001
Conidae	*Conus*	*oniscus*	Woodring, 1928	Extinct	22	6	<0.001
Conidae	*Conus*	*adversarius*	Conrad, 1840	Extinct	56	14	<0.001
Fasciolariidae	*Cinctura*	*rhomboidea*	Rogers & Rogers, 1839	Extinct	45	11	<0.001
Fasciolariidae	*Fasciolaria*	*okeechobensis*	Tucker & Wilson, 1932	Extinct	6	4	<0.001
Fasciolariidae	*Heilprinia*	*florida*	Olsson & Harbison, 1953	Extinct	10	4	<0.001
Fasciolariidae	*Heilprinia*	*carolinensis*	Dall, 1892	Extinct	5	4	0.0020
Fasciolariidae	*Heilprinia*	*caloosaensis*	Heilprin, 1886	Extinct	15	5	<0.001
Fasciolariidae	*Pliculofusus*	*scalarinus*	Heilprin, 1886	Extinct	24	4	<0.001
Fasciolariidae	*Triplofusus*	*giganteus*	Kiener, 1840	Extant	31	8	<0.001
Muricidae	*Calotrophon*	*ostrearum*	Conrad, 1846	Extant	32	9	<0.001
Muricidae	*Chicoreus*	*shirleyae*	Vokes, 1966	Extinct	6	3	0.016
Muricidae	*Chicoreus*	*floridanus*	Vokes, 1965	Extinct	33	5	<0.001
Muricidae	*Dermomurex*	*alabstrum*	A. Adams, 1864	Extant	7	3	<0.001
Muricidae	*Ecphora*	*bradleyae*	Petuch, 1988	Extinct	4	2	NA
Muricidae	*Ecphora*	*quadricostata*	Say, 1824	Extinct	28	9	<0.001
Muricidae	*Eupleura*	*metae*	Petuch, 1994	Extinct	6	3	0.015
Muricidae	*Eupleura*	*caudata*	Say, 1822	Extant	9	5	<0.001
Muricidae	*Eupleura*	*leonensis*	Mansfield, 1930	Extinct	12	4	<0.001
Naticidae	*Neverita*	*duplicata*	Say, 1822	Extant	51	15	<0.001
Olividae	*Oliva*	*sayana*	Ravenel, 1834	Extant	16	9	<0.001
Terebridae	*Terebra*	*dislocata*	Say, 1822	Extant	21	9	<0.001

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.

mPWP (~3.1 Ma) Formations	
Duplin	Jackson Bluff
Goose Greek	Mare
Guaiguaza	Raysor
Hopegate	Tamiami/Pinecrest
Intracoastal	Yorktown

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* 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 constricts 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).

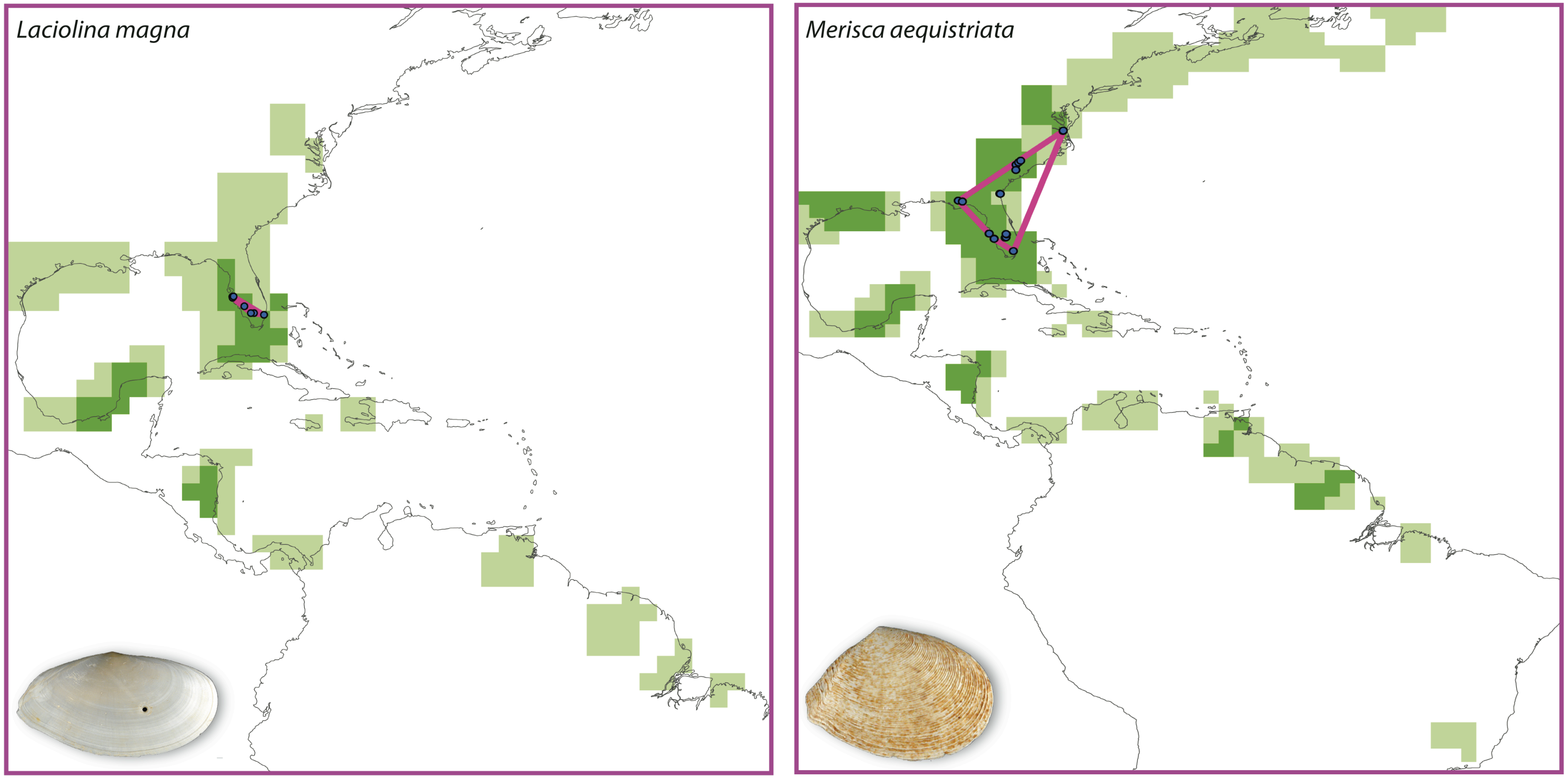


Figure 3.1 Distributional data (blue dots), area polygons (pink), and thresholded niche model projections for FN (light green) and RN (dark green) estimates for two representative bivalve species: *Laciolina magna* and *Merisca aequistriata* in the mPWP. Note that because of differences in distributional 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).

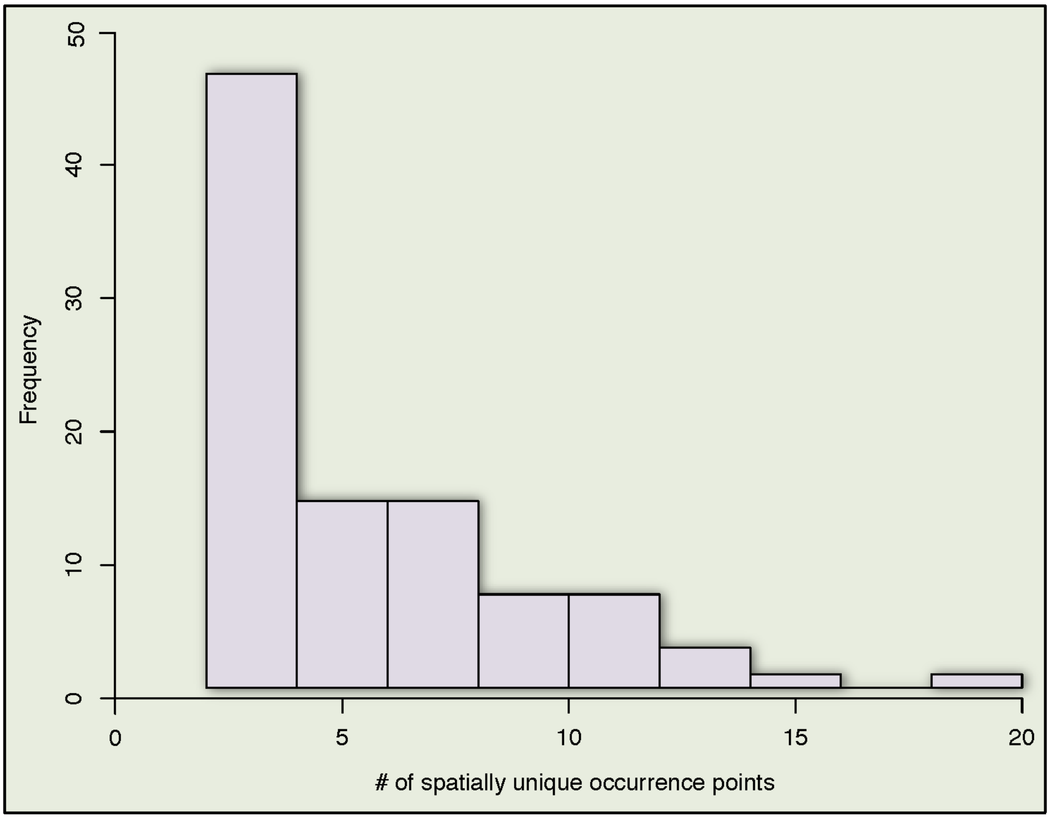


Figure 3.2 Histogram of number of occurrences per species at 1.25° resolution in the mPWP. Note the right-skewed nature of the frequency distribution, which mirrors that for many extant taxa (Gaston, 1998; Gaston & He, 2002).

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 ≥ 3 spatially unique points at 1.25^{o} 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 “≥ 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 1.25º resolution.

Analysis	**Calculation method**	One-tailed test		Two-tailed test		≥ 3 points	
		W	**P-value**	**W**	**P-value**	**W**	**P-value**
FN breadth							
Mean niche model	CPH	1272.5	0.071	1272.5	0.142	970.5	0.106
Mean niche model	MVE	1257.5	0.088	1257.5	0.176	962.5	0.120
RN breadth							
Occurrences	CPH	1406	0.006	1406	0.012	1023	0.041
Occurrences	MVE	1389	0.009	1389	0.018	1011	0.052
LTP niche model	CPH	1380	0.011	1380	0.021	1035	0.032
LTP niche model	MVE	1354	0.018	1354	0.036	1011	0.052
Rarefaction	Distance	1302.5	0.044	1302.5	0.089	1006.5	0.057
Geographic area							
Polygons analyses	Area (sq km)	1452	0.002	1452	0.004	1052	0.022
Mean model projection	Pixel count	1325	0.030	1325	0.061	1011	0.052
LGM projection							
Amount of suitable area	Pixel count	1343.5	0.022	1343.5	0.044	1024	0.040

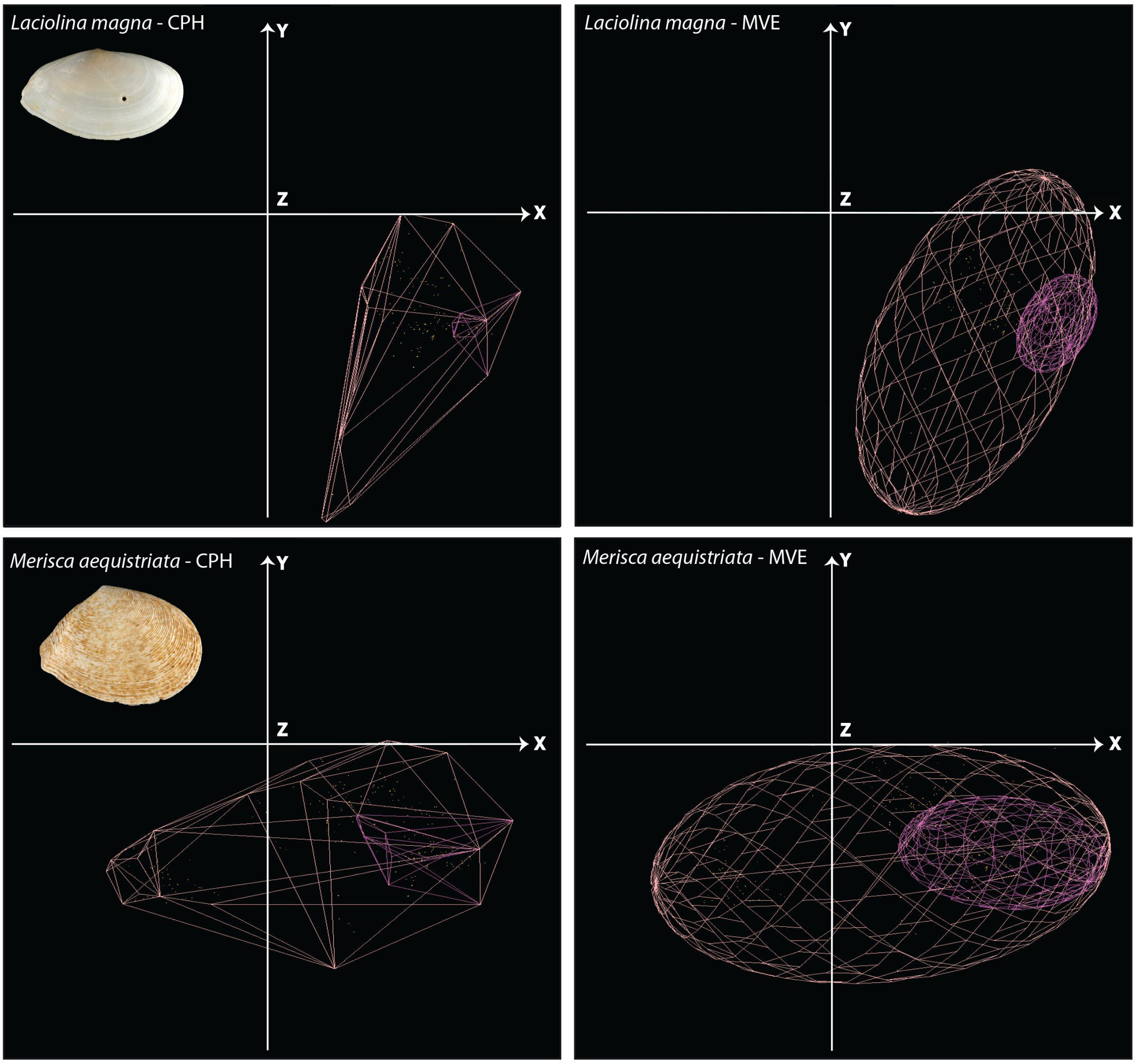


Figure 3.3 Representations of niche volumes in three-dimensional principle component space for the same two representative species, *Laciolina magna* and *Merisca aequistriata*. The left column depicts the minimum volume complex polyhedrons (CPH) for both thresholded mean niche models (FN; light pink) 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

Allmon, W.D. (2001) Nutrients, temperature, disturbance, and evolution: a model for the late Cenozoic marine record of the western Atlantic. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **166**, 9–26.

Allmon, W.D., Rosenberg, G., Portell, R.W. & Schindler, K. (1993) Diversity of Pliocene to Recent Atlantic coastal plain mollusks. *Science*, **260**, 1626–1628.

Anderson, B.J., Akçakaya, H.R., Araújo, M.B., Fordham, D.A., Martinez-Meyer, E., Thuiller, W. & Brook, B.W. (2009) Dynamics of range margins for metapopulations under climate change. *Proceedings of the Royal Society B*, **276**, 1415–1420.

Angilletta, M. (2009) *Thermal Adaptation: A Theoretical and Empirical Synthesis*. Oxford University Press, Oxford.

Araújo, M.B. & Pearson, R.G. (2005) Equilibrium of species' distributions with climate. *Ecography*, **28**, 693–695.

Araújo, M.B. & Luoto, M. (2007) The importance of biotic interactions for modelling species distributions under climate change. *Global Ecology and Biogeography*, **16**, 743–753.

Araújo, M.B. & Peterson, A.T. (2012) Uses and misuses of bioclimatic envelope modeling. *Ecology*, **93**, 1527–1539.

Austin, M.P. (1985) Continuum concept, ordination methods and niche theory. *Annual Review of Ecology and Systematics*, **16**, 39–61.

Austin, M.P., Nicholls, A.O., Doherty, M.D. & Meyers, J.A. (1994) Determining species response functions to an environmental gradient by means of a beta-function. *Journal of Vegetation Science*, **5**, 215–228.

Barnosky, A.D., Carrasco, M.A. & Davis, E.B. (2005) The impact of the species-area relationship on estimates of paleodiversity. *PLoS Biology*, **3**, e266.

Barnosky, A.D., Matzke, N., Tomiya, S., Wogan, G.O.U., Swartz, B., Quental, T.B., Marshall, C., McGuire, J.L., Lindsey, E.L., Maguire, K.C., Mersey, B. & Ferrer, E.A. (2011) Has the Earth's sixth mass extinction already arrived? *Nature*, **471**, 51–57.

Barnosky, A.D., Hadly, E.A., Bascompte, J., Berlow, E.L., Brown, J.H., Fortelius, M., Getz, W.M., Harte, J., Hastings, A., Marquet, P.A., Martinez, N.D., Mooers, A., Roopnarine, P., Vermeij, G., Williams, J.W., Gillespie, R., Kitzes, J., Marshall, C., Marzke, N., Mindell, D.P., Revilla, E. & Smith, A.B. (2012) Approaching a state shift in Earth's biosphere. *Nature*, **486**, 52–58.

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

Barve, N., Barve, V., Jiménez-Valverde, A., Lira-Noriega, A., Maher, S.P., Peterson, A.T., Soberón, J. & Villalobos, F. (2011) The crucial role of the accessible area in ecological niche modeling and species distribution modeling. *Ecological Modelling*, **222**, 1810–1819.

Blonder, B., Lamanna, C., Violle, C. & Enquist, B.J. (2014) The n-dimensional hypervolume. *Global Ecology and Biogeography*. DOI: 10.1111/geb.12146.

Boulangeat, I., Lavergne, S., Van Es, J., Garraud, L. & Thuiller, W. (2012) Niche breadth, rarity and ecological characteristics within a regional flora spanning large environmental gradients. *Journal of Biogeography*, **39**, 204–214.

Broennimann, O., Thuiller, W., Hughes, G., Midgley, G.F., Alkemade, J.R. & Guisan, A. (2006) Do geographic distribution, niche property and life form explain plants' vulnerability to global change? *Global Change Biology*, **12**, 1079–1093.

Brown, J.H., Mehlman, D.W. & Stevens, G.C. (1995) Spatial variation in abundance. *Ecology*, **76**, 2028–2043.

Colles, A., Liow, L.H. & Prinzing, A. (2009) Are specialists at risk under environmental change? Neoecological, paleoecological and phylogenetic approaches. *Ecology Letters*, **12**, 849–863.

Colwell, R.K. & Futuyma, D.J. (1971) On the measurement of niche breadth and overlap. *Ecology*, **52**, 567–576.

Cornwell, W.K., Schwilk, D.W. & Ackerly, D.D. (2006) A trait-based test for habitat filtering: convex hull volume. *Ecology*, **87**, 1465–1471.

Crampton, J.S., Cooper, R., Beu, A.G., Foote, M. & Marshall, B.A. (2010) Biotic influences on species duration: interactions between traits in marine molluscs. *Paleobiology*, **36**, 204–223.

Davis, A.J., Jenkinson, L.S., Lawton, J.H., Shorrocks, B. & Wood, S. (1998) Making mistakes when predicting shifts in species range in response to global warming. *Science*, **391**, 783–786.

Devictor, V., Clavel, J., Julliard, R., Lavergne, S., Mouillot, D., Thuiller, W., Venail, P., Villéger, S. & Mouquet, N. (2010) Defining and measuring ecological specialization. *Journal of Applied Ecology*, **47**, 15–25.

Dudík, M., Schapire, R.E. & Phillips, S.J. (2005) Correcting sample selection bias in maximum entropy density estimation. *Advances in Neural Information Processing Systems*, pp. 323-330. The MIT Press.

Eldredge, N. (1979) Alternative approaches to evolutionary theory. *Bulletin of the Carnegie Museum of Natural History*, **13**, 7–19.

Eldredge, N. (1989) *Macroevolutionary dynamics: species, niches and adaptive peaks*. McGraw Hill, New York.

Eldredge, N., Thompson, J.N., Brakefield, P.M., Gavrilets, S., Jablonski, D., Jackson, J.B.C., Lenski, R.E., Lieberman, B.S., McPeek, M.A. & Miller, W.I. (2005) The dynamics of evolutionary stasis. *Paleobiology*, **31**, 133–145.

Elith, J., Phillips, S.J., Hastie, T., Dudik, M., Chee, Y.E. & Yates, C.J. (2011) A statistical explanation of MaxEnt for ecologists. *Diversity and Distributions*, **17**, 43–57.

Essl, F., Staudinger, M., Stöhr, O., Schratt-Ehrendorfer, L., Rabitsch, W. & Niklfeld, H. (2009) Distribution patterns, range size and niche breadth of Austrian endemic plants. *Biological Conservation*, **142**, 2547–2558.

Fernandez, M.H. & Vrba, E.S. (2005) Macroevolutionary processes and biomic specialization: testing the resource-use hypothesis. *Evolutionary Ecology*, **19**, 199–219.

Fithian, W. & Hastie, T. (2012) Statistical models for presence-only data: finite-sample equivalence and addressing observer bias. *arXiv preprint arXiv*, **1207**, 6950.

Foote, M., Crampton, J.S., Beu, A.G. & Cooper, R.A. (2008) On the bidirectional relationship between geographic range and taxonomic duration. *Paleobiology*, **34**, 421–433.

Fordham, D.A., Mellin, C., Russell, B.D., Akçakaya, R.H., Bradshaw, C.J.A., Aiello-Lammens, M.E., Caley, J.M., Connell, S.D., Mayfield, S., Shepherd, S.A. & Brook, B.W. (2013) Population dynamics can be more important than physiological limits for determining range shifts under climate change. *Global Change Biology*, **19**, 3224–3237.

Fordham, D.A., Akçakaya, H.R., Araújo, M.B., Elith, J., Keith, D.A., Pearson, R., Auld, T.D., Mellin, C., Morgan, J.W., Regan, T.J., Tozer, M., Watts, M.J., White, M., Wintle, B.A., Yates, C. & Brook, B.W. (2012) Plant extinction risk under climate change: are forecast range shifts alone a good indicator of species vulnerability to global warming? *Global Change Biology*, **18**, 1357–1371.

Freeman, E.A. & Moisen, G.G. (2008) A comparison of the performance of threshold criteria for binary classification in terms of predicted prevalence and kappa. *Ecological Modelling*, **217**, 48–58.

Fritz, S.A., Bininda-Emonds, O.R.P. & Purvis, A. (2009) Geographical variation in predictors of mammalian extinction risk: big is bad, but only in the tropics. *Ecology Letters*, **12**, 538–549.

Gaston, K.J. (1998) Species-range size distributions: products of speciation, extinction, and transformation. *Philosophical Transactions of the Royal Society of London B*, **353**, 219–230.

Gaston, K.J. (2003) *The structure and dynamics of geographic ranges*. Oxford University Press, Oxford.

Gaston, K.J. & He, F. (2002) The distribution of species range size: a stochastic process. *Proceedings of the Royal Society of London B*, **269**, 1079–1086.

Gaston, K.J. & Fuller, R.A. (2009) The sizes of species' geographic ranges. *Journal of Applied Ecology*, **46**, 1–9.

Gordon, C., Cooper, C., Senior, C.A., Banks, H., Gregory, J.M., Johns, T.C., Mitchell, J.F.B. & Wood, R.A. (2000) The simulation of SST, sea ice extents and ocean heat transports in a version of the Hadley Centre coupled model without flux adjustments. *Climate Dynamics*, **16**, 147–168.

Grinnell, J. (1917) The niche-relationships of the California Thrasher. *The Auk*, **34**, 427–433.

Harnik, P.G. (2011) Direct and indirect effects of biological factors on extinction risk in fossil bivalves. *Proceedings of the National Academy of Sciences USA*, **108**, 13594–13599.

Harnik, P.G., Simpson, C. & Payne, J.L. (2012) Long-term differences in extinction risk among the seven forms of rarity. *Proceedings of the Royal Society of London B*, **279**, 4969–4976.

Harris, G. & Pimm, S.L. (2008) Range size and extinction risk in forest birds. *Conservation Biology*, **22**, 163–171.

Haywood, A.M., Dowsett, H.J., Robinson, M.M., Stoll, D.K., Dolan, A.M., Lunt, D.J., Otto-Bliesner, B. & Chandler, M.A. (2011) Pliocene Model Intercomparison Project (PlioMIP): experimental design and boundary conditions (Experiment 2). *Geoscientific Model Development*, **4**, 571–577.

Heim, N.A. & Peters, S.E. (2011) Regional environmental breadth predicts geographic range and longevity in fossil marine genera. *PLoS ONE*, **6**, e18946.

Hendricks, J.R., Lieberman, B.S. & Stigall, A.L. (2013) *The Digital Atlas of Ancient Life*. Available at: http://www.geosun.sjsu.edu/~jhendricks/AtlasTemp/TheHomePage.html (accessed 2014).

Hendriks, I.E., Duarte, C.M. & Álvarez, M. (2010) Vulnerability of marine biodiversity to ocean acidification: a meta-analysis. *Estuarine, Coastal and Shelf Science*, **86**, 157–164.

Hernandez, P.A., Graham, C.H., Master, L.L. & Albert, D.L. (2006) The effect of sample size and species characteristics on performance of different distribution modeling methods. *Ecography*, **29**, 773–785.

Holm, S. (1979) A simple sequentially rejective multiple test procedure. *Scandinavian Journal of Statistics*, **6**, 65–70.

Hooper, H.L., Connon, R., Callaghan, A., Fryer, G., Yarwood-Buchanan, S., Biggs, J., Maund, S.J., Hutchinson, T.H. & Sibly, R.M. (2008) The ecological niche of *Daphnia magna* characterized using population growth rate. *Ecology*, **89**, 1015–1022.

Hutchinson, G.E. (1957) Concluding remarks. *Cold Spring Harbor Symposia on Quantitative Biology*, **22**, 415–427.

Jablonski, D. (2008) Extinction and the spatial dynamics of biodiversity. *Proceedings of the National Academy of Sciences USA*, **105**, 11528–11535.

Jablonski, D. & Roy, K. (2003) Geographical range and speciation in fossil and living molluscs. *Proceedings of the Royal Society of London B*, **270**, 401–406.

Jablonski, D. & Hunt, G. (2006) Larval ecology, geographic range, and species survivorship in Cretaceous mollusks: organismic versus species-level explanations. *The American Naturalist*, **168**, 556–564.

Jablonski, D., Belanger, C.L., Berke, S.K., Huang, S., Krug, A.Z., Roy, K., Tomasovych, A. & Valentine, J.W. (2013) Out of the tropics, but how? Fossils, bridge species, and thermal ranges in the dynamics of the marine latitudinal diversity gradient. *Proceedings of the National Academy of Sciences USA*, **110**, 10487–10494.

Jackson, J.B.C., Todd, J.A., Fortunato, H. & Jung, P. (1999) Diversity and assemblages of Neogene Caribbean mollusca of lower Central America. *Bulletins of American Paleontology*, **357**, 193–230.

Jackson, S.T. & Overpeck, J.T. (2000) Responses of plant populations and communities to environmental changes of the late Quaternary. *Paleobiology*, **26**, 194–220.

Jiménez-Valverde, A. & Lobo, J.M. (2007) Threshold criteria for conversion of probability of species presence to either–or presence–absence. *Acta oecologica*, **31**, 361–369.

Johnson, C.N. (1998) Species extinction and the relationship between distribution and abundance. *Nature*, **394**, 272–274.

Jones, M.C., Dye, S.R., Fernandes, J.A., Frölicher, T.L., Pinnegar, J.K., Warren, R. & Cheung, W.W.L. (2013) Predicting the impact of climate change on threatened species in UK waters. *PLoS ONE* **8**, e54216.

Kammer, T.W., Baumiller, T.K. & Ausich, W.I. (1997) Species longevity as a function of niche breadth: evidence from fossil crinoids. *Geology*, **25**, 219–222.

Kearney, M. & Porter, W. (2009) Mechanistic niche modelling: combining physiological and spatial data to predict species' ranges. *Ecology Letters*, **12**, 334–350.

Kearney, M.R., Wintle, B.A. & Porter, W.P. (2010) Correlative and mechanistic models of species distribution provide congruent forecasts under climate change. *Conservation Letters*, **3**, 203–213.

Kearney, M.R., Simpson, S.J., Raubenheimer, D. & Kooijman, S.A.L.M. (2013) Balancing heat, water and nutrients under environmental change: a thermodynamic framework. *Functional Ecology*, **27**, 950–966.

Keller, G., Adatte, T., Stinnesbeck, W., Luciani, V., Karoui-Yaakoub, N. & Zaghbib-Turki, D. (1997) Paleoecology of the Cretaceous-Tertiary mass extinction in planktonic foraminifera. *Palaeogeograpgy, Palaeoclimatology, Palaeoecology*, **178**, 257–297.

Kiessling, W. & Aberhan, M. (2007) Geographical distribution and extinction risk: lessons from Triassic–Jurassic marine benthic organisms. *Journal of Biogeography*, **34**, 1473–1489.

Klaus, J.S., Lutz, B.P., McNeill, D.F., Budd, A.F., Johnson, K.G. & Ishman, S.E. (2011) Rise and fall of Pliocene free-living corals in the Caribbean. *Geology*, **39**, 375–378.

Kotiaho, J.S., Kaitala, V., Komonen, A. & Päivinen, J. (2005) Predicting the risk of extinction from shared ecological characteristics. *Proceedings of the National Academy of Sciences USA*, **102**, 1963–1967.

Lavergne, S., Thompson, J.D., Garnier, E. & Debussche, M. (2004) The biology and ecology of narrow endemic and widespread plants: a comparative study of trait variation in 20 congeneric pairs. *Oikos*, **107**, 505–518.

Lawton, J.H., Nee, S., Letcher, A.J. & Harvey, P.H. (1994) Animal distributions: patterns and processes. *Large-Scale Ecology and Conservation Biology* (ed. by P.J. Edwards, R.M. May and N.R. Webb), pp. 41–58. Blackwell Scientific Publications, Oxford.

Lee, T.M. & Jetz, W. (2011) Unravelling the structure of species extinction risk for predictive conservation science. *Proceedings of the Royal Society London B*, **278**, 1329–1338.

Liow, L.H. (2007) Does versatility as measured by geographic range, bathymetric range and morphological variability contribute to taxon longevity? *Global Ecology and Biogeography*, **16**, 117–128.

Liu, C., White, M. & Newell, G. (2013) Selecting thresholds for the prediction of species occurrence with presence-only data. *Journal of Biogeography*, **40**, 778–789.

Liu, C., Berry, P.M., Dawson, T.P. & Pearson, R.G. (2005) Selecting thresholds of occurrence in the prediction of species distributions. *Ecography*, **28**, 385–393.

Ludbrook, J. (1998) Multiple comparison procedures updated. *Clinical and Experimental Pharmacology and Physiology*, **25**, 1032–1037.

Mace, G.M., Collar, N.J., Gaston, K.J., Hilton-Taylor, C., Akçakaya, H.R., Leader-Williams, N., Milner-Gulland, E.J. & Stuart, S.N. (2008) Quantification of extinction risk: IUCN's system for classifying threatened species. *Conservation Biology*, **22**, 1424–1444.

Martínez-Meyer, E. & Peterson, A.T. (2006) Conservatism of ecological niche characteristics in North American plant species over the Pleistocene-to-Recent transition. *Journal of Biogeography*, **33**, 1779–1789.

McKinney, M.L. (1997) Extinction vulnerability and selectivity: combining ecological and paleontological views. *Annual Review of Ecology and Systematics*, **28**, 495–516.

Miller, A.I. & Foote, M. (1996) Calibrating the Ordovician Radiation of marine life: implications for Phanerozoic diversity trends. *Paleobiology* **22**, 304–309.

Monahan, W.B. & Tingley, M.W. (2012) Niche tracking and rapid establishment of distributional equilibrium in the House Sparrow show potential responsiveness of species to climate change. *PLoS ONE*, **7**, e42097.

Myers, C.E. & Saupe, E.E. (2013) A macroevolutionary expansion of the modern synthesis and the importance of extrinsic abiotic factors. *Palaeontology*, **56**, 1179–1198.

Myers, C.E., MacKenzie III, R.A. & Lieberman, B.S. (2012) Greenhouse biogeography: the relationship of geographic range to invasion and extinction in the Cretaceous Western Interior Seaway. *Paleobiology*, **39**, 135–148.

Norris, R.D. (1992) Extinction selectivity and ecology in planktonic foraminifera. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **95**, 1–17.

Nürnberg, S. & Aberhan, M. (2013) Habitat breadth and geographic range predict diversity dynamics in marine Mesozoic bivalves. *Paleobiology*, **39**, 360–372.

Owens, H.L., Campbell, L.P., Dornak, L.L., Saupe, E.E., Barve, N., Soberón, J., Ingenloff, K., Lira-Noriega, A., Hensz, C.M., Myers, C.E. & Peterson, A.T. (2013) Constraints on interpretation of ecological niche models by limited environmental ranges on calibration areas. *Ecological Modelling*, **263**, 10-18.

Patzkowsky, M.E. & Holland, S.M. (2012) *Stratigraphic Paleobiology: Understanding the Distribution of Fossil Taxa in Time and Space*. University of Chicago Press, Chicago.

Payne, J.L. & Finnegan, S. (2007) The effect of geographic range on extinction risk during background and mass extinction. *Proceedings of the National Academy of Sciences USA*, **104**, 10506–10511.

Pearman, P.B., Guisan, A., Broennimann, O. & Randin, C.F. (2008) Niche dynamics in space and time. *Trends in Ecology & Evolution*, **23**, 149–158.

Pearson, R.G., Raxworthy, C.J., Nakamura, M. & Peterson, A.T. (2007) Predicting species distributions from small numbers of occurrence records: a test case using cryptic geckos in Madagascar. *Journal of Biogeography*, **34**, 102–117.

Peterson, A.T., Soberón, J., Pearson, R.G., Anderson, R.P., Martínez-Meyer, E., Nakamura, M. & Araújo, M.B. (2011) *Ecological niches and geographic distributions* Princeton University Press, Princeton.

Phillips, S.J., Anderson, R.P. & Schapire, R.E. (2006) Maximum entropy modeling of species geographic distributions. *Ecological Modelling*, **190**, 23–259.

Phillips, S.J., Dudík, M., Elith, J., Graham, C.H., Lehmann, A., Leathwick, J. & Ferrier, S. (2009) Sample selection bias and presence-only distribution models: implications for background and pseudo-absence data. *Ecological Applications*, **19**, 181–197.

Pope, V.D., Gallani, M.L., Rowntree, P.R. & Stratton, R.A. (2000) The impact of new physical parameterizations in the Hadley Centre Climate model: HadAM3. *Climate Dynamics*, **16**, 123–146.

Powell, M.G. (2007) Geographic range and genus longevity of late Paleozoic brachiopods. *Paleobiology*, **33**, 530–546.

Pulliam, R. (2000) On the relationship between niche and distribution. *Ecology Letters*, **3**, 349–361.

Purvis, A., Gittleman, J.L., Cowlishaw, G. & Mace, G.M. (2000) Predicting extinction risk in declining species. *Proceedings of the Royal Society of London B*, **267**, 1947–1952.

Qiao, H., Soberón, J., Campbell, L. & Peterson, A.T. (2012) *Biodiversity Informatic Application: Niche Analyst User Guide*. Available at: http://biodiversity-informatics-training.org/software-data-sources/nichea/ - Availability.

Renner, I.W. & Warton, D.I. (2013) Equivalence of MAXENT and Poisson point process models for species distribution modeling in ecology. *Biometrics*, **69**, 274–281.

Roopnarine, P.D. & Beussink, A. (1999) Extinction and naticid predation of the bivalve *Chione* von Mühlfeld in the late Neogene of Florida. *Palaeontologia Electronica*, **2**, 1–14.

Royle, J.A., Chandler, R.B., Yackulic, C. & Nichols, J.D. (2012) Likelihood analysis of species occurrence probability from presence-only data for modelling species distributions. *Methods in Ecology and Evolution*, **3**, 545–554.

Russell, B.D., Connell, S.D., Mellin, C., Brook, B.W., Burnell, O.W. & Fordham, D.A. (2012) Predicting the distribution of commercially important invertebrate stocks under future climate. *PLoS ONE*, **7**, e46554.

Saupe, E.E., Hendricks, J.R., Townsend, A.T. & Lieberman, B.S. (2014) Climate change and marine molluscs of the western North Atlantic: future prospects and perils. *Journal of Biogeography*. DOI: 10.1111/jbi.12289.

Saupe, E.E., Hendricks, J.R., Portell, R.W., Dowsett, H.F., Haywood, A., Hunter, M.E. & Lieberman, B.S. (in review) Macroevolutionary consequences of profound climate change on niche evolution in marine mollusks over the past 3 million years *Proceedings of the National Academy of Sciences USA*.

Schwartz, M.W., Iverson, L.R., Prasad, A.M., Matthews, S.N. & O'Connor, R.J. (2006) Predicting extinctions as a result of climate change. *Ecology*, **87**, 1611–1615.

Simpson, G.G. (1944) *Tempo and Mode in Evolution*. Columbia University Press, New York.

Singarayer, J.S. & Valdes, P.J. (2010) High-latitude climate sensitivity to ice-sheet forcing over the last 120kyr. *Quaternary Science Reviews*, **29**, 43–55.

Singarayer, J.S., Valdes, P.J., Friedlingstein, P., Nelson, S. & Beerling, D.J. (2011) Late Holocene methane rise caused by orbitally controlled increase in tropical sources. *Nature*, **470**, 82–85.

Smith, E.P. (1982) Niche breadth, resource availability, and inference. *Ecology*, **63**, 1675–1681.

Soberón, J. & Nakamura, M. (2009) Niches and distributional areas: concepts, methods, and assumptions. *Proceedings of the National Academy of Sciences USA*, **106**, 19644–19650.

Stanley, S.M. (1979) *Macroevolution: pattern and process*. Freeman, San Francisco.

Stanley, S.M. (1986a) Anatomy of a regional mass extinction: Plio-Pleistocene decimation of the western Atlantic bivalve fauna. *Palaios*, **1**, 17–36.

Stanley, S.M. (1986b) Population size, extinction, and speciation; the fission effect in Neogene Bivalvia. *Paleobiology*, **12**, 89–110.

Stanley, S.M. (1990) The general correlation between rate of speciation and rate of extinction: fortuitous causal linkages. *Causes of evolution: a paleontological perspective* (ed. by R.M. Ross and W.D. Allmon), pp. 103–127. University of Chicago Press, Chicago.

Stigall, A.L. (2010) Using GIS to assess the biogeographic impact of species invasions on native brachiopods during the Richmondian Invasion in the type-Cincinnatian (Late Ordovician, Cincinnati region). *Palaeontologia Electronica*, **13**, 1–19.

Strubble, D., Broennimann, O., Chiron, F. & Matthysen, E. (2013) Niche conservatism in non-native birds in Europe: niche unfilling rather than niche expansion. *Global Ecology and Biogeography*, **22**, 962–970.

Svenning, J.-C., Fløjgaard, C., Marske, K.A., Nógues-Bravo, D. & Normand, S. (2011) Applications of species distribution modeling to paleobiology. *Quaternary Science Reviews*, **30**, 2930–2947.

Tewksbury, J.J., Huey, R.B. & Deutsch, C.A. (2008) Putting the heat on tropical animals. *Science*, **320**, 1296–1297.

Thomas, C.D., Cameron, A., Green, R.E., Bakkenes, M., Beaumont, L.J., Collingham, Y.C., Erasmus, B.F.N., de Siqueira, M.F., Grainger, A., Hannah, L., Hughes, L., Huntley, B., van Jaarsveld, A.S., Midgley, G.F., Miles, L., Ortega-Huerta, M.A., Peterson, A.T., Phillips, O.L. & Williams, S.E. (2004) Extinction risk from climate change. *Nature*, **427**, 145–148.

Thuiller, W., Lavorel, S. & Araújo, M.B. (2005) Niche properties and geographical extent as predictors of species sensitivity to climate change. *Global Ecology and Biogeography*, **14**, 347–357.

Todd, J.A., Jackson, J.B.C., Johnson, K.G., Fortunato, H.M., Heitz, A., Alvarez, M. & Jung, P. (2002) The ecology of extinction: molluscan feeding and faunal turnover in the Caribbean Neogene. *Proceedings of the Royal Society of London B*, **269**, 571–577.

Van Aelst, S. & Rousseeuw, P. (2009) Minimum volume ellipsoid. *Wiley Interdisciplinary Reviews: Computational Statistics*, **1**, 71–82.

Van der Putten, W.H., Macel, M. & Visser, M.E. (2010) Predicting species distribution and abundance responses to climate change: why it is essential to include biotic interactions across trophic levels. *Philosophical Transactions of the Royal Society B*, **365**, 2025–2034.

VanDerWal, J., Shoo, L.P., Graham, C. & Williams, S.E. (2009) Selecting pseudo-absence data for presence-only distribution modeling: how far should you stray from what you know? *Ecological Modelling*, **220**, 589–594.

Varela, S., Rodríquez, J. & Lobo, J.M. (2009) Is current climatic equilibrium a guarantee for the transferability of distribution model predictions? A case study of the spotted hyena. *Journal of Biogeography*, **36**, 1645–1655.

Vermeij, G.J. (1989) Interoceanic differences in adaptation: effects of history and productivity. *Marine Ecology Progress Series*, **57**, 293–305.

Vermeij, G.J. (1993) Biogeography of recently extinct marine species: Implications for conservation. *Conservation Biology*, **7**, 391–397.

Vermeij, G.J. (2005) One-way traffic in the western Atlantic: causes and consequences of Miocene to early Pleistocene molluscan invasions in Florida and the Caribbean. *Paleobiology*, **31**, 624–642.

Vrba, E.S. (1987) Ecology in relation to speciation rates: some case histories of Miocene–Recent mammal clades. *Evolutionary Ecology*, **1**, 283–300.

Worm, B., Barbier, E.B., Beaumont, N., Duffy, J.E., Folke, C., Halpern, B.S., Jackson, J.B.C., Lotze, H.K., Micheli, F., Palumbi, S., Sala, E., Selkoe, K.A., Stachowicz, J.J. & Watson, R. (2006) Impacts of biodiversity loss on ocean ecosystem services. *Science*, **314**, 787–790.

Yackulic, C.B., Chandler, R., Zipkin, E.F., Royle, J.A., Nichols, J.D., Campbell Grant, E.H. & Veran, S. (2013) Presence-only modelling using MAXENT: when can we trust the inferences? *Methods in Ecology and Evolution*, **4**, 236–243.

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*.

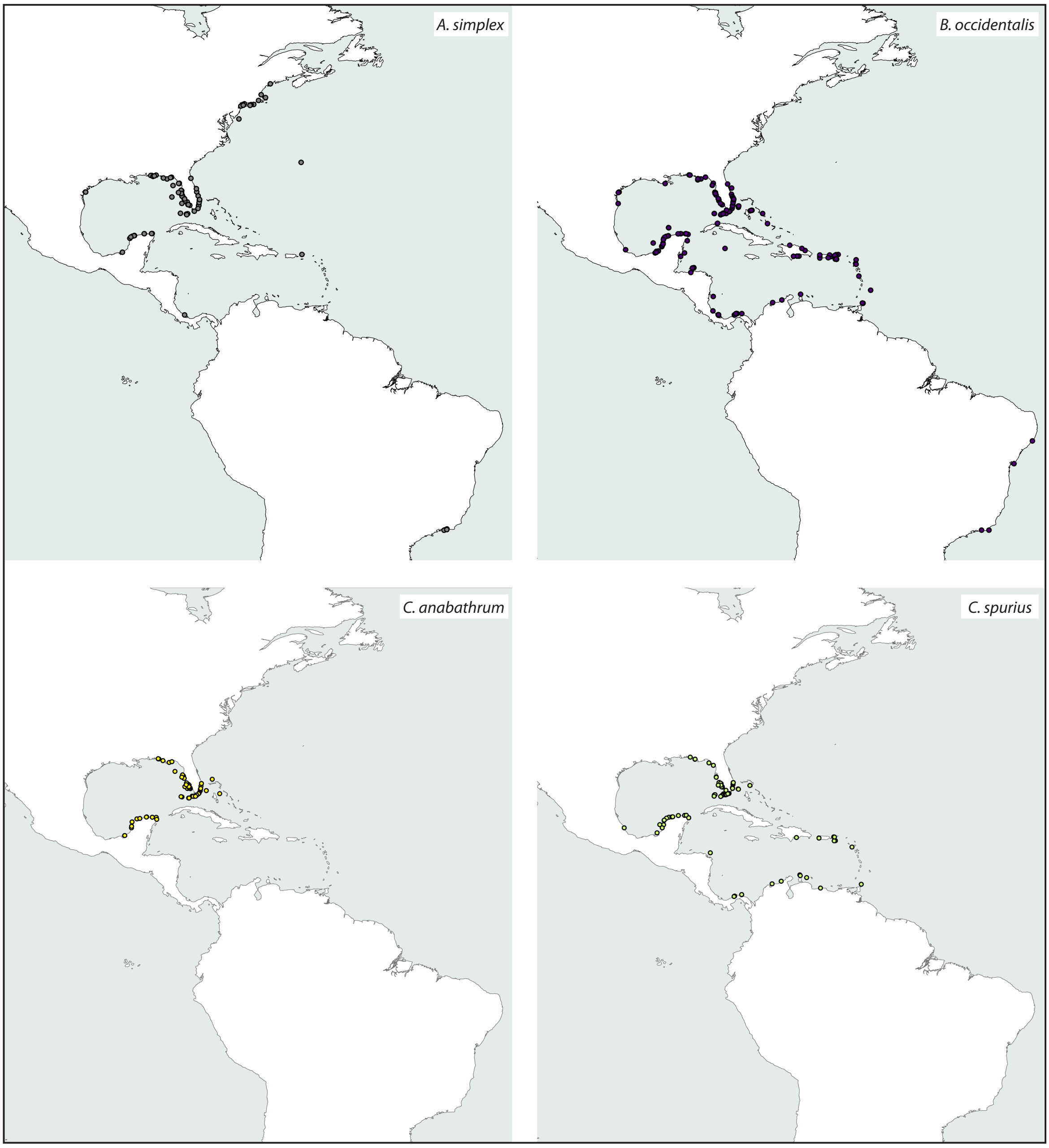


Figure S1.1.2 Distributional data for *Crassostrea virginica*, *Crepidula fornicata*, *Dinocardium robustum* and *Lucina pensylvanica*.

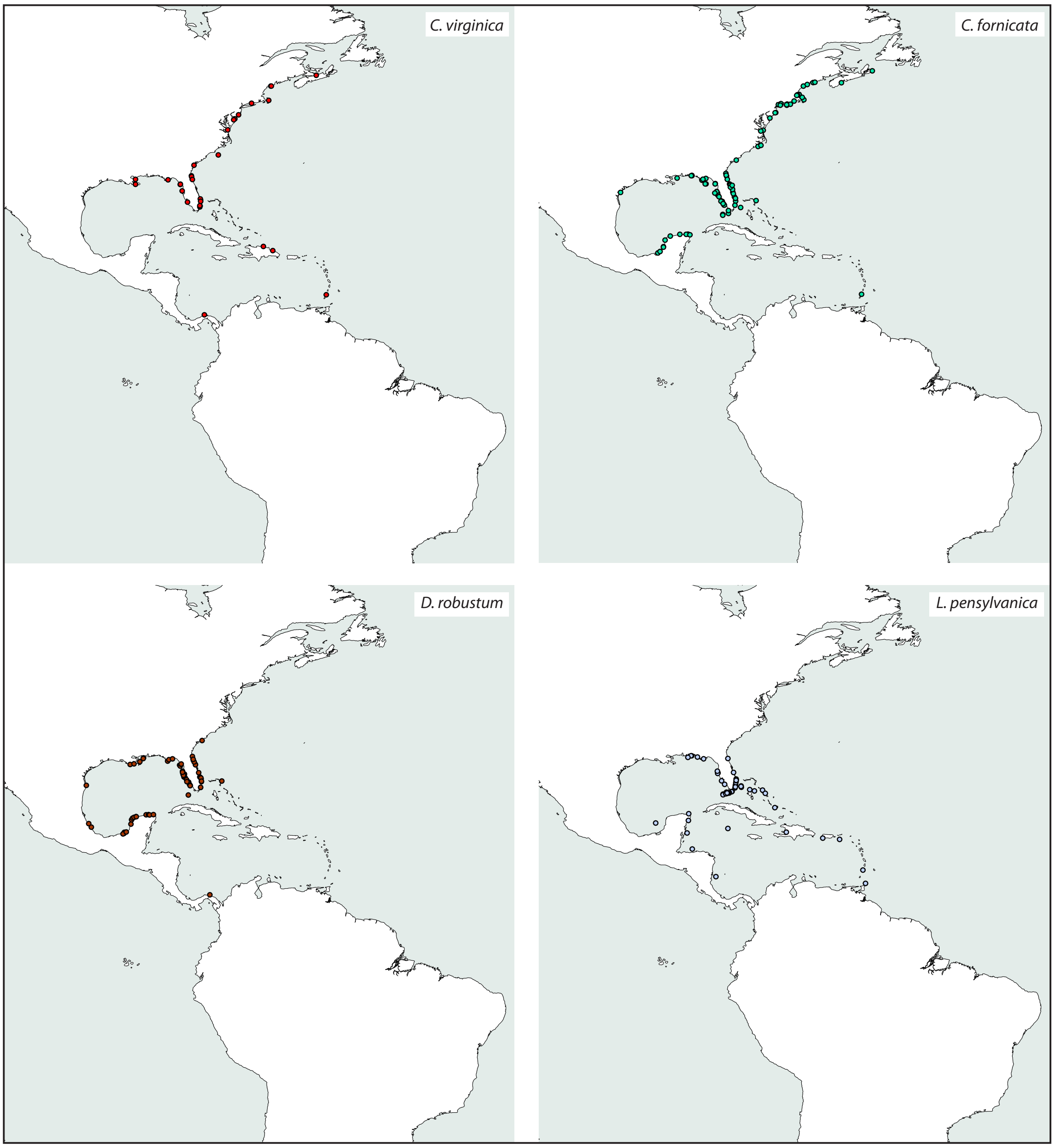


Figure S1.1.3 Distributional data for *Melongena corona*, *Mercenaria campechiensis*, *Neverita duplicata* and *Oliva sayana*.

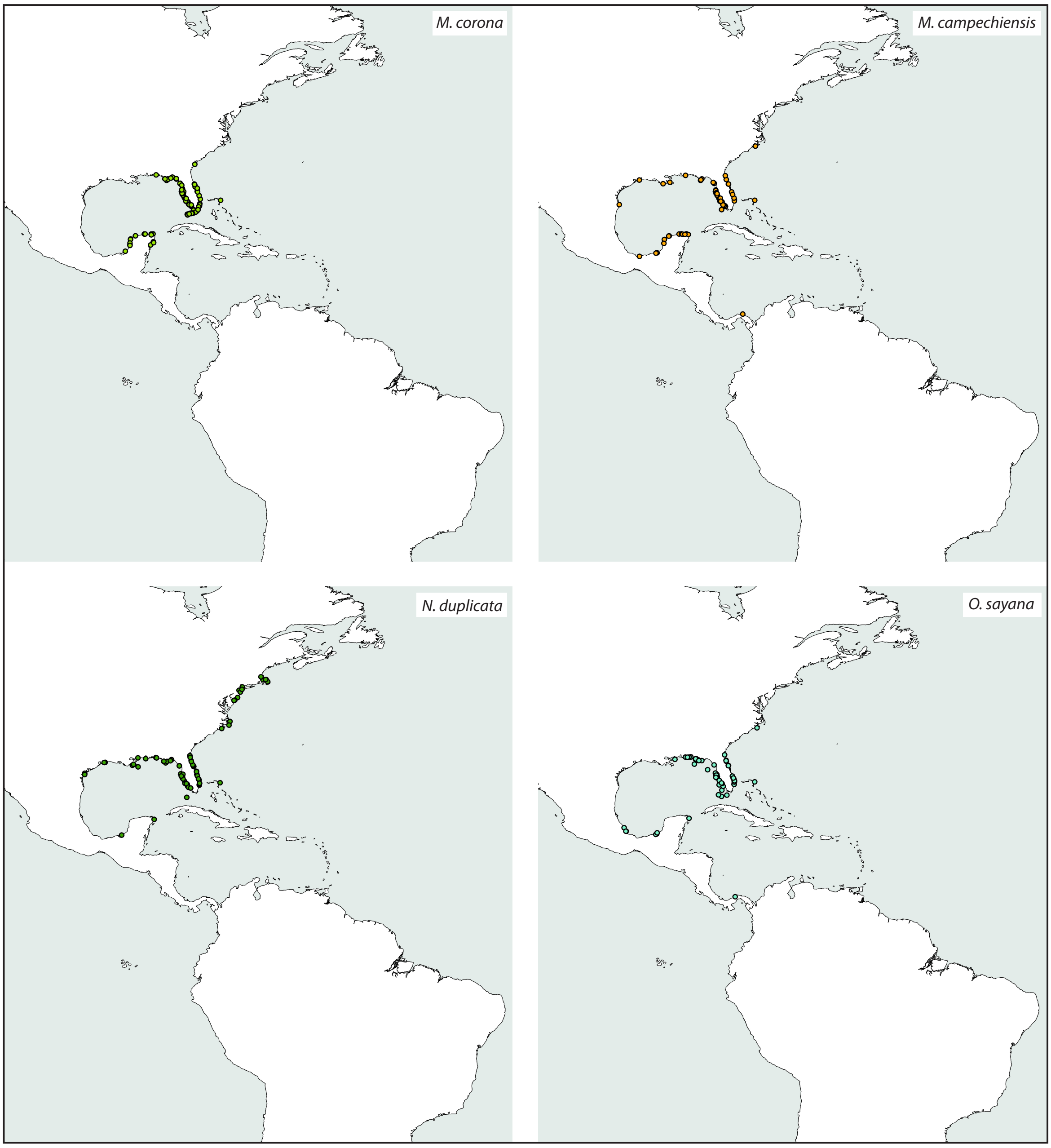
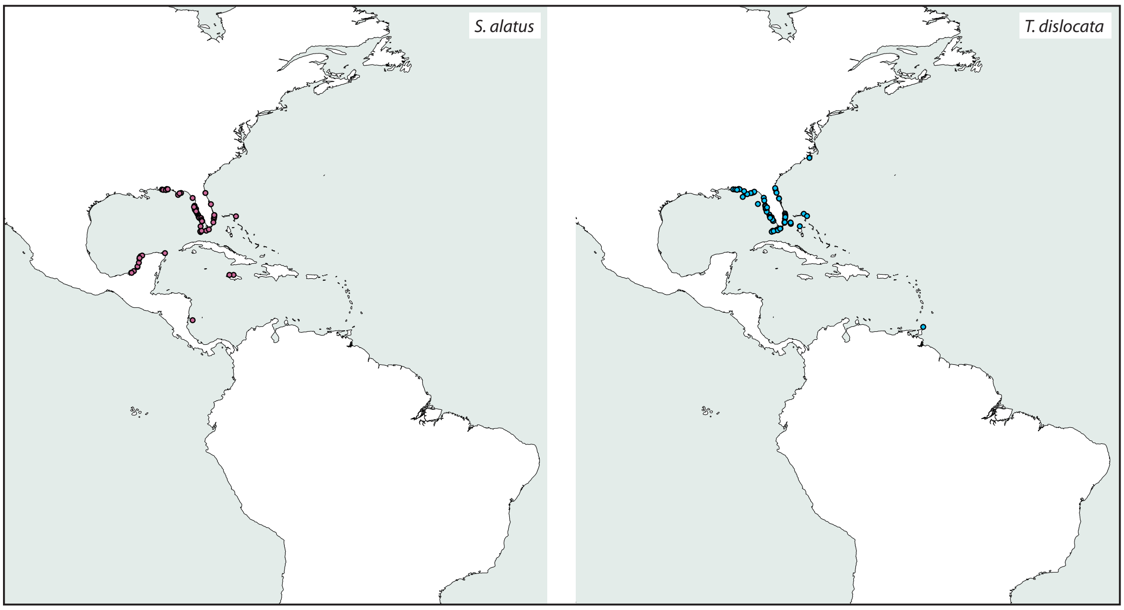


Figure S1.1.4 Distributional data for *Strombus alatus* and *Terebra dislocata*.



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.

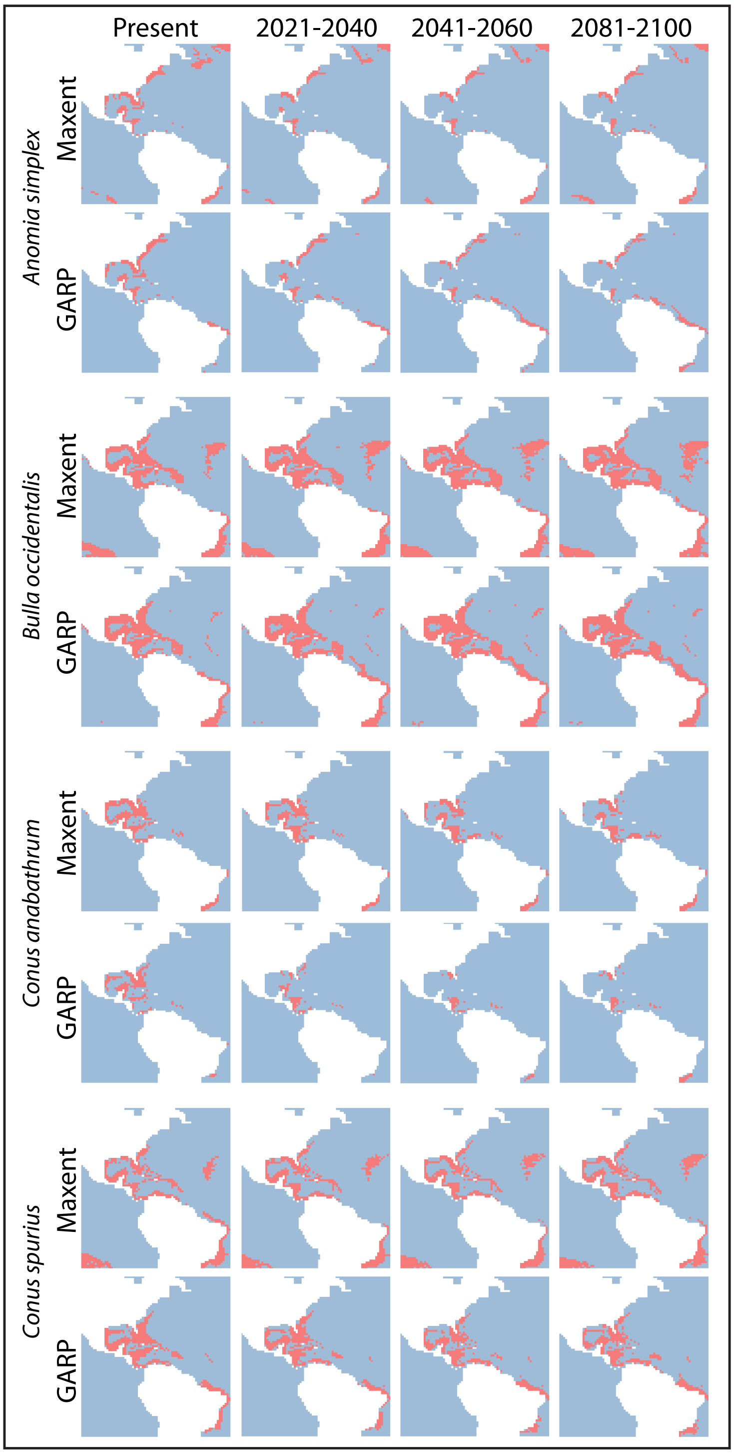


Figure S1.1.6 Niche modeling results for *C. virginica*, *C. fornicata*, *D. robustum* and *L. pensylvanica*. Four time slices are shown: present day (1991–2010) and three future projections (2021–2040, 2041–2060 and 2081–2100) from the most conservative scenario of future change (RCP 2.6). A threshold has been applied, allowing for a maximum of 5% omission error based on presence data.

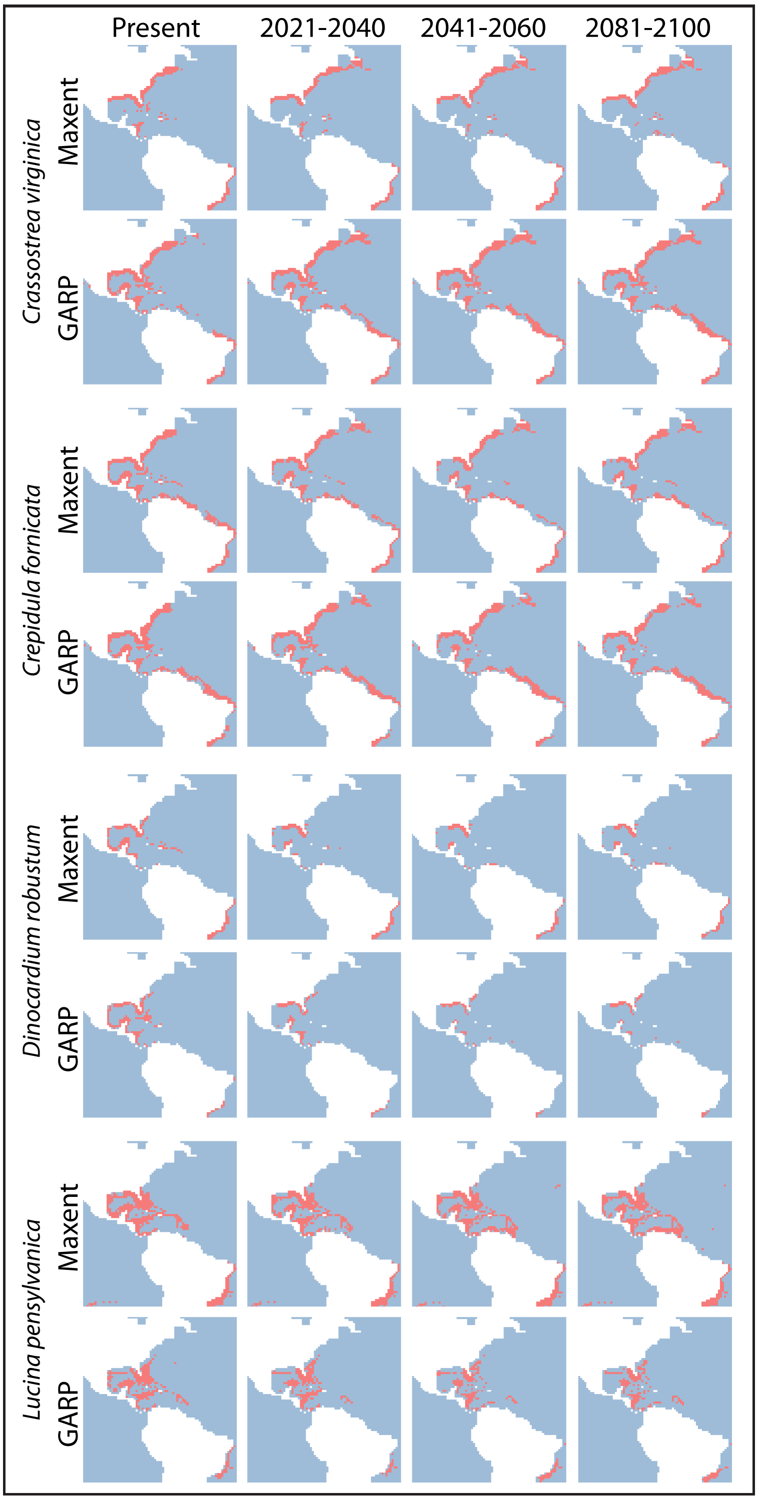


Figure S1.1.7 Niche modeling results for *M. corona*, *M. campechiensis*, *N. duplicata* and *O. sayana*. Four time slices are shown: present day (1991–2010) and three future projections (2021–2040, 2041–2060 and 2081–2100) from the most conservative scenario of future change (RCP 2.6). A threshold has been applied, allowing for a maximum of 5% omission error based on presence data.

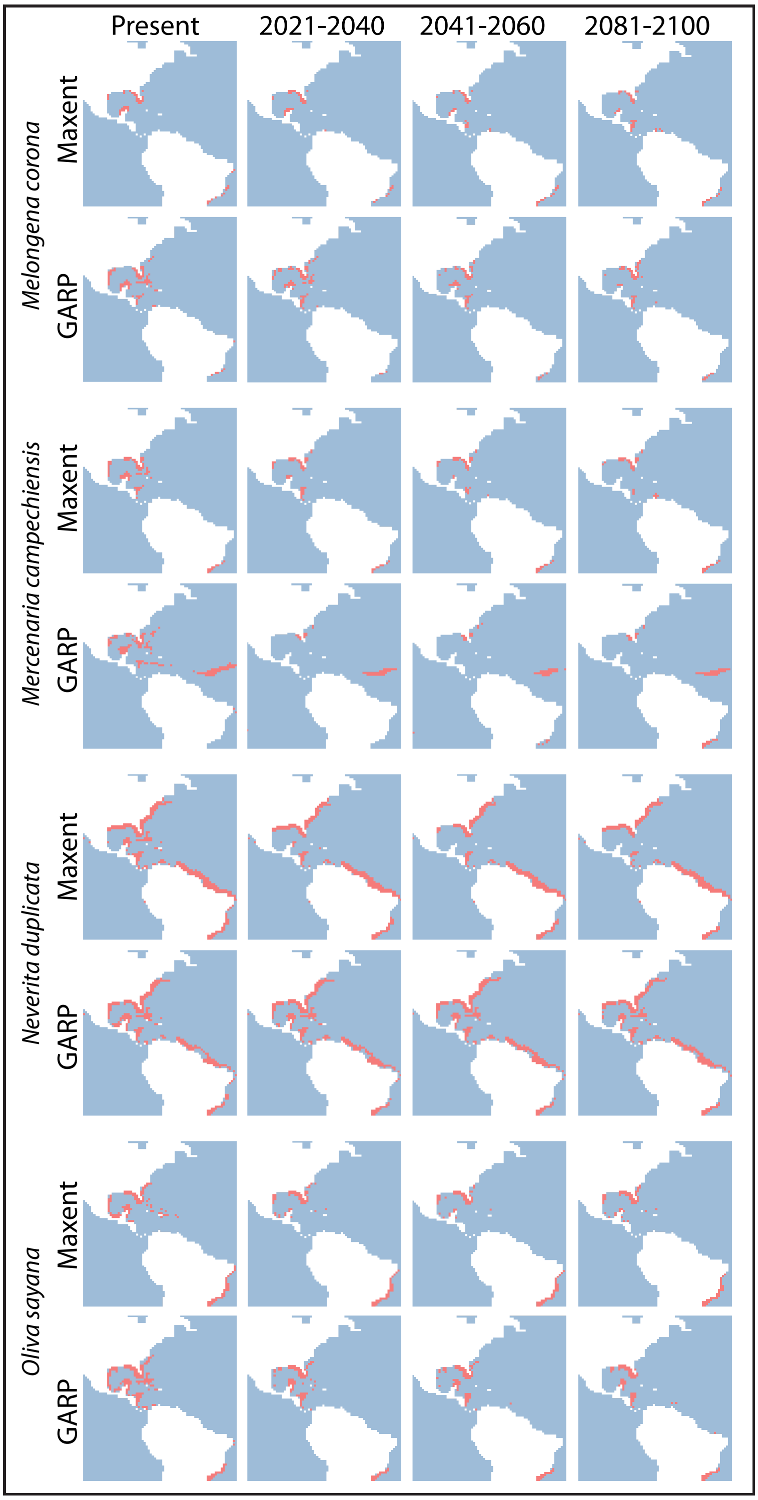


Figure S1.1.8 Niche modeling results for *S. alatus* and *T. dislocata*. Four time slices are shown: present day (1991–2010) and three future projections (2021–2040, 2041–2060 and 2081–2100) from the most conservative scenario of future change (RCP 2.6). A threshold has been applied, allowing for a maximum of 5% omission error based on presence data.

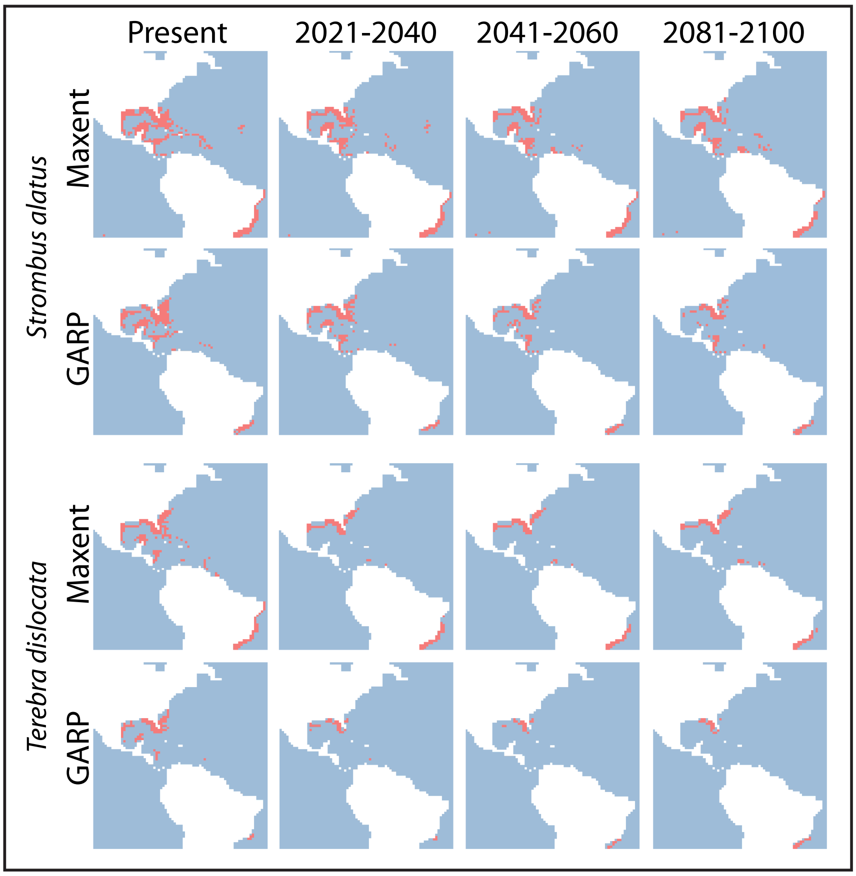


Table S1.1.1 Comparison of models to previously published distributional descriptions. We included multiple descriptions only if they conflicted. Models are congruent if all areas occupied by a species are predicted as suitable. We were less concerned about areas predicted suitable but not thought to be occupied by species, as these regions may be habitable, but the species is prevented from occupying them due to biological or dispersal limitations.

Table S1.1.1: Part 1

Species	Refs	Previously published distribution*	Depth (m)	Zone	Congruence	
					MAXENT	GARP
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 with 2nd & 3rd references – may be missing suitability in Venezuela and Colombia, but references do not mention such areas
	[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
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

Species	Refs	Previously published distribution*	Depth (m)	Zone	Congruence MAXENT	Congruence GARP
	[2]	Maryland to Florida, Bermuda, Bahamas, West Indies, Gulf of Mexico, Caribbean Central America, South America (Colombia)				
Mercenaria campechiensis	[1,3]	39° N to 20° N; 91° W to 76° W; New Jersey to Florida, Texas; Cuba	0–36; live 3–6	Subtropical to tropical	Not congruent – model does not predict as far north as actual distribution (FL/GA vs. NJ/Chesapeake Bay)	Not congruent – model does not predict as far north as actual distribution (FL/GA vs. NJ/Chesapeake Bay)
	[4]	Chesapeake Bay to Florida, Texas and the Yucatán Peninsula to Cuba				
	[2,6]	New Jersey to Gulf of Mexico, Caribbean Central America and the West Indies				
Gastropoda						
Bulla occidentalis	[3]	Texas, Louisiana, Florida, Cuba, Yucatán, Tabasco, Brazil	0–80; live 0–15	Tropical	Congruent, but predicts suitable area further north than realized distribution	Congruent, but predicts suitable area further north than realized distribution
	[1,7]	34.5° N to 34° S; 97.28° W to 0° W; USA: Florida: East Florida, West Florida; USA: Louisiana, Texas; Mexico: Veracruz, Tabasco, Campeche State, Cayos Arcas, Campeche, Yucatán State, Alacran Reef, Quintana Roo; Colombia: offshore islands; Costa Rica, Colombia, Venezuela: Falcón, Isla Margarita; Bermuda, Cuba: North Havana Province, North Matanzas, Camagüey, Holguín; Jamaica, Puerto Rico, Guadeloupe; St Vincent and the Grenadines: Mustique, Grenada; Barbados, Brazil: Maranhão, Ceará, Rio Grande do Norte, Pernambuco, Alagoas, Espírito Santo, Rio de Janeiro, São Paulo, Paraná, Santa Catarina, Rio Grande do Sul				
Conus anabathrum	[1]	35° N to 14.5° N; 91° W to 61° W; USA: Florida: West Florida; Mexico: Campeche State, Yucatán State, Alacran Reef, Quintana Roo	0–122	Tropical	Congruent with 1st reference	Congruent with 2nd reference
	[3]	North Carolina, Florida, Texas				

Table S1.1.1: Part 3

					Congruence	
Species	Refs	Previously published distribution*	Depth (m)	Zone	MAXENT	GARP
Conus spurius	[1]	28° N to 9° N; 94° W to 64.4° W; USA: Florida: East Florida, West Florida, Florida Keys; Mexico: Campeche State, Yucatán State, Alacran Reef, Quintana Roo; Panama; Venezuela; Cuba: Havana Province	0–65; live 1–8	Tropical	Congruent, but predicts suitable area further north than realized distribution	Congruent, but predicts suitable area further north than realized distribution
	[3]	Florida, Texas, Gulf of Mexico				
Crepidula fornicata	[1,3]	48° N to 25° N; 97.2° W to 25° W; Canada to Florida, Texas and Louisiana	0–70; live 0–49	Temperate to tropical	Congruent, but no mention of a Brazilian distribution	Congruent, but no mention of a Brazilian distribution
Melongena corona	[1,4,8]	30.4° N to 24° N; 87.7° W to 80.04° W; 0–2 m; USA: Florida: East Florida, West Florida, Florida Keys; USA: Louisiana, Texas; Mexico: Tamaulipas	0–2; live 0–1.2	Tropical	Congruent	Congruent
Neverita duplicata	[1,3]	42.5° N to 16° N; 97.2° W to 70° W; Cape Ann, MA, to Florida to Texas	0–58; live 0–26	Temperate to tropical	Congruent, but no mention of a Brazilian distribution	Congruent, but no mention of a Brazilian distribution
Oliva sayana	[1,3]	35.34° N to 18.7° N; 97° W to 75.33° W; N. Carolina to Florida to Texas, Gulf of Mexico, Brazil	0–130; live 0–27	Tropical	Not congruent – model does not predict as far north as actual distribution (FL vs. NC)	Congruent

Table S1.1.1: Part 4

Species	Refs	Previously published distribution*	Depth (m)	Zone	Congruence Maxent	 GARP
Strombus alatus	[1,3]	34.42°N to 18.7°N; 97°W to 76.68°W; 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	0–183; live 0–46	Tropical	Not congruent – model does not predict as far north as actual distribution (SC vs. NC	Congruent
Terebra dislocata	[1,3]	38°N to 6°S; 97°W to 37°W; 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	0–146; live 0–22	Subtropical to tropical	Congruent, with exception of potential missing areas in Colombia & Venezuela	Congruent, with exception of potential missing areas in Colombia & Venezuela

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

REFERENCES

1 Rosenberg, G. (2009) *Malacolog 4.1.1: a database of western Atlantic marine Mollusca*. Available at: http://www.malacolog.org/.

2 Mikkelsen, P.M. & Bieler, R. (2008) *Seashells of Southern Florida: living marine mollusks of the Florida Keys and adjacent regions: bivalves.* Princeton University Press, Princeton, NJ.

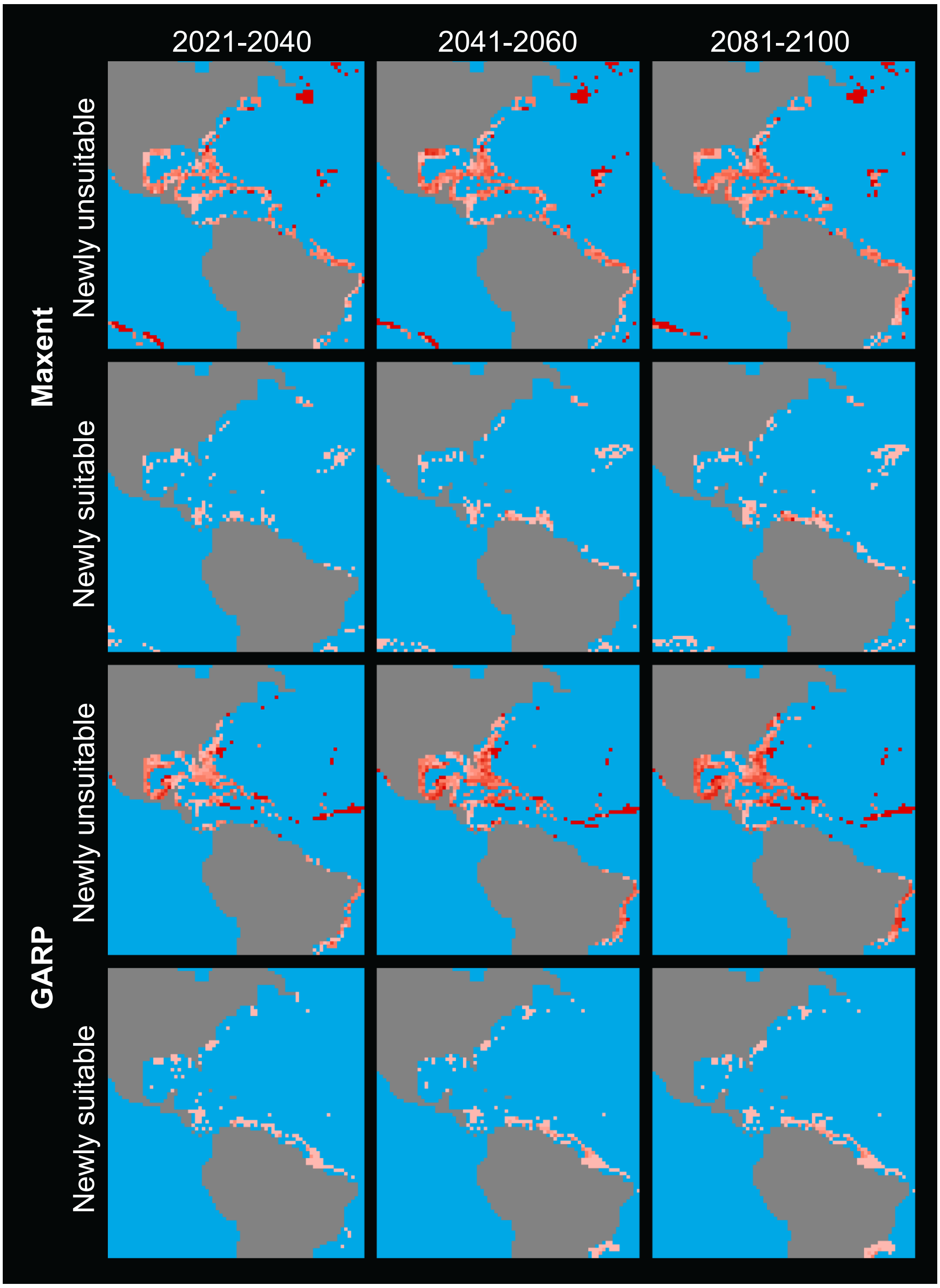
3 Tunnell, J.W., Andrews, J., Barrera, N.C. & Moretzsohn, F. (2010) *Encyclopedia of Texas seashells: identification, ecology, distribution and history*. Texas A&M University Press, College Station, TX.

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.

5 Buroker, N.E. (1983) Population genetics of the American oyster *Crassostrea virginica* along the Atlantic coast and the Gulf of Mexico. *Marine Biology*, **75**, 99–112.

6 Menzel, R.W. (1989) The biology, fishery and culture of quahog clams, *Mercenaria*. *Clam mariculture in North America* (ed. by J.J. Manzi and M. Castagna), pp. 201–242. Elsevier, Amsterdam.

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 e*quatorward* 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.

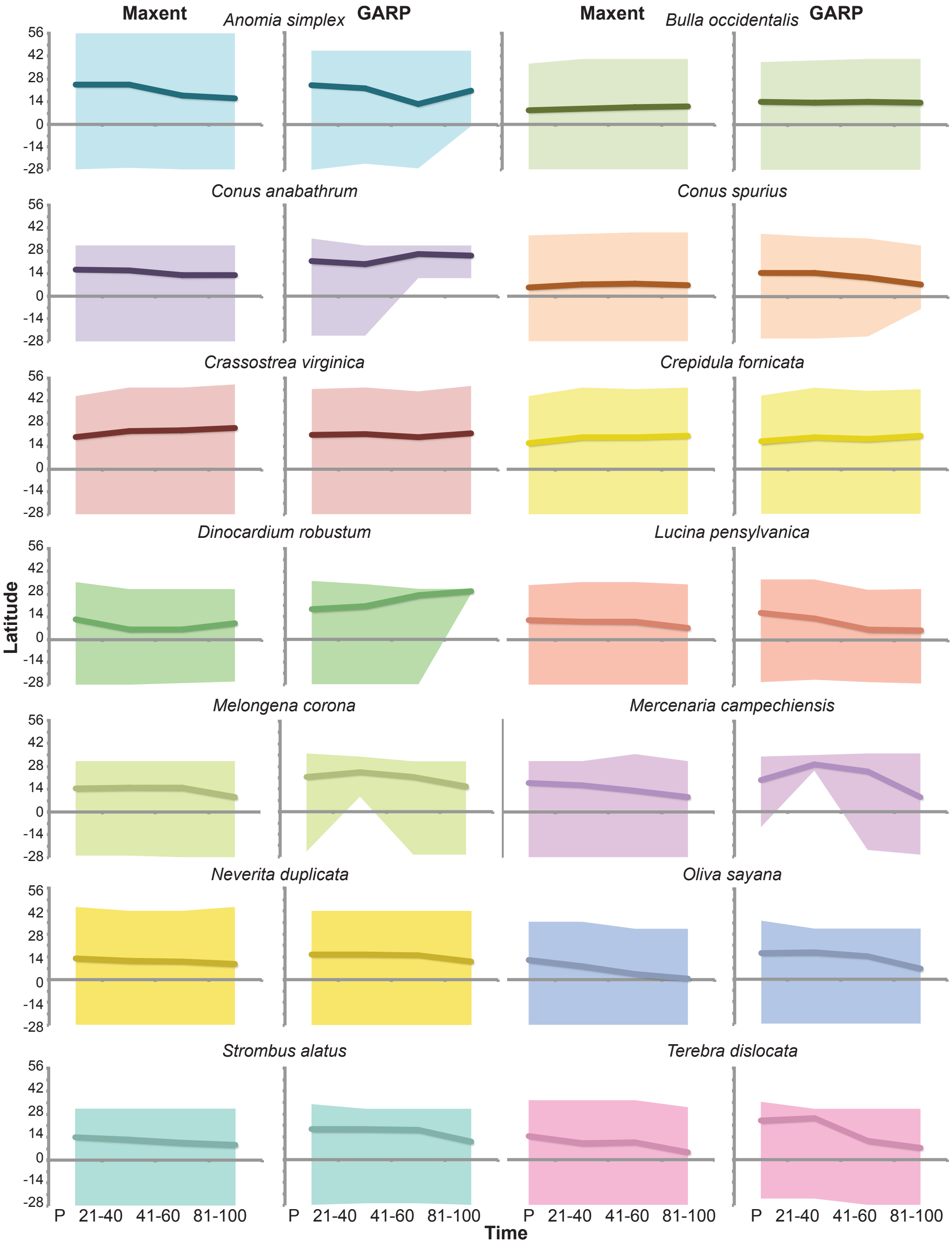


Figure S1.1.11 Latitudinal extent (light shading) and change in centroid of suitable conditions (dark line) from the present (P) to each time slice (2021–2040, 2041–2060 and 2081–2100) for the RCP 8.5 scenario. There is more change in centroid position in this scenario, but the change occurs, for the 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.

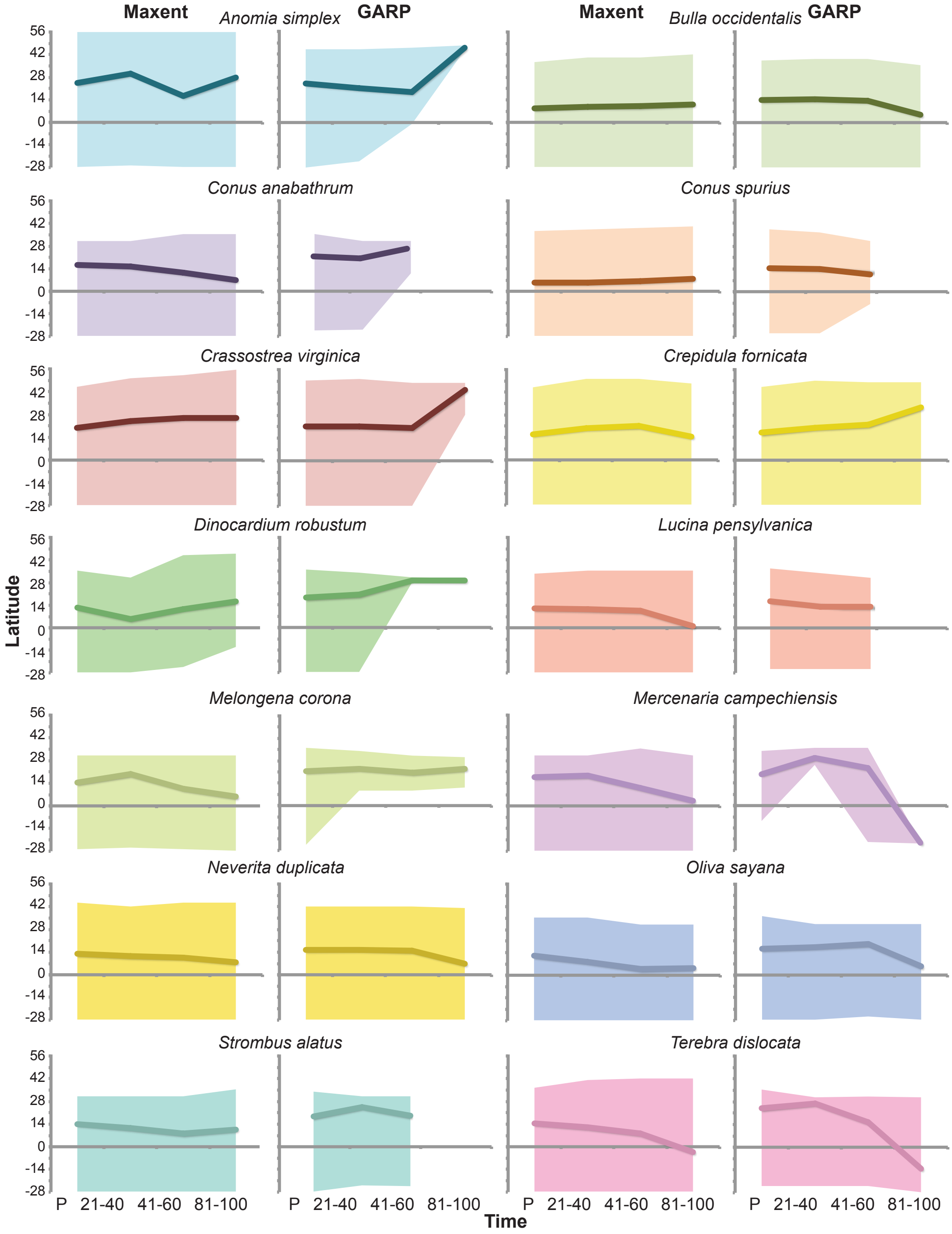


Figure S1.1.12 Cumulative potential suitable area loss and gain for the moderate-emission scenario of change (RCP 4.5). Darker reds indicate higher potential suitable area loss or gain. Results are derived from binary model output and have been normalized based on present-day suitability.

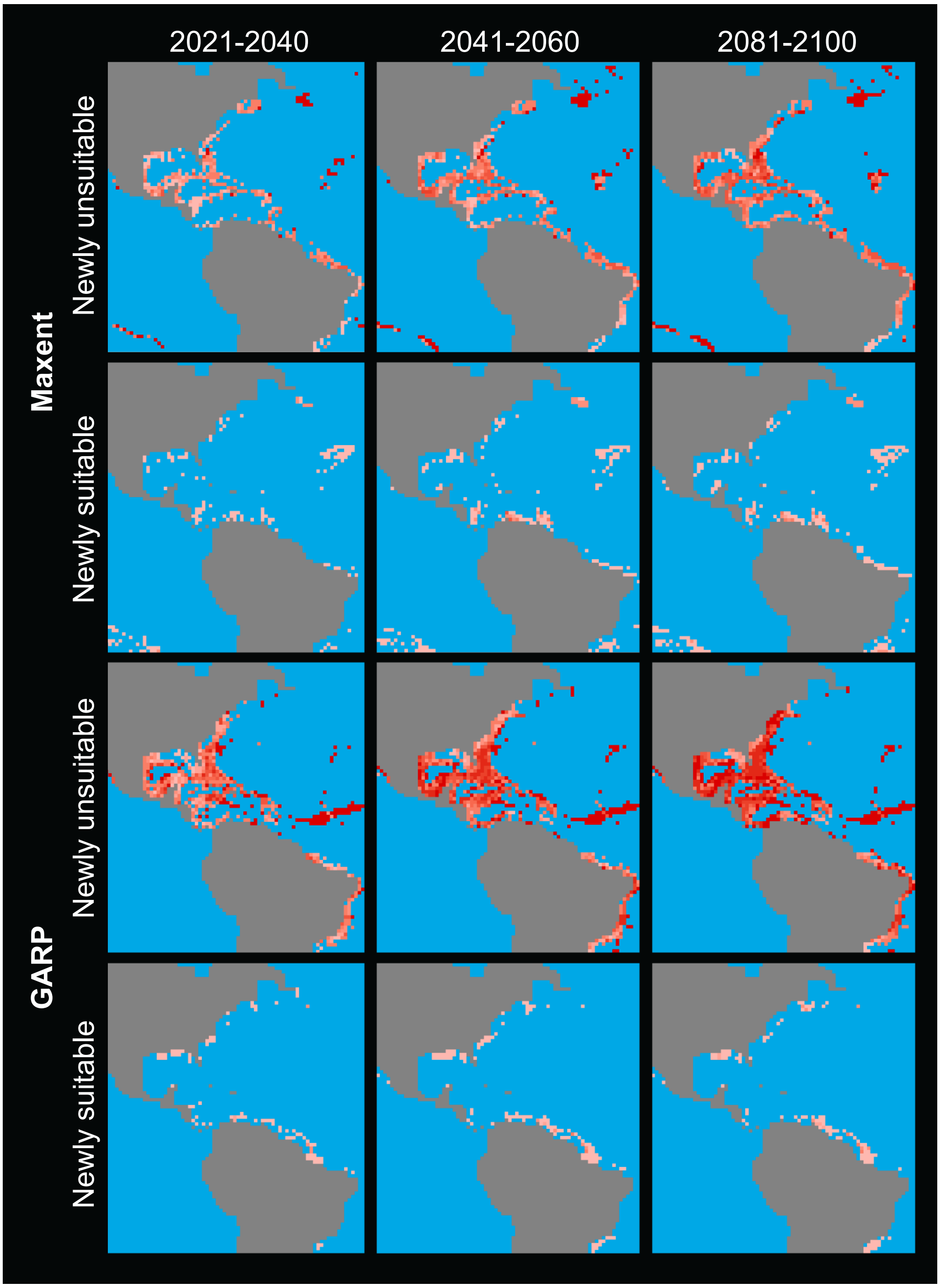
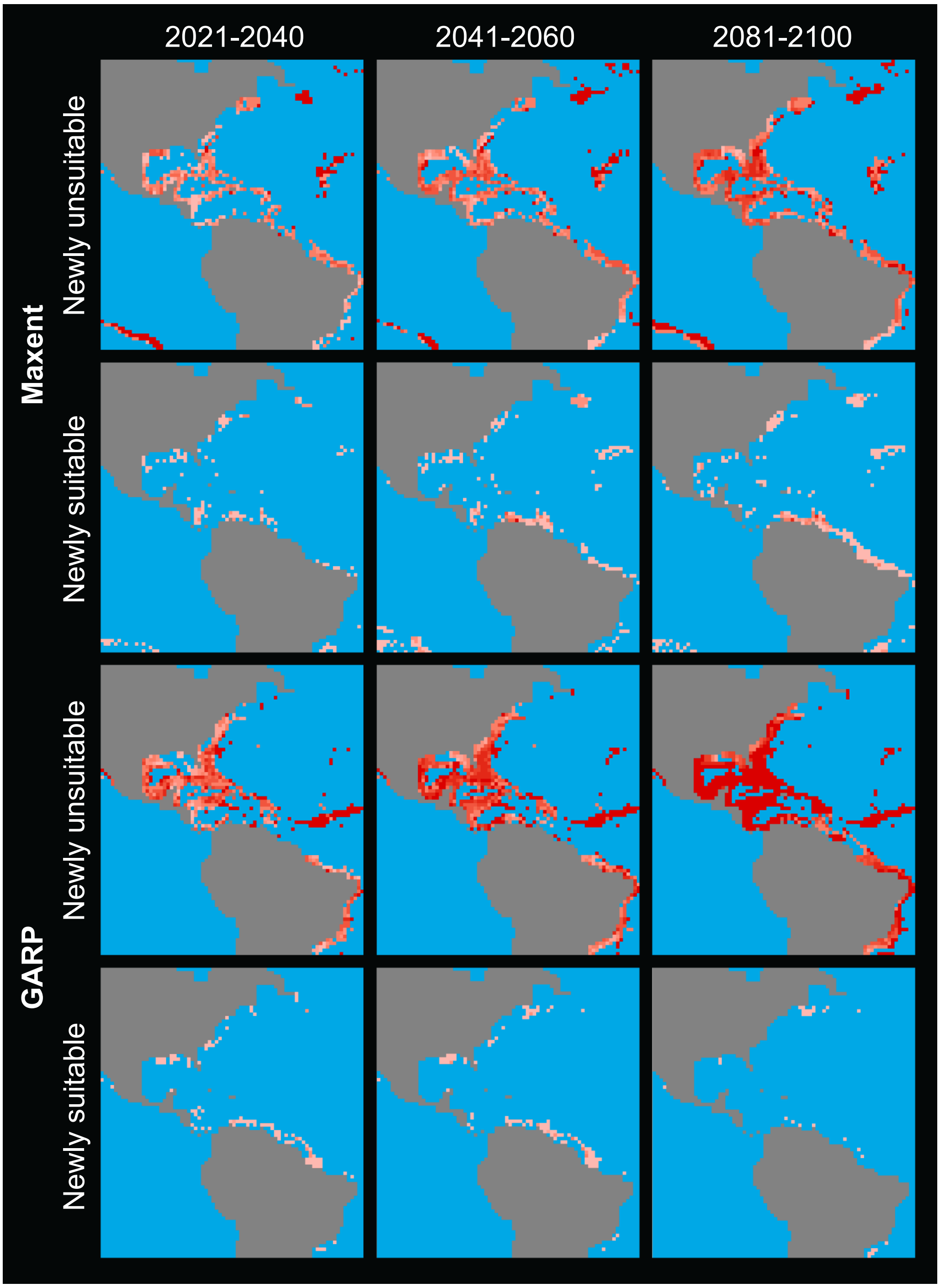


Figure S1.1.13 Cumulative potential suitable area loss and gain over three time slices (2021–2040, 2041–2060 and 2081–2100) for the extreme scenario of change (RCP 8.5). Darker reds indicate higher potential suitable area loss or gain. Results are derived from binary model output and have been normalized 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.

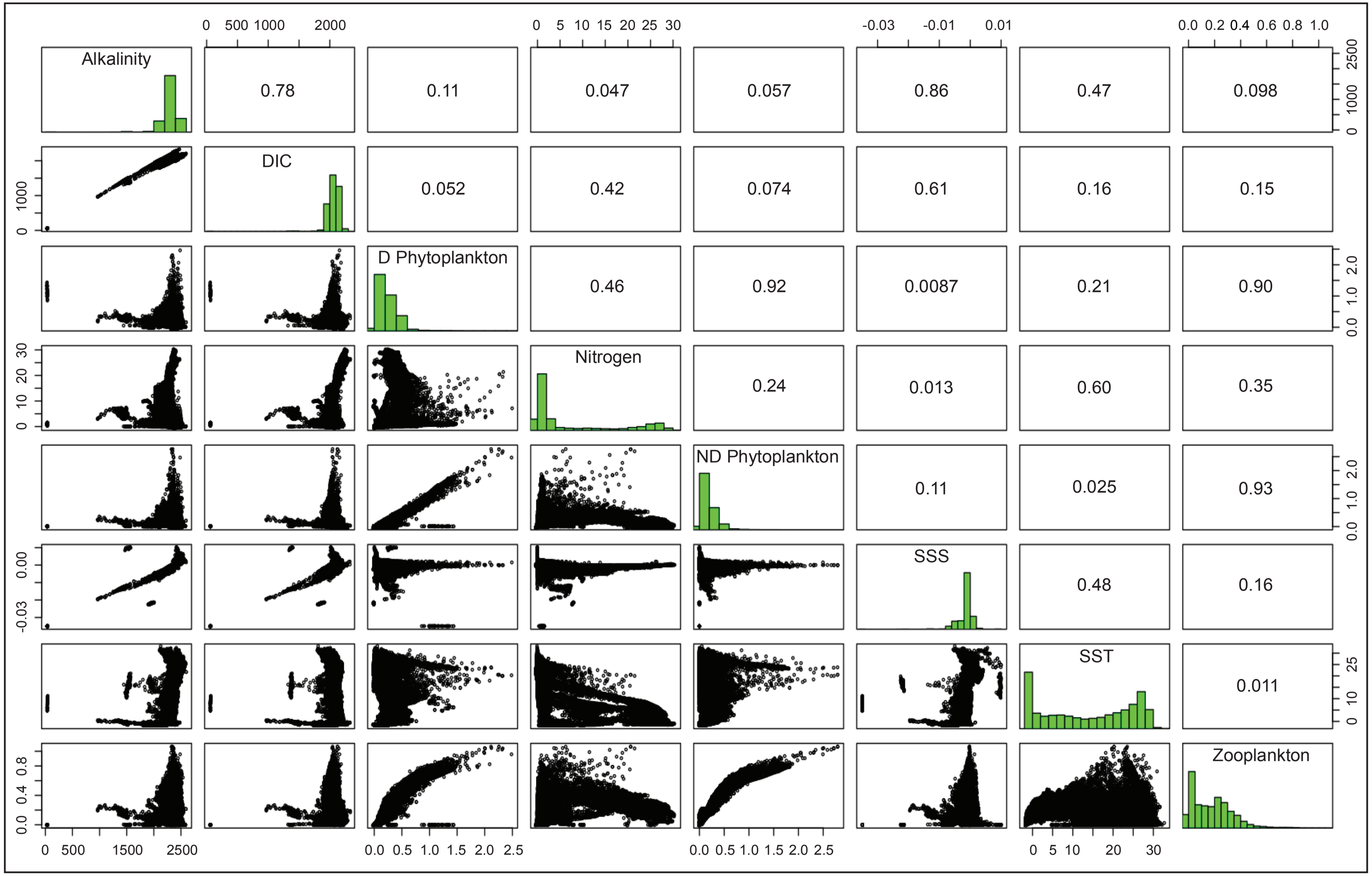


Figure S1.2.1 Pearson correlation of the environmental variables used in this study, performed with the ‘cor’ function in R.

		MAXENT									GARP								
		2021–2040			2041–2060			2081–2100			2021–2040			2041–2060			2081–2100		
Species	RCP	All	No bathy	Red.	All	No bathy	Red.	All	No bathy	Red.	All	No bathy	Red.	All	No bathy	Red.	All	No bathy	Red.
Bivalvia																			
Anomia simplex	2.6	−40.1	−35.1	−30.3	−44.7	−37.9	−35.2	−32.5	−34.8	−29.7	−30.3	−43.9	−14.0	−29.2	−48.1	−14.0	−24.7	−44.4	−11.7
	8.5	−41.8	−27.3	−32.4	−41.4	−49.4	−49.4	−73.8	−76.0	−78.2	−42.1	−57.0	−16.1	−73.0	−88.9	−20.7	−98.9	−100.0	−48.5
Crassostrea	2.6	1.6	−29.2	−6.5	5.3	−15.6	−13.9	2.0	−11.9	−14.7	12.4	−5.2	−8.2	16.3	−8.1	−8.2	17.9	−7.1	−2.7
virginica	8.5	12.2	−17.2	−6.1	22.3	−26.6	−23.7	9.6	−51.2	−33.5	7.8	−13.5	−10.9	−26.1	−12.4	−16.4	−78.5	−54.3	−49.2
Dinocardium	2.6	−38.0	−45.3	−1.9	−49.1	−55.2	−1.9	−44.2	−57.2	5.7	−43.6	−43.0	−4.3	−63.8	−53.0	−8.6	−65.1	−53.5	−9.9
robustum	8.5	−47.9	−56.7	−4.8	−77.9	−63.3	−12.4	−87.1	−62.9	1.0	−75.2	−79.3	−13.7	−94.0	−97.7	−30.5	−98.7	−100.0	−51.1
Lucina	2.6	−5.4	−0.1	−6.2	−0.5	−11.3	−1.4	0.0	−15.3	2.0	−21.9	−25.5	−30.3	−27.5	−32.5	−34.5	−29.5	−32.0	−34.1
pensylvanica	8.5	−5.1	−14.1	−7.6	−11.3	−23.3	−16.7	−57.9	−46.2	−69.2	−59.0	−58.8	−39.8	−86.1	−86.3	−59.8	−100.0	−99.2	−83.0
Mercenaria	2.6	−35.2	−23.0	−26.8	−42.9	−37.4	−29.1	−44.0	−32.5	−25.2	−66.7	−66.9	−23.7	−66.7	−73.3	−26.3	−58.5	−63.2	−27.0
campechiensis	8.5	−40.7	−27.1	−29.9	−57.1	−44.3	−48.0	−84.6	−63.4	−78.7	−87.8	−92.3	−30.3	−92.5	−99.3	−35.5	−99.3	−100.0	−52.6
Gastropoda																			
Bulla	2.6	10.3	1.8	6.2	18.1	4.0	15.9	25.8	8.6	21.3	10.5	−19.2	6.0	17.1	−26.7	6.0	16.7	−20.8	10.3
occidentalis	8.5	5.9	−3.8	5.3	19.3	−28.8	16.8	36.8	−17.7	21.8	−8.9	−63.0	−5.4	−17.3	−93.9	−1.0	−77.8	−100.0	−8.5
Conus	2.6	−12.7	−10.6	−5.0	−18.8	−25.9	−7.6	−25.4	−27.3	−2.5	−52.6	−46.5	−3.5	−68.4	−55.5	−6.0	−59.1	−54.5	−8.5
anabathrum	8.5	−13.5	−13.7	−9.2	−28.1	−29.8	−6.7	−45.4	−26.1	−38.7	−73.7	−72.9	−8.5	−97.1	−92.3	−16.5	−100.0	−97.2	−61.0
Conus spurius	2.6	−1.6	−7.9	2.8	−1.8	−14.0	4.3	4.2	−10.7	13.3	−8.6	−18.6	7.2	−17.7	−29.2	12.0	−12.0	−26.6	15.1
	8.5	−10.8	−15.0	−2.5	−3.8	−17.5	6.8	−8.2	−6.7	22.3	−45.0	−49.0	−7.2	−90.2	−84.0	−10.8	−100.0	−100.0	−36.1
Crepidula	2.6	−14.7	−7.8	−11.3	−25.4	−12.6	−16.5	−22.0	−9.2	−15.2	−2.5	−24.4	0.3	−10.8	−33.8	0.7	−11.7	−32.1	0.0
fornicata	8.5	−19.9	−9.4	−15.9	−37.9	−14.9	−32.9	−53.5	−36.6	−41.8	−21.1	−38.7	−4.7	−40.0	−53.7	−4.4	−70.3	−66.8	−34.9
Melongena	2.6	−17.3	−18.7	−17.5	−11.5	−29.1	−21.1	−7.7	−46.9	−12.3	−12.1	−50.0	−25.2	−36.3	−54.7	−31.0	−39.6	−47.0	−28.4
corona	8.5	−19.2	−28.8	−28.1	−46.2	−37.1	−47.4	−65.4	−72.7	−73.7	−28.6	−95.7	−34.2	−74.7	−99.1	−41.9	−93.4	−100.0	−68.4
Neverita	2.6	−22.8	−30.6	−17.5	−29.1	−33.3	−26.5	−29.6	−32.3	−29.8	−5.1	−26.7	−3.8	−4.7	−30.7	−3.1	−9.4	−33.5	−2.7
duplicata	8.5	−22.8	−30.3	−19.9	−35.4	−37.7	−44.4	−55.8	−51.5	−76.2	−4.7	−38.5	−4.6	−15.2	−57.4	−22.1	−54.2	−83.9	−69.1
Oliva sayana	2.6	−32.4	−57.9	−14.5	−37.2	−67.7	−15.6	−32.4	−60.2	−9.7	−36.2	−55.9	−7.0	−41.8	−65.0	−5.6	−46.3	−61.7	−4.8
	8.5	−31.1	−68.3	−15.1	−49.3	−90.9	−46.8	−70.3	−99.8	−56.5	−42.9	−88.7	−12.6	−68.9	−99.5	−19.3	−80.2	−100.0	−59.6
Strombus alatus	2.6	−20.7	−16.0	−11.7	−32.5	−28.9	−13.1	−31.4	−29.6	−1.7	−23.2	−54.9	−24.9	−45.3	−65.8	−29.1	−48.1	−61.8	−25.4
	8.5	−25.5	−24.0	−14.4	−45.8	−34.1	−23.7	−45.0	−24.6	−33.7	−64.1	−92.8	−46.6	−80.7	−99.6	−66.7	−100.0	−100.0	−83.6
Terebra	2.6	−47.3	−34.2	−50.8	−47.8	−39.2	−54.2	−46.7	−33.4	−55.4	−56.8	−58.6	−36.4	−65.9	−67.6	−43.6	−56.8	−62.0	−46.7
dislocata	8.5	−49.5	−39.9	−52.9	−60.3	−48.7	−63.3	−85.3	−58.7	−82.1	−65.9	−85.2	−41.2	−75.0	−99.4	−64.8	−90.9	−100.0	−91.5

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.

Species/layer	Alkal.		DIC		D phyt.		ND phyt.		Nitrogen		SSS		SST		Zoopl.	
	Pres. Δ	Fut. Δ	Pres. Δ	Fut. Δ	Pres. Δ	Fut. Δ	Pres. Δ	Fut. Δ	Pres. Δ	Fut. Δ	Pres. Δ	Fut. Δ	Pres. Δ	Fut. Δ	Pres. Δ	Fut. Δ
Bivalvia																
A. simplex	−9.0	2.3	12.1	−11.6	23.0	−17.9	−17.2	4.1	21.1	−12.1	−17.2	26.6	−28.5	20.8	−16.0	36.4
C. virginica	0.0	0.0	29.0	−25.3	12.9	−10.0	12.9	−5.3	18.8	−19.0	−20.4	27.9	−24.7	40.5	−19.4	23.2
D. robustum	0.0	0.0	−42.1	85.9	3.9	−8.2	−37.5	61.2	29.6	−30.6	3.9	−14.1	−21.1	42.4	11.8	−12.9
L. pensylvanica	0.0	0.0	3.4	−6.0	0.0	0.0	−5.7	6.0	13.9	−20.3	−5.7	7.7	−10.8	18.1	2.6	−7.5
M. campechiensis	0.0	0.0	0.0	0.0	0.0	0.0	−57.1	84.8	10.7	−21.7	−3.6	2.2	−29.8	34.8	15.5	−19.6
Gastropoda																
B. occidentalis	7.8	−5.2	0.0	0.0	2.1	−1.9	−12.6	13.9	28.1	−22.7	0.3	1.0	−1.3	2.8	4.6	−3.8
C. anabathrum	0.0	0.0	0.0	0.0	2.9	−19.1	−74.7	94.9	10.2	−26.4	−0.8	−0.6	−5.3	7.3	17.1	−57.3
C. spurius	−5.1	7.6	0.0	0.0	0.2	1.0	−12.6	12.5	26.9	−29.2	6.2	−5.1	−6.0	6.3	0.0	0.0
C. fornicata	−7.0	10.2	0.0	0.0	5.5	−14.7	−21.8	24.5	23.3	−38.9	−1.5	1.9	−22.1	31.3	0.0	0.0
M. corona	−6.3	15.6	0.0	0.0	0.0	0.0	−52.1	77.8	97.9	−64.4	4.2	−11.1	−18.8	37.8	0.0	0.0
N. duplicata	0.0	0.5	0.0	0.5	1.7	−4.7	−10.6	13.1	3.4	0.5	−13.0	17.8	−7.5	8.4	2.4	−7.5
O. sayana	−38.0	59.8	0.0	0.0	0.0	0.0	−8.8	14.1	9.5	−13.0	0.0	2.2	−29.2	50.0	38.7	−31.5
S. alatus	0.0	0.0	2.4	−4.1	0.0	0.0	−17.8	30.6	11.5	−27.2	−7.9	14.5	−26.1	39.3	2.8	−10.4
T. dislocata	0.0	0.0	0.0	0.0	0.0	0.0	−12.1	3.2	4.6	−5.3	−26.0	9.6	−46.2	47.9	12.7	−100

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.

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.

Species/variable	Bathy.	Alkal.	DIC	D phyt.	ND phyt.	Nitrogen	SSS	SST	Zoopl.
Bivalvia									
A. simplex	56.9	0.2	7.5	3.0	2.7	6.6	4.7	9.3	9.0
C. virginica	72.1	0.0	0.4	0.2	0.2	10.7	2.6	12.4	1.5
D. robustum	66.2	0.4	0.5	1.4	2.9	10.8	9.3	4.1	4.4
L. pensylvanica	64.2	0.0	0.0	0.0	0.6	6.7	8.8	3.5	16.1
M. campechiensis	70.6	0.0	0.0	0.0	2.0	10.1	3.8	6.5	7.1
Gastropoda									
B. occidentalis	60.9	0.6	14.7	1.7	2.4	15.1	0.5	0.2	3.8
C. anabathrum	54.8	5.4	0.0	0.5	7.9	15.3	0.6	1.1	14.4
C. spurius	68.6	0.9	11.5	0.1	2.7	8.8	4.8	2.6	0.0
C. fornicata	65.6	0.5	0.0	0.2	4.3	8.4	4.9	16.2	0.0
M. corona	66.3	0.3	0.0	0.0	5.6	13.9	11.1	2.8	0.2
N. duplicata	75.7	0.0	0.0	0.3	6.0	2.0	11.4	4.5	0.0
O. sayana	75.5	1.5	3.7	0.0	0.1	6.6	5.5	4.0	3.1
S. alatus	57.5	0.0	1.0	0.0	2.4	9.8	19.3	7.2	2.7
T. dislocata	58.9	0.0	0.0	2.5	3.6	5.7	12.1	15.3	1.9

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.

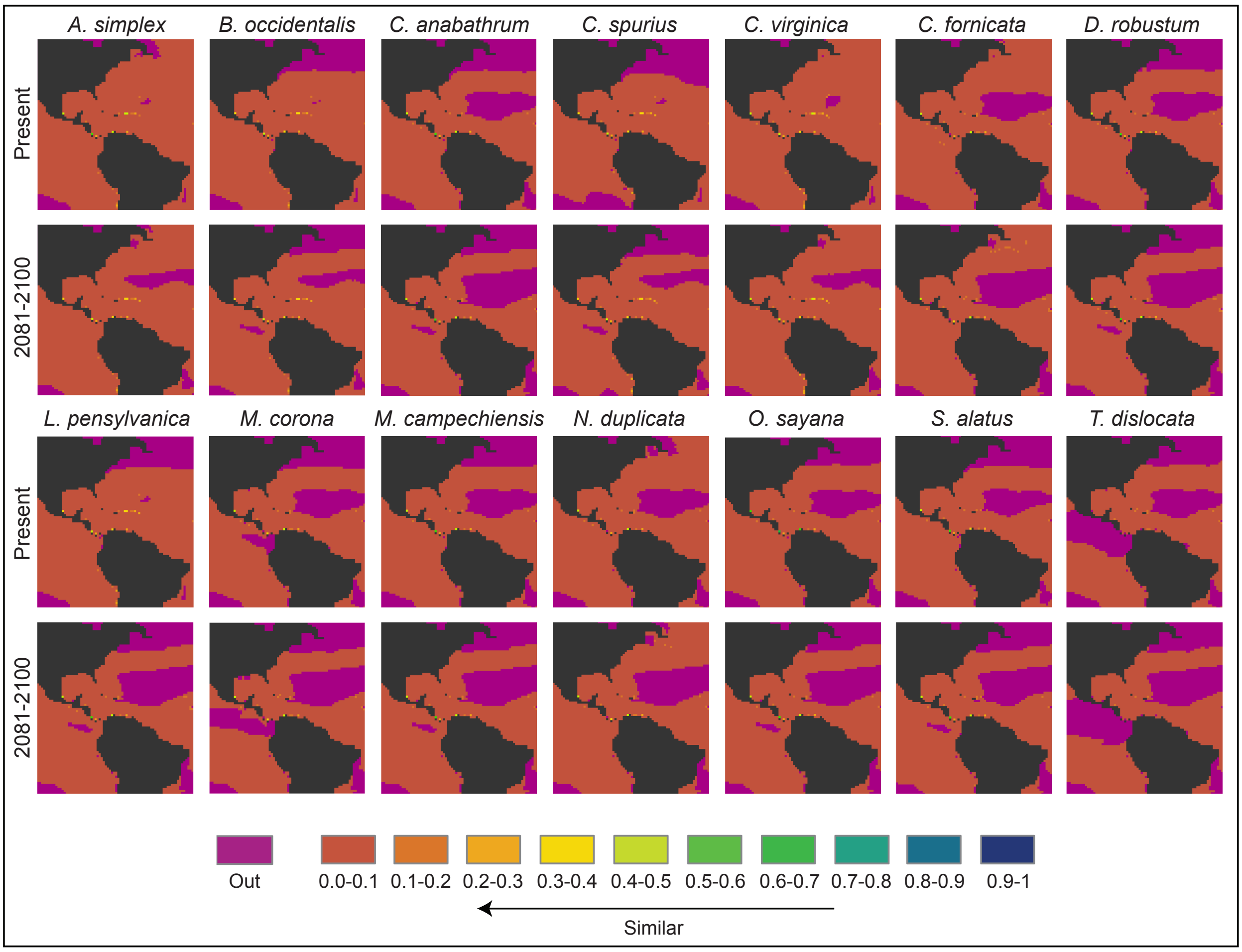


Table S1.3.1 Indication of model extrapolation in specified regions. Crosses indicate cases where the model predicts suitable area in that region, but the area also contains values for environmental variables that are outside those found in the training region. For most species, only a few suitable pixels are implicated in the respective regions.

	Present			(RCP 8.5) 2081–2100		
Species	SW Pacific	mid-Atlantic	Brazilian coast	SW Pacific	mid-Atlantic	Brazilian coast
Bivalvia						
Anomia simplex	×		×			
Crassostrea virginica			×			×
Dinocardium robustum		×	×		×	×
Lucina pensylvanica	×		×	×	×	×
Mercenaria campechiensis						
Gastropoda						
Bulla occidentalis	×		×	×	×	×
Conus anabathrum						
Conus spurius	×		×	×	×	×
Crepidula fornicata		×	×		×	×
Melongena corona			×			
Neverita duplicata			×			
Oliva sayana		×	×			×
Strombus alatus	×	×	×	×	×	
Terebra dislocata			×			

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.

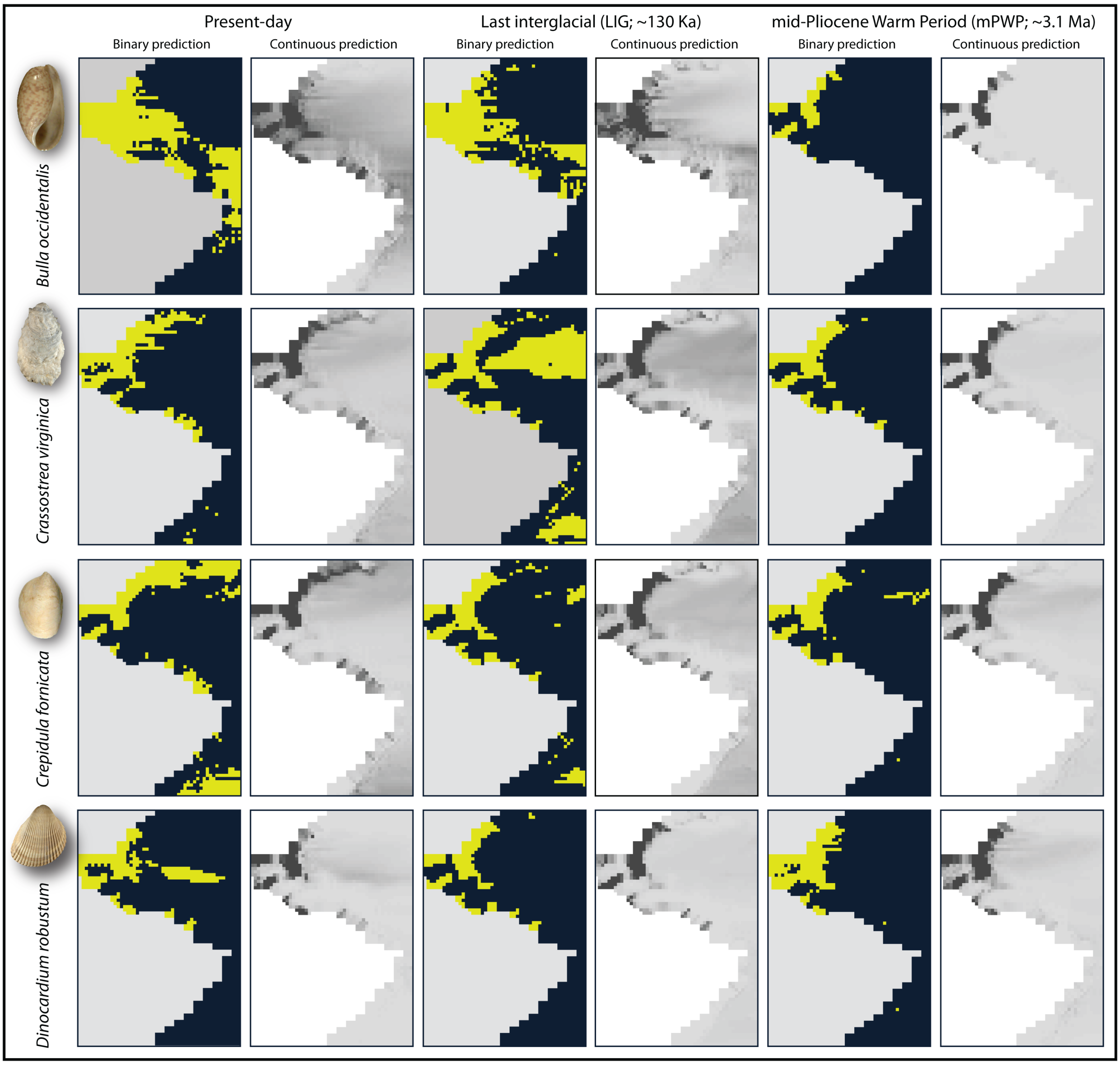


Figure S2.1.2 Ecological niche models for the present, LIG, and mPWP time slices for *Lucina pensylvanica*, *Mercenaria campechiensis*, *Neverita duplicata*, and *Terebra dislocata.* Binary and continuous predictions are presented, with binary predictions thresholded using the mean suitability value from the continuous output. For the binary predictions, yellow=suitable and dark blue=unsuitable, whereas for the continuous predictions, darker grays indicate higher suitability.

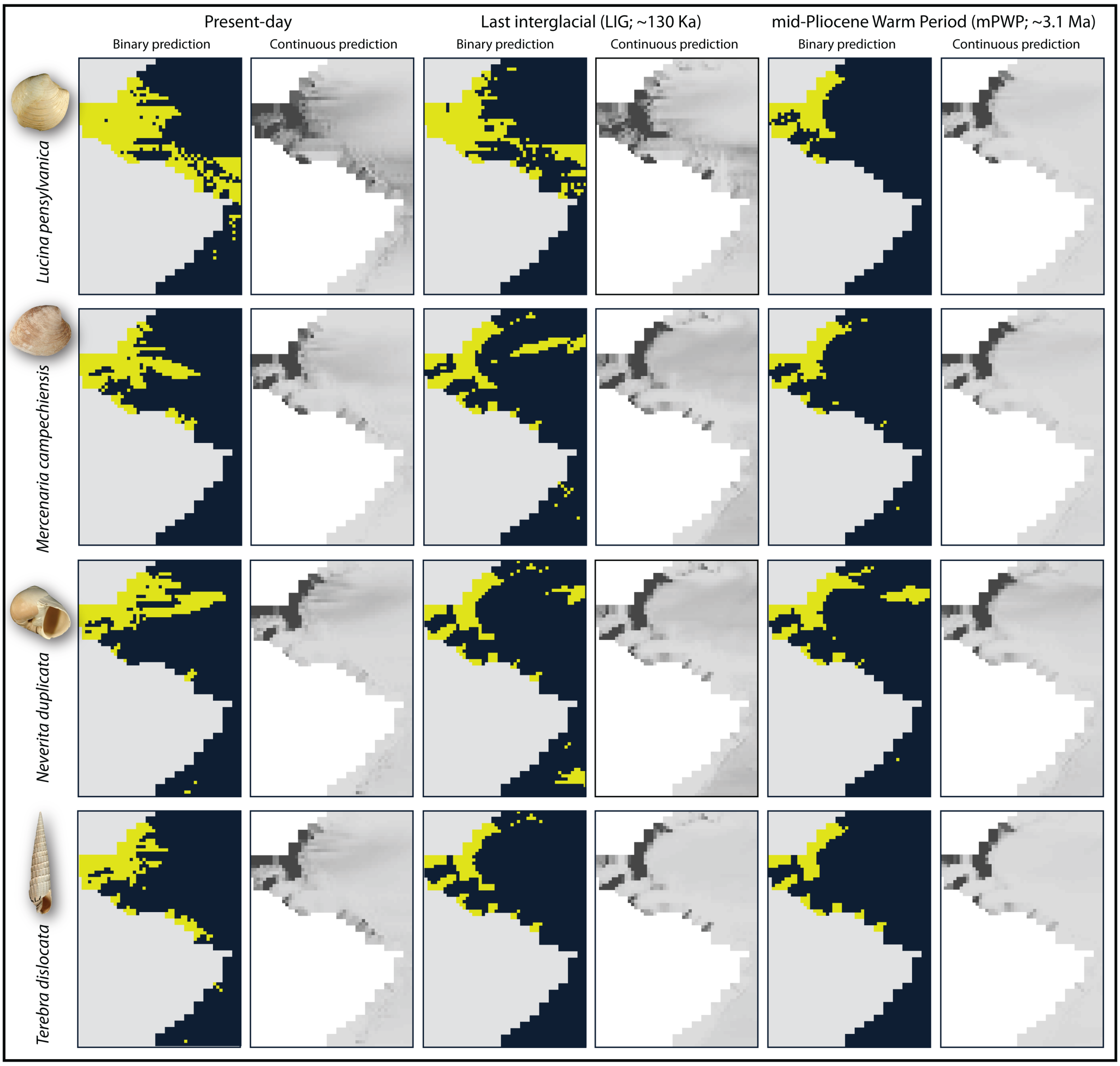


Figure S2.1.3 Distributional data for *Anomia simplex*, *Bulla occidentalis*, *Crassostrea virginica* and *Crepidula fornicata* for the three time slices: mid-Pliocene Warm Period (mPWP; ~3.1 Ma), Last Interglacial (LIG; ~ 130 Ka), and present-day (PI).

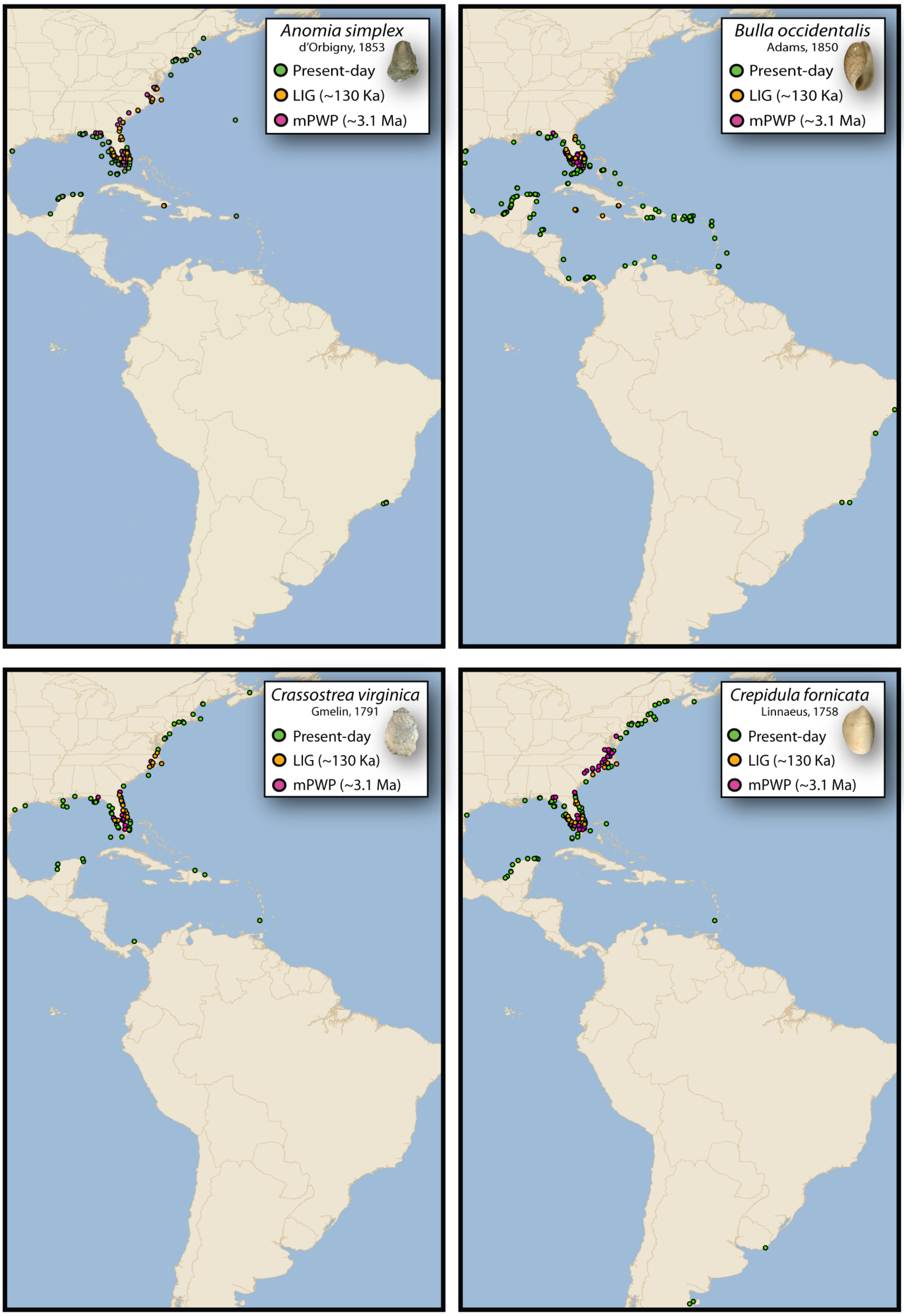


Figure S2.1.4 Distributional data for *Dinocardium robustum*, *Lucina pensylvanica*, *Mercenaria campechiensis* and *Neverita duplicata* the three time slices: mid-Pliocene Warm Period (mPWP; ~3.1 Ma), Last Interglacial (LIG; ~ 130 Ka), and present-day (PI).

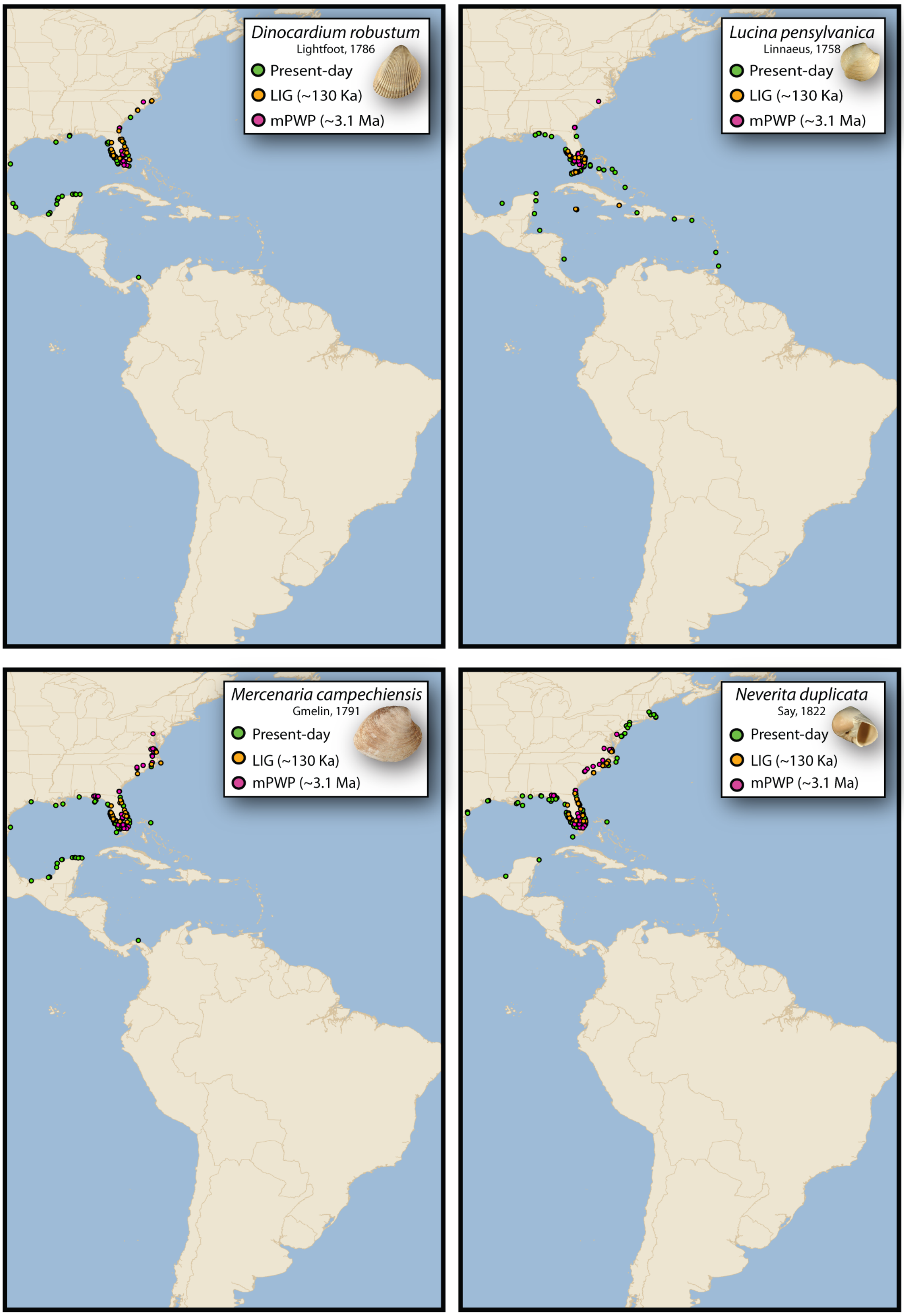


Figure S2.1.5 Distributional data for *Oliva sayana* and *Terebra dislocata* for the three time slices: mid-Pliocene Warm Period (mPWP; ~3.1 Ma), Last Interglacial (LIG; ~ 130 Ka), and present-day (PI).

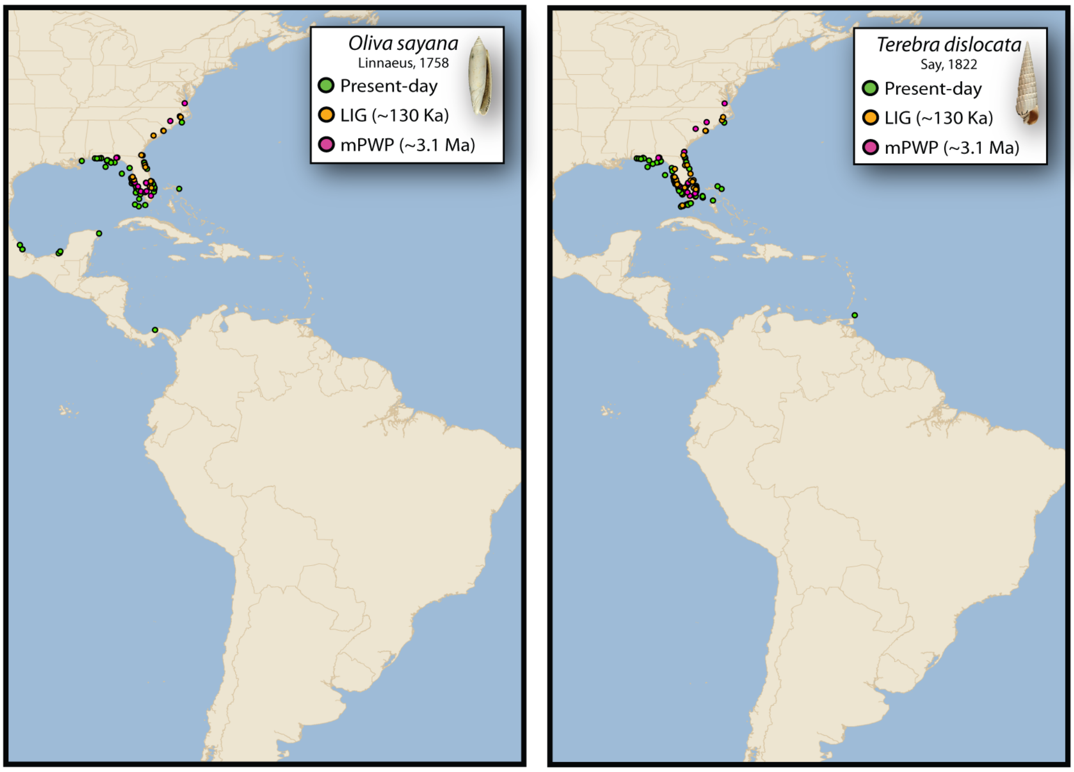


Table S2.1.1 Data on climatic preference and larval strategy for the species analyzed. Distributional data are shown for each time slice: mid-Pliocene Warm Period (mPWP; ~3.1 Ma), Last Interglacial (LIG; ~ 130 Ka), and present-day (PI). The "all" column indicates the total number of distributional records for each time slice/species, and the "unique" column specifies the spatially explicit distributional records used for modeling.

	Species	**Climatic Zone**	**Larval Strategy**	**Distributional Data**					
				mPWP		LIG		PI	
				All	Unique	All	Unique	All	Unique
Bivalvia	*Anomia simplex*	Temperate—Tropical	Planktonic	219	13	85	15	96	31
	Crassostrea virginica	Temperate—Tropical	Planktonic	42	7	24	10	62	37
	Dinocardium robustum	Subtropical—Tropical	Planktonic	59	7	46	11	74	22
	Lucina pensylvanica	Tropical	Benthic	127	7	29	8	79	37
	Mercenaria campechiensis	Subtropical—Tropical	Planktonic	198	14	94	12	70	24
Gastropoda	*Bulla occidentalis*	Tropical	Planktonic	82	6	60	9	191	58
	Crepidula fornicata	Temperate—Tropical	Planktonic	157	16	31	10	103	42
	Neverita duplicata	Temperate—Tropical	Planktonic	134	16	54	14	88	28
	Oliva sayana	Tropical	Planktonic	76	9	28	8	81	25
	Terebra dislocata	Subtropical—Tropical	Benthic	58	9	37	13	89	20

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.

	Species	Time Slice	Set	AUC Ratio/ Success Rate	P-value
Bivalvia	*Anomia simplex*	mPWP	NA	0.92	0.00
		LIG	NA	0.93	0.00
		PI	1	1.81	0.00
			2	1.81	0.00
			3	1.82	0.00
			4	1.31	0.03
			5	1.19	0.05
	Crassostrea virginica	mPWP	NA	0.71	0.00
		LIG	NA	0.90	0.00
		PI	1	1.29	0.01
			2	1.77	0.00
			3	1.65	0.00
			4	1.52	0.00
			5	1.79	0.00
	Dinocardium robustum	mPWP	NA	0.86	0.00
		LIG	NA	0.91	0.00
		PI	NA	0.95	0.00
	Lucina pensylvanica	mPWP	NA	0.86	0.00
		LIG	NA	0.75	0.00
		PI	1	1.61	0.00
			2	1.59	0.00
			3	1.54	0.00
			4	1.91	0.00
			5	1.76	0.00
	Mercenaria campechiensis	mPWP	NA	0.93	0.00
		LIG	NA	0.92	0.00
		PI	NA	0.96	0.00
Gastropoda	*Bulla occidentalis*	mPWP	NA	0.50	0.00
		LIG	NA	0.89	0.00
		PI	1	1.53	0.00
			2	1.18	0.04
			3	1.61	0.00
			4	1.59	0.00
			5	1.22	0.02
	Crepidula fornicata	mPWP	NA	0.88	0.00
		LIG	NA	0.90	0.00
		PI	1	1.79	0.00
			2	1.20	0.02
			3	1.20	0.04
			4	1.78	0.00
			5	1.26	0.03
	Neverita duplicata	mPWP	NA	0.88	0.00
		LIG	NA	0.93	0.00
		PI	1	1.82	0.00
			2	1.70	0.00
			3	1.88	0.00
			4	1.90	0.00
			5	1.57	0.00
	Oliva sayana	mPWP	NA	0.89	0.00
		LIG	NA	0.88	0.00
		PI	NA	0.96	0.00
	Terebra dislocata	mPWP	NA	0.78	0.00
		LIG	NA	0.92	0.00
		PI	NA	0.95	0.00

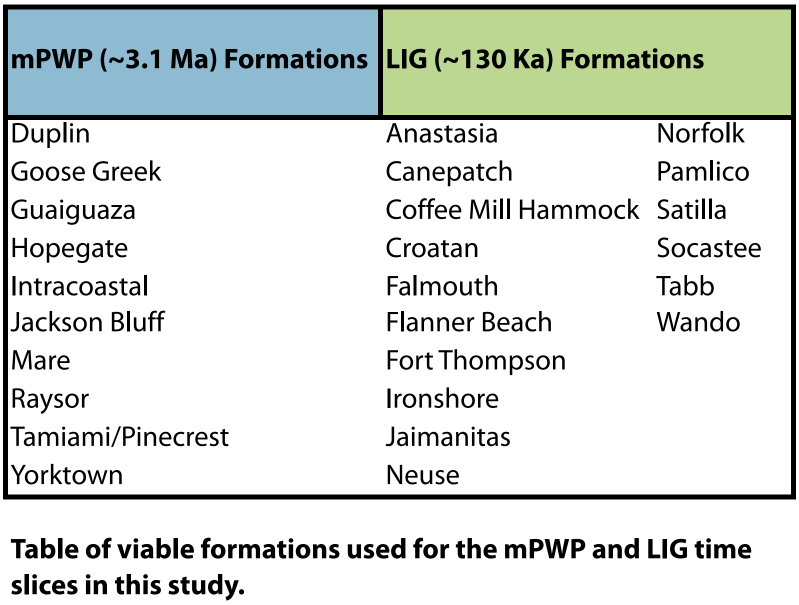
Appendix S2.2

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 provide a useful reference for those working on Pliocene—recent material from the Atlantic Coastal Plain.

Table 2.2.1 Table of viable formations used for the mPWP and LIG time slices in this study.



mPWP (~3.1 Ma) Formations	**LIG (~130 Ka) Formations**	
Duplin	Anastasia	Norfolk
Goose Greek	Canepatch	Pamlico
Guaiguaza	Coffee Mill Hammock	Satilla
Hopegate	Croatan	Socastee
Intracoastal	Falmouth	Tabb
Jackson Bluff	Flanner Beach	Wando
Mare	Fort Thompson	
Raysor	Ironshore	
Tamiami/Pinecrest	Jaimanitas	
Yorktown	Neuse	

Table of viable formations used for the mPWP and LIG time slices in this study.

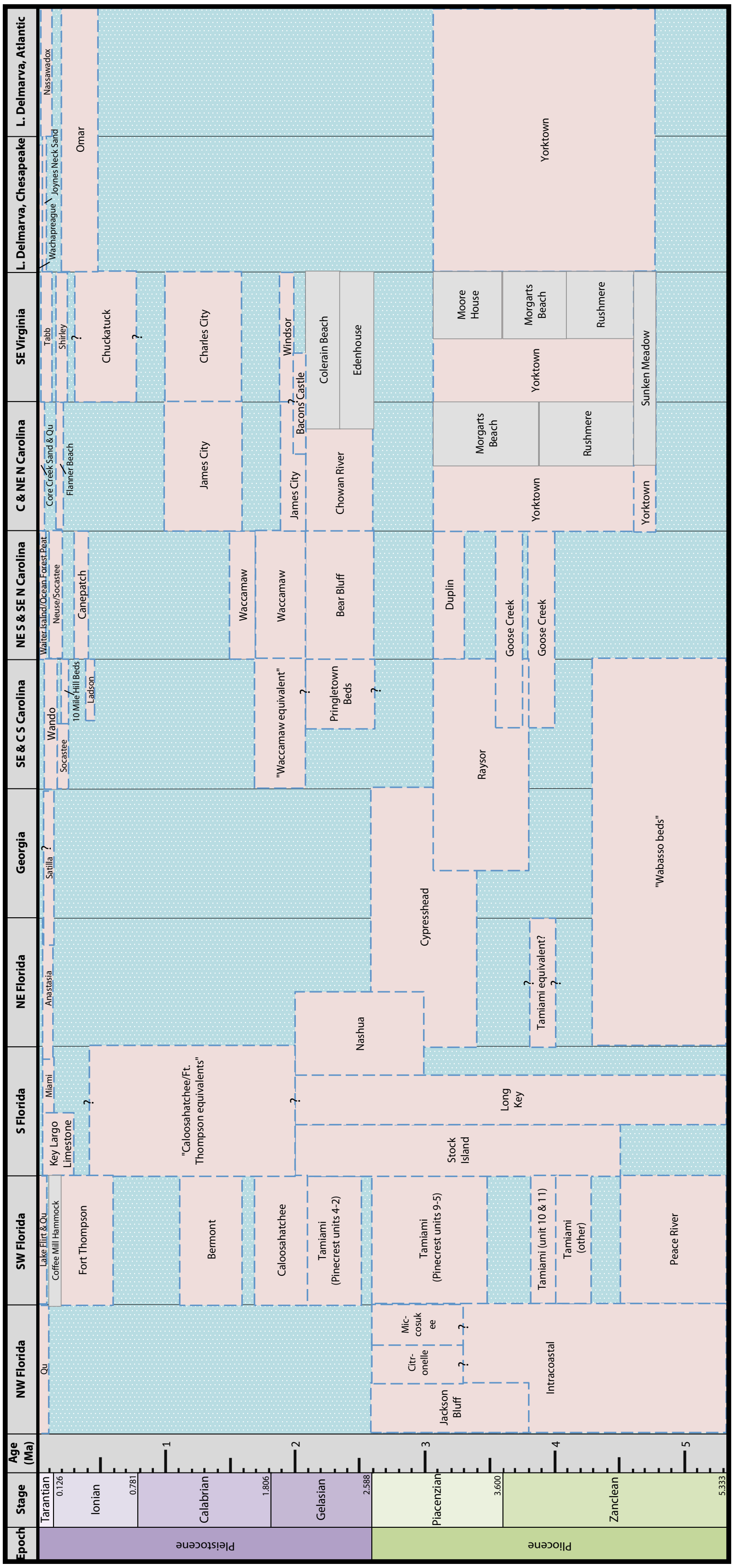


Figure 2.2.1 Correlational chart of Pliocene to recent geological units of the Atlantic Coastal Plain.

Table S2.2.2: Part 1. Northwest Florida

Region	Formation	Member	Unit	Age (Ma)	Supporting References	Notes	Other age details or opinions	Correlation	Other opinions on correlations	General regional notes
	Qu			**<0.135**	The Prairie Frm (135-60 Ka) (Mateo 2005; Otvos 2005, 2009; Shen et al 2008); Biloxi Frm (132-116 Ka) (Otvos 2005, 2009, 2013); and Gulfport Frm (132-118 Ka) (Otvos 2013) 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 Otvos (1992), the Prairie Frm deposits interfinger with transgressive Biloxi units; they cover Biloxi deposits and the landward flank of the Gulfport Belt. According to Otvos (2009, 2013), the Biloxi is partially correlated with the above-lying Gulfport Frm. Kolbe et al (2011) cite these as present in NW Florida. Huddlestun (pers comm 2013) also indicated the Biloxi Frm of Otvos is present in the coastal area as far east as St. George Island and is in the same stratigraphic position as the Satilla Frm of GA.					
	Miccosukee			**~3.3-2.6**	Cooke and Mossom (1929); Otvos (1998)	Found in E and Citronelle to W; Miccosukee Frm is more clayey; the transition between these two units occurs around central Gladson County (Means, pers comm 2013); unit could be a member or facies of the Citronelle Frm. Huddlestun (pers comm 2013) indicated he has no reasonable evidence that the Citronelle, Miccosukee, and Jackson Bluff Frms are anything but lithofacies of one depositional event: the Citronelle/Miccosukee Frms are a shore/shoreface deposit or lithofacies, whereas the Jackson Bluff Frm is an offshore, shelf bottom deposit or lithofacies. The Intracoastal Frm 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 unfossiliferous; 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 Frms (2.4-1.7 Ma).	Considered time-equivalent of Cypresshead Frm (GA) and correlated in part with Nashua Frm in NE Florida (Huddlestun 1988); time equivalent with Citronelle Frm (Rupert 1990; Otvos 1988, 1998); Huddlestun (pers comm 2013) indicated Miccosukee, Citronelle, Jackson Bluff, Cypresshead and Intracoastal Frms are time equivalents.	Note that in this compilation, the Miccosukee Frm is only partially correlated with the Cypresshead Frm.	
	Citronelle			**~3.3-2.6***	Stringfield and LaMoreaux (1957); Huddlestun (1988); Otvos (1988); Means (2009)	Citronelle found only in the uplands from S GA to TX (Otvos 1995, 2004). There is a questionable, thin bed that may be younger and perhaps eolian atop the Citronelle Frm. Huddlestun (pers comm 2013) indicated he has no reasonable evidence that the Citronelle, Miccosukee, and Jackson Bluff Frms are anything but lithofacies of one depositional event: the Citronelle/Miccosukee Frms are a shore/shoreface deposit or lithofacies, whereas the Jackson Bluff Frm is an offshore, shelf bottom deposit or lithofacies. The Intracoastal Frm 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). Otvos (1992) indicated that in the western panhandle of FL and southern AL, the unit unconformably overlies the Perdido Key Frm, 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 Frm; however, Huddlestun (pers comm 2013) indicated the Citronelle and Jackson Bluff Frms are time-equivalent.	*Age range is an estimate. Age of the Citronelle Frm has been debated for years because of the lack of index fossils and has been variously assigned to the Miocene, Pliocene or Pleistocene (Rupert 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 Pliocene, but this was before the Plio-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).	Frm grades into Miccosukee Frm (Cooke and Mossom 1929); correlated with Cypresshead Frm (Huddlestun 1988; Otvos 1988, 1998; Means 2009); Huddlestun (pers comm 2013) indicated the Miccosukee, Citronelle, Jackson Bluff, Cypresshead and Intracoastal Frms are time equivalents.	Note that in this compilation, the Citronelle Frm is only partially correlated with the Cypresshead Frm.	

Table S2.2.2: Part 2. Northwest Florida

Region	Formation	Member	Unit	Age (Ma)	Supporting References	Notes	Other age details or opinions	Correlation	Other opinions on correlations	General regional notes
Northwest Florida	**Jackson Bluff**			**3.8-2.6**	Otvos (1992); Markewich et al (1992); Otvos (1998); Otvos (2009); Kolbe et al (2011); Huddlestun (pers comm 2013)	Otvos (1988, 1992) cited the Perdido Key Frm as being correlative with the Jackson Bluff and Intracoastal Frms, but the Perdido Key Frm is not recognized by the Florida Geological Survey (Means, pers comm 2013); Huddlestun (pers comm 2013) indicated he has no reasonable evidence that the Citronelle, Miccosukee, and Jackson Bluff Frms are anything but lithofacies of one depositional event: the Citronelle/Miccosukee Frms are a shore/shoreface deposit or lithofacies, whereas the Jackson Bluff Frm is an offshore, shelf bottom deposit or lithofacies. The Intracoastal Frm 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). According to Huddlestun, the Jackson Bluff Frm is fully encompassed within the Intracoastal Frm, which represents a new relationship from previously-cited literature.	The unit is cited as within zones: N18-19 (Akers 1972; Otvos 1992), N20 (Otvos 1988), N19-21 or PL3-PL5 (Otvos 1998); Huddlestun (pers comm 2013) indicated Frm is overwhelmingly within zone PL3 and slightly into PL4 in Washington County. Markewich et al (1992) cited age from ~3.5-3 Ma, but the slight difference from the age here probably reflects changes in Berggren Zones; age here differs from Scott (2011), who indicated base age of 5.3 Ma.	Equivalent wholly or in part to Duplin and Raysor Frms, and to the Rushmere Member of the Yorktown Frm in southeastern VA and northeastern NC (Markewich et al 1992); correlated with the lower Pinecrest Beds, Duplin Marl, Raysor Marl, Rushmere and Morgarts Beach Members of the Yorktown Frm (Allmon et al 1996a); Huddlestun (pers comm 2013) indicated Miccosukee, Citronelle, Jackson Bluff, Cypresshead and Intracoastal Frms are time equivalents.	Campbell et al (2011) indicated the lower Jackson Bluff Frm is correlated with the lower Goose Creek Limestone of SC, Unit 3 of the Yorktown, and the Tamiami Limestone by a *Leptopecten* unit (Early Pliocene); however, in this compilation, the Jackson Bluff Frm is correlated with the upper Goose Creek, not the lower, and the Tamiami Limestone is below the Jackson Bluff Frm.	
	Intracoastal			**~5.54-2.6**	Huddlestun (pers comm 2013)	The distinction between the Jackson Bluff and Intracoastal Frms is not always clear, although Portell (pers comm 2013) indicated the units can be easily distinguished because the Jackson Bluff Frm is primarily of clastic lithologically, while the Intracoastal Frm is primarily carbonate. Scott (2011) indicated the Intracoastal Frm is above the Jackson Bluff Frm in his stratigraphic chart, but Schmidt and Clark (1980) and Otvos (1988) indicated the unit underlies or interfingers with the Jackson Bluff Frm, and Means (pers comm 2013) confirmed this relationship for at least a pit just north of Carrabelle. Means and Portell (pers comm 2013) have never seen the Intracoastal overlying the Jackson Bluff Frm. Huddlestun (pers comm 2013), however, suggested the Intracoastal, Jackson Bluff, Citronelle, and Miccosukee Frms are all correlative: the Citronelle/Miccosukee Frms are a shore/shoreface deposit or lithofacies, whereas the Jackson Bluff Frm is an offshore, shelf bottom deposit or lithofacies. The Intracoastal Frm 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). According to Huddlestun (pers comm 2013), the Jackson Bluff Frm is fully encompassed within the Intracoastal Frm.	The age cited for the Frm is variable: unit has been cited as Miocene and as young as 1.6 Ma. Donoghue (1992), Locker and Doyle (1992), and Scott (1992) cited a Middle Miocene to Late Pliocene age for the unit [Donoghue (1992) indicated the Chipola Frm sits above the Intracoastal Frm, but this relationship does not match most other publications, which placed the Chipola Frm in the Middle Miocene. Portell (pers comm 2013) indicated no cores or exposures are found where the Intracoastal Frm sits below the Chipola Frm. Rupert (1990) indicated that "Chipola-like" sediments are found above the Intracoastal Frm in Gulf County, which may be the root of some of the confusion]. Others suggest a significantly younger age; e.g., Clark and Wright (1979) placed the unit within the *Globorotalia margaritae* zone and the older *G. fohsi fohsi* zone, which represent an age of 4.4-3.8 Ma for the *G. margaritae* zone in the updated Berggren Zone scheme of Wade et al (2011). Otvos (1998) cited a younger top age of 1.6 Ma, as did Scott (2011), who indicated the Frm is within zone PL3-5 (~3.8-2.2). Huddlestun (pers comm 2013) indicated the Frm is in zone PL1-PL4 to PL5.	In downdip direction, the Frm partly underlies and laterally interfingers with the Jackson Bluff Frm (Otvos 1988); Huddlestun (pers comm 2013) indicated the Miccosukee, Citronelle, Jackson Bluff, Cypresshead and Intracoastal Frms are time equivalents.		

Table S2.2.2: Part 3. Southwest Florida

Region	Formation	Member	Unit	Age (Ma)	Supporting References	Notes	Other age details or opinions	Correlation	Other opinions on correlations	General regional notes
	Lake Flirt Formation &			<0.1						
	Fort Thompson	Coffee Mill Hammock		0.14-0.11	Puri and Vanstrum (1969); Lyons (1991)	Considered a unit of the Ft. Thompson Frm, although others have argued for formational status (e.g., Brooks 1968, 1974; Lyons 1991); the validity of the Ft. Thompson Frm as a lithological unit has been debated by the Florida Geological Survey in their most recent map of Florida (2001).	Petuch and Roberts (2007) indicated the Coffee Mill Hammock Member and the Ft. Thompson Frm are younger (from 0.6-0.01 Ma).	Correlated with the Princess Anne Frm (Lyons 1991) [this Frm is included within the Satilla Frm by Huddlestun (1988) and is correlated in part in this compilation]. Lyons (1991) indicated the Socastee, Pamlico (in part), Norfolk [now Shirley, Tabb or Acredale Frms], Sandbridge, Princess Anne, Silver Bluff, and Anastasia Frms have been cited within Blackwelder interval zone M1, which Lyons (1991) does not agree with. Lyons (1991) argued only the Princess Anne Frm and Coffee Mill Hammock Member of the Ft. Thompson Frm are in interval M1.		
		Undifferentiated		0.6-0.12	Wehmiller and Belknap (1978); Karrow et al (1996); Missimer (2001a); Hickey et al (2010); Missimer and Wise (2012)	The Ft. Thompson Frm has also been said to include an Okaloacoochee 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.	Hickey et al (2010) indicated that reliable dates for the Ft. Thompson Frm are difficult to obtain, but placed the interval around 0.6-0.4 Ma; Brooks (1974) cited an age of 0.22+ Ma; others cited slightly older ages: 0.95-0.55 Ma (Webb et al 1989) and 0.9-0.1 Ma (Kolbe et al 2011). Petuch and Roberts (2007) cited a younger top age for the Frm (0.01 Ma).	Ward and Blackwelder (1987) considered the Ft. Thompson Frm (including the Coffee Mill Hammock) as correlative with the Socastee Frm, but Lyons (1991) disagreed; however, in this report, the Ft. Thompson does correlate in part with the Socastee Frm. The Ft. Thompson, Anastasia and Key Largo Frms are equivalent (DuBar 1991). The Ft. Thompson Frm grades into the Anastasia Frm in the E and the Miami Limestone to the SW (Kittle and Portell 2010).		

Table S2.2.2: Part 4. Southwest Florida

Region	Formation	Member	Unit	Age (Ma)	Supporting References	Notes	Other age details or opinions	Correlation	Other opinions on correlations	General regional notes
	Bermont			**1.6-1.1**	Hulbert and Morgan (1989); Webb et al (1989); Campbell and Campbell (1995); Knorr and Harries (2007); Kolbe et al (2011)	The unit is only found in southern Florida.	Younger ages have been cited previously for the Bermont Frm, including: 1-0.5 Ma (DuBar 1974; Willard et al 1993; Blackwelder 1981a); and 0.5-0.4 Ma (Mitterer 1974, 1975); however, these younger ages may be suspect for a number of reasons, see Lyons (1991). Petuch and Roberts (2007) also indicated a younger top age for Frm (of 0.6 Ma).	Partially correlated with the James City and Waccamaw Frms (NC and SC) (Ward et al 1991).	DuBar (1991) indicated that the unit correlates with the Canepatch Frm (SC), but this is not supported in this compilation, with the Canepatch Frm younger than the Bermont Frm here.	
	Caloosahatchee			**2.1-1.7**	Cunningham et al (2001); Missimer (2001a,b); Kolbe et al (2011); Missimer and Wise (2012)	A "lower" and "upper" Caloosahatchee have been referred to in publications, but the Frm in places (e.g., the Sarasota mine) can have 2 to 3 discontinuities/unconformities.	Missimer (2001b) cited an age of 2.1 or 1.77 Ma to 0.6 Ma, but the latter age does not accord with other dates for the Caloosahatchee Frm or with other formations in the sequence. Furthermore, a more up-to-date GSA abstract (Missimer and Wise 2012) indicated the Frm straddles the Gelasian-Calabrian boundary. Older ages cited for the Frm include: 2.35-1.71 and 2.5-2 Ma in the same publication (Missimer 1993); 2.4-2 Ma (Willard et al 1993); 2.5-1.8 Ma, but there was no provenance data for the sample (Bender 1972, 1973; Lyons 1991); 2.55-2.35 Ma for the lower Caloosahatchee and 1.9-1.7 Ma for the upper Caloosahatchee (Campbell and Campbell 1995).	Correlated with the Waccamaw and Nashua Frms (DuBar 1991) [only partially correlated with the Nashua Frm in this compilation: here, the Nashua Frm is primarily older]; correlated with the James City and Waccamaw Frms (Blackwelder 1981a; Allmon et al 1996a).	DuBar (1991) indicated the Frm is correlated with the Nashua Frm, but the Nashua Frm is primarily older in this report; Lyons (1991) indicated the Frm is correlated with the Chowan River Frm (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 Frm is younger here.	

Table S2.2.2: Part 5. Southwest Florida

Region	Formation	Member	Unit	Age (Ma)	Supporting References	Notes	Other age details or opinions	Correlation	Other opinions on correlations	General regional notes
Southwest Florida		Pinecrest Sand	Units 4-2	**2.5-2.1**	Allmon et al (1996a); Jones et al (1991)	Beds *sensu* Petuch (1982) and modified by Zullo and Harris (1992); Zullo and Harris (1992) placed Petuch's Unit 0 and 1 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 11 were placed into the lower Tamiami Formation. *Indicates these units are no longer included in the Pinecrest (Unit 10 and 11) (Portell et al 2012).	Campbell and Campbell (1995) cited an age of 3.0-2.8 Ma for Beds 3-1; Allmon et al (1996a,b) cited a slightly younger top age of 2.5-2.0 Ma (Matuyama Chron).	The "upper Pinecrest" correlated with the Chowan River Frm (VA and Carolinas) (Jones et al 1991; Dowsett and Cronin 1996; Williams et al 2009).		
			Units 10*-5	**3.5-2.6**	Allmon et al (1996a); Jones et al (1991)		Cronin (1991) indicated an age of 3.5-3.0 Ma for Beds 10-5. Campbell and Campbell (1995) cited an age of 3.3-3.1 Ma for the "middle beds" of the Pinecrest. Knowles et al (2009) and Williams et al (2009) have the Pinecrest Beds 10-5 at ~3.7-3.5 Ma.	The unit is correlated with the Duplin Frm (NC and SC), Raysor Frm (GA) and Jackson Bluff Frm (Florida Panhandle) (Dowsett and Cronin 1990); the "lower Pinecrest" correlated with the Duplin and Raysor Frms (NC, SC, and GA) and Rushmere, Morgarts Beach and Moore House Members of the Yorktown Frm (Cronin 1991); correlated with the lower and upper Yorktown of VA and NC (Lyons 1991) [in this report correlated primarily with the upper]; lower Pinecrest correlated with the Jackson Bluff, Duplin, and Raysor Frms, and the Rushmere and Morgarts Beach Members of the Yorktown Frm (Allmon et al 1996a); lower Tamiami and lower Pinecrest Beds correlated with the Jackson Bluff Frm (Zullo and Harris 1992; Zullo and Portell 1993).		
			Unit 11* (& 10*)	**4.0-3.8**	Cronin et al (1984); Lyons (1991)		Knowles et al (2009) and Williams et al (2009) placed this unit at 4.2-3.9 Ma, suggesting the authors did not revise the age of interval zone M6. Campbell and Campbell (2005) placed the age at 3.75-3.55 Ma for Bed 10 (= Bed 11?)		Jones et al (1991), Willard et al (1993), and Williams et al (2009) indicated the Frm is equivalent to the Sunken Meadow Member of the Yorktown Frm, but this correlation is not supported in this compilation; here, the Sunken Meadow Member is older; others (e.g., Scott 1995) indicated the Sunken Meadow Member is not correlated with any Tamiami sediments, at least not in S Florida.	

Table S2.2.2: Part 6. Southwest Florida

Region	Formation	Member	Unit	Age (Ma)	Supporting References	Notes	Other age details or opinions	Correlation	Other opinions on correlations	General regional notes
	Tamiami		Undifferentiated	**3.2-2.2**	Missimer (2001a,b); Missimer and Wise (2012)	Missimer (2001a) indicated the "Pinecrest" is 3.22-2.15 Ma; however, when Beds 10 and 11 are removed from traditional definitions of the "Pinecrest", this age range seems to match the ages of the sequences fairly well; Missimer and Wise (2012) indicated the Pinecrest is 3-2 Ma.	Bender (1972, 1973) found a date of 3.9-3.5 Ma for the Pinecrest, but the location within the section was not specified. Cronin (1991) cited that the entire Pinecrest spans from 4.5-1.8 Ma. The older dates cited by these authors probably reflect the fact that the authors included lower units (Units 10 and 11) in their estimation, which are now removed from the Pinecrest *sensu* Zullo and Harris (1992).	Correlated with the Bear Bluff (NC, SC, and GA) and Chowan River Frms (Colerain Beach and Edenhouse Members) Frms (VA and NC) (Cronin 1991).		
		Ochopee Limestone		**3.83-3.62**	Cunningham et al (2001)	The Ochopee Limestone is present in southern Florida; an undifferentiated sand lies above it, which is probably equivalent to the Long Key Frm of the Keys or the Pinecrest Beds (Cunningham et al 2001); Hunter (1968) suggested that the Pinecrest 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 Pinecrest appear time-equivalent based on the molluscan assemblages.	Petuch and Roberts (2007) placed the Ochopee Limestone as younger than 3.6 Ma and equivalent to the Pinecrest Beds. Conversely, Missimer (1990) and others cited the Ochopee Limestone as older than the Pinecrest Beds.	Former Beds 10 and 11 of the Pinecrest are probably equivalent in age to the Ochopee Limestone (Waldrup and Wilson 1990; Lyons 1991; Zullo and Harris 1992), but Waller (1996) indicated that the Ochopee Limestone might be older than Bed 11 based on *Chesapecten* relationships; the "Tamiami Limestone" was correlated with the lower Goose Creek Limestone (SC), Unit 3 of the Yorktown and the lower Jackson Bluff Frm on the basis of a *Lectopecten* unit (Campbell et al 2011).		
		Buckingham Limestone		**~4.3-3.8**	Missimer (1990)	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 Pinecrest Sand, Ochopee Limestone and Buckingham Limestone are lateral equivalents.				

Table S2.2.2: Part 7. Southwest Florida

Region	Formation	Member	Unit	Age (Ma)	Supporting References	Notes	Other age details or opinions	Correlation	Other opinions on correlations	General regional notes
		Undifferentiated		**4.3-2.1**	Missimer (1984); Meeder (1987); Missimer (1990); Scott (1992); Missimer (1993); Missimer (1997); Missimer (1999); Guertin et al (2000); Missimer (2001b); Cunningham et al (2003); Knowles et al (2009); Williams et al (2009); Kolbe et al (2011)	According to Missimer (1990, 1993), the definition of the Hawthorn is used to establish the base of the Tamiami Frm. He suggested that the Tamiami Frm may underlie the Caloosahatchee or the Ft. Thompson Frms. Missimer (1993) defined 9 or more members of the Tamiami Frm; however, correlation among them is problematic. These 9 units can be mapped on the basis of dominant lithology in southwest FL, including: the Pinecrest Sand Member, the unnamed limestone facies, the Golden Gate Reef Member (of Meeder 1987), the Bonita Springs Marl Member (of Missimer 1984), the HYOTISSA facies, the Ochopee Limestone Member, the sand facies, the Buckingham Limestone Member, and the tan clay and sand facies. Only 1 to 4 of these occur in a vertical stratigraphic section at any given locality. In contrast to Missimer (1990, 1993), Hunter (1968) indicated the Pinecrest Sand, Ochopee Limestone and Buckingham Limestone were lateral equivalents. Missimer (1990), 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 Frm additionally has been broken into at least three other members (Fruitville, Golden Gate Reef, and Bonita Springs Marl, cited youngest to oldest) by Meeder (1987) and Petuch and Roberts (2007), but these remain controversial. Meeder (1987) did not formally define the Golden Gate Reef Member in terms of the stratigraphy and relationships with other major lithological units, and Missimer (1984) only informally suggested the Bonita Springs Marl Member. Much controversy and confusion surrounds the surface and near-surface deposits of southern Florida, especially the Tamiami Frm. This is for a variety of reasons, see Jones et al (1991) and Scott (1992) for details. Based on the sequence stratigraphic framework of Zullo and Harris (1992) at the APAC and SMR Pits, the authors concluded that Petuch's Units 0-1 belong to the Caloosahatchee Frm and Units 2-11 were within the Tamiami Frm. Units 2-9 were divided into the upper Tamiami Frm, and Units 10-11 were within the lower Tamiami Frm. Further subdivision placed Units 2-3 into the upper Pinecrest Beds and Units 4-9 into the lower Pinecrest Beds. Petuch and Drolshagen (2011), however, now consider Units 2-4 to belong to the Fruitville Member (Tamiami Frm), Units 5-9 to belong to the Pinecrest Member (Tamiami Frm), Unit 10 to belong to the Buckingham Member (Tamiami Frm) and Unit 11 to be the Sarasota Member (Murdock Station Frm).	Missimer (1993) cited the Frm as 4.2-2.8 Ma, while Campbell and Campbell (1995) indicated the Tamiami Limestone is 4-3.8 Ma; Petuch and Roberts (2007) placed the Tamiami Frm older than 2.1 Ma; Williams et al (2000) and Knowles et al (2009) also cited the Tamiami Formation as older, from 5.3-4.3 Ma; Kolbe et al (2011) indicated an age of 4.3-2.5 Ma in parts of both NE and S Florida; Scott (2011) placed an older bottom age for the Tamiami at 5.3 Ma.	The lower Tamiami and lower Pinecrest Beds are correlated with the Jackson Bluff Frm (Zullo and Harris 1992; Zullo and Portell 1993) [note that the lower Tamiami Frm, depending on the definition, does not correlate with the Jackson Bluff Frm in this compilation].		
	Peace River Formation			**11-4.5**	Emslie and Morgan (1994); McCartan et al (1995); Missimer (1999); Guertin et al (2000); Kolbe et al (2011)	The unconformity between the Peace River Frm and the overlying Tamiami Frm is likely only 0.2 Ma (Missimer 1999), and deposition may have stopped as late as 4.3 Ma (not 4.5 Ma), an age which Guertin et al (2000) also cited.				

Table S2.2.2: Part 8. Southern Florida

Region	Formation	Member	Unit	Age (Ma)	Supporting References	Notes	Other age details or opinions	Correlation	Other opinions on correlations	General regional notes
	Qu			<0.090						
	Miami Limestone			0.13-0.09	Broecker and Thurber (1965); Osmond et al (1965); Guertin et al (2000); Neal et al (2008); Hickey et al (2010)	The Miami Limestone sits above the Ft. Thompson Frm, previously considered part of the Key Largo Frm (Hickey et al 2010).	Kolbe et al (2011) cited an older age of 0.9-0.1 Ma, while Scott (2011) indicated a younger top age of 0.01 Ma.	DuBar (1991) indicated the Miami Limestone interfingers with the Anastasia Frm in the N, the Key Largo Frm in the S, and the Ft. Thompson Frm in the NW, but according to Neal et al (2008) and Hickey et al (2010), the unit sits above the Ft. Thompson Frm; here the Ft. Thompson is above and partially interfingers/correlative. Hickey et al (2010) indicated the unit is a lateral equivalent to the upper part of the Key Largo Limestone.		
	Anastasia			0.132-0.0	Osmond et al (1970); Murphy (1973); Mitterer (1974); McNeil (1985); Portell et al (2003); Banks et al (2007); Burdette et al (2009); Burdette (2010)	Portell (pers comm 2013) indicated the unit is present from St. Augustine to southern Palm Beach County.	Kolbe et al (2011) cited an older age for this Frm (0.9-0.1 Ma); publications such as Osmond et al (1970), Murphey (1973), and Mitterer (1974) cited slightly younger top ages (around 90 to 100 Ka) compared to the others of around 115 to 116 Ka (e.g., Banks et al 2007; Finkle et al 2008; Burdette 2010); Petuch and Roberts (2007) indicated an age of 0.1-0.01 Ma.	The Miami Oolite of the Miami Limestone is considered contemporaneous with the Anastasia Frm (Cooke and Mossom 1929); the Anastasia Frm interfingers with the Miami Limestone at the top of the section and probably correlates with the Caloosahatchee and Ft. Thomson Frms (Missimer et al 2000) [however, the Caloosahatchee Frm is too old in this compilation to correlate]; if congruent with OIS 5e, the unit correlates with the Biloxi and Gulfport Frms (ME).	Missimer et al (2000) indicated the unit probably correlates with the Caloosahatchee and Ft. Thomson Frms, but the Caloosahatchee Frm is too old in this report.	

Table S2.2.2: Part 9. Southern Florida

Region	Formation	Member	Unit	Age (Ma)	Supporting References	Notes	Other age details or opinions	Correlation	Other opinions on correlations	General regional notes
Southern Florida	**Key Largo Limestone**			**0.3-0.09**	Broecker and Thurber (1965); Osmond et al (1965); Multer et al (2002)	The Key Largo Frm is a fossil coral reef that forms the Florida Keys from Soldier Key southwest to the New Found Harbor Channel (DuBar 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 (Multer et al 2002). Ages found: single data points of 0.139 Ma (Harmon et al 1979), 0.145 Ma (Szabo and Halley 1988), 0.144 Ma +/- 10 Ka (Muhs et al 1992); 0.138-0.125 Ma (Fruijtier et al 2000), but these dates have error bars of probably 5 Ka; a generally accepted age is 0.125 Ma (Shin 2001; Means pers comm 2013), but recent work indicates 0.135 Ma (Henderson and Slowey 2000). Petuch 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).	The upper part of the Key Largo Limestone is the same age as the Miami Limestone (DuBar 1991); the Ft. Thompson Frm is recognized as a lateral equivalent of the Key Largo Limestone (Cunningham et al 1998).	Hickey et al (2010) indicated the Key Largo and Miami are equivalent, with the Ft. Thompson Frm below these two units. In this report, the Ft. Thompson is primarily below but also partially correlated.	
	upper limestone deposits			**2.0-1.7?***	Guertin (1998); Missimer (1997); Guertin et al (2000)	*Placed around 2 Ma and referred to as Ft. Thompson and Caloosahatchee Frm equivalents (Guertin et al 2000), and thus the upper age boundary is set at 0.4 Ma, which is within the Ft. Thompson Frm.		Suggested to be a Ft. Thompson-Caloosahatchee equivalent (Missimer 1997; Guertin 1998; Guertin et al 2000).		

Table S2.2.2: Part 10. Southern Florida

Region	Formation	Member	Unit	Age (Ma)	Supporting References	Notes	Other age details or opinions	Correlation	Other opinions on correlations	General regional notes
	Nashua			**3.0-1.9**	Huddlestun (1988); Markewich et al (1992); Scott (1992)	Cooke and Mossom (1929) abandoned the Nashua Frm name and used the Caloosahatchee instead, but Huddlestun (1988) reintroduced the Nashua Frm of Matson and Clapp (1909); the Frm disconformably overlies the Coosawhatchie Frm. In the coastal area, the Frm may be overlain by the Satilla Frm (Huddlestun 1988). Kolbe et al (2011) included the Tamiami Frm as a unit below the Cypresshead/Nashua Frms in NE Florida, but the unit is not included in this region by Scott (2011) and Fountain (2010). Portell (pers comm 2013) indicated the Nashua Frm is well established in St. Lucie and Okeechobee Counties.	Noted to be within Berggren zone PL5 (~3-2.3 Ma, based on updated zonation's from Wade et al 2011) and a Cypresshead equivalent (Huddlestun 1988; Markewich et al 1992); Kolbe et al (2011) cited a younger age (2.4-1.7 Ma), as does Petuch and Roberts (2007) (~2.5-1.6 Ma). Cited age differs from Scott (2011) (5.3-1.8 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).	The Cypresshead (and thus Citronelle) and Bear Bluff (SC) Frms are equivalents (Huddlestun 1988; Markewich et al 1992; Means pers comm 2013).	DuBar (1991) indicated the unit is correlative with the Waccamaw Frm, but the Waccamaw Frm is younger in this compilation.	
	Stock Island (West)			**4.5-2.0**	Cunningham et al (1998); Guertin (1998)	Fine-grained limestone underlying the lower and part of the middle of the Florida Keys (Guertin et al 2000).		Correlated with a portion of the Long Key Frm and with the Ochopee Limestone (Cunningham et al 1998; Cunningham et al 2001).		
	Long Key (East)			**5.6-2.0**	Warzeski et al (1996); Guertin (1998); Guertin et al (1999); Guertin et al (2000)	The Long Key Frm has three depositional intervals (Guertin et al 2000).		Correlated with the Ochopee Limestone and with the Stock Island Frm (Cunningham et al 1998; Cunningham et al 2001); the Long Key Frm has three intervals, which correlate with the Peace River Frm, the Tamiami Frm, and the Pinecrest Member of the Tamiami Frm (Guertin et al 2000).		

Table S2.2.2: Part 11. Northeast Florida

Region	Formation	Member	Unit	Age (Ma)	Supporting References	Notes	Other age details or opinions	Correlation	Other opinions on correlations	General regional notes
	Qu			**<0.090**		According to Parker and Cooke (1944), the Satilla Frm overlies the Anastasia Frm in Florida, but Means (pers comm 2013) indicated the Satilla Frm is only in Georgia.				
	Anastasia			**0.132-0.0**	Osmond et al (1970); Murphy (1973); Mitterer (1974); McNeil (1985); Portell et al (2003); Banks et al (2007); Burdette (2010)	Scott (2011) does not include the Anastasia Frm in the N Florida stratigraphic column and instead placed the unit in S Florida; however, the unit is present in N Florida *sensu* Scott (1992).	Kolbe et al (2011) cited an older age for this Frm (0.9-0.1 Ma); publications such as (Osmond et al 1970; Murphey 1973; Mitterer 1974) cited a slightly younger top age (around 90 to 100 Ka) compared to others of 115 to 116 Ka (e.g., Banks et al 2007; Finkle et al 2008; Burdette 2010); Petuch and Roberts (2007) indicated 0.1-0.01 Ma.	The Miami Oolite of the Miami Limestone is contemporaneous with the Anastasia Frm (Cooke and Mossom 1929); the Anastasia Frm interfingers with the Miami Limestone at the top of the section and probably correlates to the Caloosahatchee and Ft. Thomson Frms (Missimer et al 2000) [however, the Caloosahatchee Frm is too old in this compilation to correlate]; if congruent with OIS 5e, the unit correlates with the Biloxi and Gulfport Frms (ME).	Missimer et al (2000) indicated the unit probably correlates to the Caloosahatchee and Ft. Thomson Frms, but the Caloosahatchee Frm is too old in this report.	
	Satilla			**~0.126-0.**	Huddlestun (1988); Alber et al (2003); Huddlestun (pers comm 2013)	The Satilla Frm in GA, SC and FL includes the Pamlico Frm of Cooke (1943), the Princess Anne Frm and the Silver Bluff Frms (Hails and Hoyt 1969) and Holocene shoreline complexes, as redefined by Huddlestun (1988); these were rejected by Huddlestun (1988) because they simultaneously referred to terrace planes–a geomorphic feature–and lithostratigraphic units. Huddlestun (pers comm 2013) indicated the relationship between the Satilla Frm and the Princess Anne, Silver Bluff and Pamlico terraces is still unclear. Portell (pers comm 2013) indicated the units mapped as "Satilla Frm" in NE Florida were based on lithology. Parker and Cooke (1944) also indicated the unit is present in NE Florida and this was accepted by Huddlestun (1988).				

Table S2.2.2: Part 12. Northeast Florida

Region	Formation	Member	Unit	Age (Ma)	Supporting References	Notes	Other age details or opinions	Correlation	Other opinions on correlations	General regional notes
Northeast Florida	**Nashua**			**3.0-1.9**	Huddlestun (1988); Markewich et al (1992); Scott (1992)	Cooke and Mossom (1929) abandoned the Nashua name and used Caloosahatchee instead, but Huddlestun (1988) reintroduced the Nashua Frm of Matson and Clapp (1909); the Frm disconformably overlies the Coosawhatchie Frm. In the coastal area, the Frm may be overlain by the Satilla Frm (Huddlestun 1988). Kolbe et al (2011) included the Tamiami Frm as a unit below the Cypresshead/Nashua Frms in NE Florida, but the unit is not included in this region by Scott (2011) and Fountain (2010).	Noted to be within Berggren zone PL5 (~3-2.3 Ma, based on updated zonation's from Wade et al 2011) and a Cypresshead Frm equivalent (Huddlestun 1988; Markewich et al 1992); Kolbe et al (2011) cited a younger age (2.4-1.7 Ma), as does Petuch and Roberts (2007) (~2.5-1.6 Ma). The cited age differs from Scott (2011) (5.3-1.8 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).	The Cypresshead Frm (and thus the Citronelle) and the Bear Bluff Frm (SC) are equivalents (Huddlestun 1988; Markewich et al 1992; Means pers comm 2013).	DuBar (1991) indicated the unit is correlative with the Waccamaw Frm, but the Waccamaw Frm is younger in this compilation.	
	Cypresshead			**~3.4-2.6**	Huddlestun (1988); Fountain (2010)	Sediments in peninsular Florida probably belong to the Cypresshead Frm, not the Citronelle Frm (Scott 1988; Means 2009). The Frm is found in coastal GA and NE Florida (Otvos 1998); reworking of the unit occurred from 2.8-1.8 Ma (Fountain 2010). The Cypresshead Frm contains both Citronelle-type and Miccosukee-type lithologies (Huddlestun pers comm 2013).	The age differs from that cited by Krantz (1991) (2.5-1.9 Ma), Alber et al (2003) (3.6-1.0 Ma) and Scott (2011) (5.3-1.8 Ma). Dating on the Frm is difficult due to the lack of fossil material (Means pers comm 2013).	The unit is equivalent with the Citronelle and Miccosukee Frms, overlies the Raysor Frm, and correlates with the Talbot of the Carolinas (Otvos 1998); Campbell and Campbell (1995) argued that the unit is coincident with the Waccamaw Frm, but Ward and Gilinsky (1993) disagreed [the unit is not correlated in this report]; equivalent to the Nashua Frm (Huddlestun 1988; Markewich et al 1992); the unit underlies the Satilla Frm (Alber et al 2003); Huddlestun (pers comm 2013) indicated the Miccosukee, Citronelle, Jackson Bluff, Cypresshead and Intracoastal Frms are time equivalents.	Krantz (1991) indicated the unit is correlated with the Chowan River and Bear Bluff Frms, but this is not supported in this compilation: these formations are younger than the Cypresshead Frm here; Markewich et al (1992) also indicated the Frm is coincident with the Bear Bluff Frm in the Carolinas, but this is not supported in this compilation, with the Cypresshead Frm older here. Otvos (1998) indicated the Frm is correlated with the Talbot Frm of the Carolinas, otherwise referred to as the Canepatch Frm [or the Tabb Frm in SE VA], but the Frm is not correlated in this report.	

Table S2.2.2: Part 13. Northeast Florida

Region	Formation	Member	Unit	Age (Ma)	Supporting References	Notes	Other age details or opinions	Correlation	Other opinions on correlations	General regional notes
	Tamiami equivalent			**~4-3.8**	Portell (pers comm 2013)	Quarries in Palatka are known to contain Tamiami-aged fossils (mostly *Encope tamiamiensis*); whether the unit below the Nashua Frm at this site is lithologically the Tamiami Frm has not yet been confirmed (Portell, pers comm 2013); Kolbe et al (2011) included the Tamiami Frm as a unit below the Cypresshead/Nashua Frms in NE Florida, but this has not been confirmed by the Florida Geological Survey.				
	Wabasso Beds			**~5.5-4.3**	Huddlestun (1988); Markewich et al (1992)	The Wabasso Beds is an informal name applied to lower Pliocene, 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 (Huddlestun 1988); Scott (2001) indicated the Wabasso Beds are also within the Peace River Frm in S Florida, but that they do not outcrop at the surface. The Wabasso Beds were treated as formational rank by Krantz (1991), but there seems to be no evidence for this, although Huddlestun (pers comm 2013) would like to see them formalized.	The unit belongs within zone PL1 or N-18 (Huddlestun 1988); the unit is no older than 5.7 Ma and no younger than 4.2-4.0 Ma (Markewich et al 1992).	The unit is probably time equivalent to the Sunken Meadow Member of the Yorktown Frm in SE VA and NE NC.	Krantz (1991) indicated the lower Duplin Frm is time equivalent with the Sunken Meadow Member of the Yorktown Frm and the Wabasso Beds, but this is not supported in this compilation; here, the Duplin Frm is younger than the Wabasso Beds and the Sunken Meadow Member.	

Table S2.2.2: Part 14. Georgia

Region	Formation	Member	Unit	Age (Ma)	Supporting References	Notes	Other age details or opinions	Correlation	Other opinions on correlations	General regional notes
	Qu			<0.0117						
	Satilla* [includes Pamlico, Princess Anne and Silver Bluff]			~0.126-0.0117	Huddlestun (1988); Alber et al (2003); Huddlestun (pers comm 2013)	The Plio-Pleistocene sediments in GA and SC were onlap, transgressive sections and lacked embayments (Markewich, pers comm 2013). The Pleistocene material up to 25 m looks very similar, which is why Huddlestun (1988), using a lithostratigraphic framework, placed all units within the Satilla Frm. The framework of Huddlestun (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 Frm in GA, SC and FL includes the Pamlico Frm of Cooke (1943), the Princess Anne and the Silver Bluff Frms (Hails and Hoyt 1969), and the Holocene shoreline complexes, redefined by Huddlestun (1988); these were rejected by Huddlestun (1988) because they simultaneously referred to terrace planes–a geomorphic feature–and lithostratigraphic units. Huddlestun (pers comm 2013) indicated the relationship between the Satilla Frm and the Princess Anne, Silver Bluff and Pamlico terraces is still unclear.	*Markewich et al (1992, pers comm 2013) preferred a different interpretation to Huddlestun's (1988, pers comm 2013) usage of only the Satilla and Cypresshead Frms, one which is more aligned to McCartan et al (1984, 1990) 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. Huddlestun's (1988) framework (here adopted) does not define units on morphological features, as does Cooke (1936, 1943) or Hoyte and Hails (1974). Huddlestun (pers comm 2013) indicated the terraces above the Cypresshead Frm are merely overprinted on the older Cypresshead Frm and not genetically related to the Frm. Huddlestun has not been able to determine discrete lithostratigraphic units uniquely related to specific marine terraces in GA.			

Table S2.2.2: Part 15. Georgia

Region	Formation	Member	Unit	Age (Ma)	Supporting References	Notes	Other age details or opinions	Correlation	Other opinions on correlations	General regional notes
Georgia	Cypresshead			~3.4-2.6*	Huddlestun (1988); Fountain (2010)	Markewich (pers comm 2013) indicated the "Cypresshead" of Huddlestun (1988) sits directly on Miocene sediments in many parts of GA. Huddlestun (pers comm 2013) indicated the terraces on top of the Cypresshead Frm [like the Wicomico, Penholoway, and Talbot] are merely overprinted on the older Cypresshead Frm and not genetically related to the Frm. Markewich et al (2013) also discussed terrace deposits within GA.	*No age data are available for Cypresshead sediments in Georgia outcrops (Markewich et al 1992); Markewich (pers comm 2013) indicated the Cypresshead Frm is at least middle Pleistocene in age. She suggested the upper part of what Huddlestun (1988) mapped as the Cypresshead Frm is called the Wicomico barrier (dated around 300 Ka, see Markewich et al 2013), but Huddlestun (pers comm 2013) indicated the Cypresshead Frm is within zone PL3 and slightly younger than PL4 and has no genetic relationship to overlying terraces/barrier complexes. The age also differs from that cited by Krantz (1991) (2.5-1.9 Ma), Alber et al (2003) (3.6-1.0 Ma) and Scott (2011) (5.3-1.8 Ma). Dating on the Frm is difficult due to lack of fossil material (Means pers comm 2013).	Equivalent with the Citronelle and Miccosukee Frms, overlies the Raysor Frm, and correlates with the Talbot Frm of the Carolinas (Otvos 1998); Campbell and Campbell (1995) think the unit is coincident with the Waccamaw Frm, but Ward and Gilinsky (1993) disagreed [the unit is not correlated in this report]; considered a Nashua equivalent (Huddlestun 1988; Markewich et al 1992); the unit underlies the Satilla Frm (Alber et al 2003); Huddlestun (pers comm 2013) indicated the Miccosukee, Citronelle, Jackson Bluff, Cypresshead and Intracoastal Frms are time equivalents.	Krantz (1991) indicated that the unit is correlated with the Chowan River and Bear Bluff Frms, but this relationship is not supported in this compilation: these formations are younger than the Cypresshead Frm here; Markewich et al (1992) also indicated the Frm is coincident with the Bear Bluff Frm in the Carolinas, but this is not supported in this compilation, with the Cypresshead Frm older here. Otvos (1998) indicated the unit is correlated with the Talbot Frm of the Carolinas, otherwise referred to as the Canepatch Frm [or the Tabb Frm in SE VA], but the Frm is not correlated in this report.	

Table S2.2.2: Part 16. Georgia

Region	Formation	Member	Unit	Age (Ma)	Supporting References	Notes	Other age details or opinions	Correlation	Other opinions on correlations	General regional notes
	Raysor			**3.8-3.1**	Huddlestun (1988); Ward and Huddlestun (1988); Cronin (1991); Markewich et al (1992); Campbell and Campbell (1995); Campbell (pers comm 2013) [for lower date]	Cooke (1936) originally named the Raysor Marl for deposits in SC that are older than the Duplin Marl (he considered them to be upper Miocene in age). Raysor deposits were left behind from eroding Miocene shorelines and are spotty in Georgia (Huddlestun pers comm 2013); these deposits are also referred to as the Duplin Frm (mostly time-equivalent) (Markewich pers comm 2013); Weems et al (1982) indicated the Raysor Marl sediments (neostratotype) designated by Blackwelder and Ward (1979) are lithologically similar to the Goose Creek Limestone and should be abandoned. Campbell (1992) rejected the Raysor Frm on the basis that the only known locality that matches the original type description is hidden by a slump, but this rejection is not in use even by these authors in subsequent publications (e.g. Campbell and Campbell 1995).	The Raysor is thought to be within zone PL3 of Berggren or N20 (Huddlestun 1988; Cronin 1991)	Correlated with the Duplin and Rushmere Member of the Yorktown Frm (Cronin et al 1984, Ward and Huddlestun 1988) and to the Jackson Bluff Frm (Huddlestun 1988); Raysor Frm interfingers with the correlative Duplin Frm in SC and extends southward into GA (Ward et al 1991); correlated with the lower Pinecrest Beds, Jackson Bluff, and Duplin Frms and the Rushmere and Morgarts Beach Members of the Yorktown Frm (Cronin 1991; Allmon et al 1996a); correlated with the Yorktown and Duplin Frms on the basis of forams (Dowsett and Wiggs 1992); Raysor Frm was placed below the Duplin Frm in Weems and Lewis (2002); Campbell and Campbell (1995) argued that the Goose Creek and Raysor Frms are older than the Duplin Frm at the Natural Well stratotype section. The Raysor Frm is equivalent to the upper Goose Creek Frm and overlies the lower Goose Creek Frm. In Ward and Huddlestun (1988), the Raysor Frm is depicted as below the Goose Creek Frm (but the authors later reversed their opinions, pers comm); the Raysor, Duplin and Jackson Bluff Frms are correlated (Huddlestun pers com 2013).	Krantz (1991) correlated the lower Duplin with the Raysor Frms, but here the Duplin Frm is correlated with the upper Raysor Frm; Ward (2008) placed the Duplin and Raysor Frms as correlative with the Yorktown Frm, but with the Yorktown Frm younger than the Duplin and Raysor Frms; however, in this compilation, the Duplin and Raysor Frms correlate with the upper part of the Yorktown Frm.	The Plio-Pleistocene framework of Georgia and South Carolina is still uncertain, partially due to the lack of fossil material in these sediments (Markewich pers comm 2013); the definition of formations depends on whether one takes a morphostratigraphic, lithostratigraphic or biostratigraphic interpretation. Huddlestun's (1988) framework (here adopted, but work is ongoing and this does not necessarily represent consensus opinion) does not define units on morphological features, as did Hoyte and Hails (1974) or Cooke (1936, 1943).
	Wabasso Beds			**~5.5-4.3**	Huddlestun (1988); Markewich et al (1992); Campbell and Campbell (1995)	The Wabasso Beds is an informal name applied to lower Pliocene, 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 (Huddlestun 1988); Scott (2001) indicated the Wabasso Beds are also in the Peace River Frm in S Florida, but that they do not outcrop at the surface. The Wabasso Beds were treated as formational rank by Krantz (1991), but there seems to be no evidence for this, although Huddlestun (pers comm 2013) would like to see them formalized.	The unit is included within zone PL1 or N-18 (Huddlestun 1988); considered no older than 5.7 Ma and no younger than 4.2-4.0 Ma (Markewich et al 1992).	The unit is probably time equivalent to the Sunken Meadow Member of the Yorktown Frm in SE VA and NE NC.	Krantz (1991) indicated the lower Duplin Frm as time equivalent with the Sunken Meadow Member of the Yorktown Frm and Wabasso Beds, but this is not supported in this compilation; here, the Duplin Frm is younger than the Wabasso Beds and the Sunken Meadow Member.	

Table S2.2.2: Part 17. Southeast and central South Carolina

Region	Formation	Member	Unit	Age (Ma)	Supporting References	Notes	Other age details or opinions	Correlation	Other opinions on correlations	General regional notes
	Qu [eolian]			**<0.070**						
	Wando	upper		**~0.087***	McCartan et al (1980); McCartan et al (1982); Szabo (1985)	Youngest of SC coastal region (Soller and Mills 1991). McCartan et al (1980) indicated the Wando Frm includes deposits formerly within the Pamlico, Princess Anne and Silver Bluff Frms; the authors argued that these names should not be used in S Carolina. The Wando Frm is divided into an upper and lower unit by Wehmiller et al (1988) equivalent to (respectively) the Princess Anne and Pamlico Terraces of Colquhoun.	*Age of unit is unclear: if younger ages for the Socastee and Canepatch Frms are assumed (see discussion below), then the dates indicated for the Wando Frm do not match this compilation. Szabo (1985) found ages of 129,000 +/- 10,000 for the lower Wando Frm and 87,000 +/- 4000 for the upper Wando Frm. The unit has generally been identified as latest Pleistocene in age (McCartan et al 1980), with dates of 126-87 Ka (McCartan et al 1982), isotope stage 5a (~80 Ka) (McCartan et al 1984), 100 Ka based on isotopic data (Soller and Mills 1991), and an older age of 250 Ka (Wehmiller and Belknap 1982), but these authors correlated the Wando Frm with the Socastee and Flanner Beach Frms, so their definition of formations may have differed. All of MIS 5 may be recorded in the Wando Frm (Muhs et al 2003), and there is evidence for multiple amino zones present, but these cannot be directly associated with U-series ages (Corrado et al 1986; Harris 2000; York et al 2001; see Muhs et al 2003); Wando is 70 - 130 Ka (Andrus et al 2009).	The unit may correlate with the Core Creek Sand of Mixon and Pilkey (1976) in northeastern NC (Soller and Mills 1991), but Corrado et al (1986) do not share this interpretation; the unit is also tentatively correlated with the Lynnhaven Member of the Tabb Frm of Johnson and Peebles (1986) (Soller and Mills 1991).		
		lower		**~0.129***	McCartan et al (1980); McCartan et al (1982); Szabo (1985); Soller and Mills (1991)			Unconformably overlies the Cooper Frm or the Santee Limestone and underlies Holocene eolian deposits (McCartan et al 1980); the unit may correlate with the Core Creek Sand (Mixon and Pilkey 1976) in NE NC and tentatively correlated with the Lynnhaven Member of the Tabb Frm (Johnson and Peebles 1986; Soller and Mills 1991).	Wehmiller and Belknap (1982) correlated the Wando Frm with the Socastee and Flanner Beach Frms, which supposedly underlie the Wando Frm in this report; the definitions of these formations may have changed or may differ from those of the authors, leading to this discrepancy.	
	Ten Mile Hill beds			**~0.25-0.20**	McCartan et al (1990); Weems et al (1994); Andrus et al (2009)	Deposited in a marsh environment near Charleston (Weems et al 1994); equivalent to unit Q3 of McCartan et al (1984) (McCartan et al 1990; Weems et al 1994).		The unit may correlate with the Socastee Frm (Szabo 1985; McCartan et al 1990; Weems et al 1994).		

Table S2.2.2: Part 18. Southeast and central South Carolina

Region	Formation	Member	Unit	Age (Ma)	Supporting References	Notes	Other age details or opinions	Correlation	Other opinions on correlations	General regional notes
	Socastee			**~0.24-0.1***	McCartan et al (1982); Wehmiller et al (1988); Soller and Mills (1991)	Dockal (1996) indicated the Neuse Frm has priority over the Socastee Frm and the two units are synonymous, but the "Socastee" name is still in use for sediments of this age in SC.	*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 Frm is typically assigned an age of ~240-180 Ka (McCartan et al 1982; Wehmiller et al 1988; Soller and Mills 1991), but Hollin and Hearty (1990) indicated the age is younger, dating to late isotope stage 5 (~90-70 Ka), which conforms with what Dockal (1996) found for the age of the Neuse Frm (Cape Fear Coquina) in southern NC, which is thought to be synonymous with the Socastee Frm (~75-55 Ka); Muhs et al (2003) indicated the dates of Hollin and Hearty (1990) would be consistent with aminostratigraphic comparison with the Sea Islands VLPG data.	Correlated with the Flanner Beach (NC), Norfolk (VA) [now Shirley, Tabb or Acredale Frms] and Omar (DE) Frms (McCartan et al 1982); correlated with the Flanner Beach Frm and with the Shirley Frm and Sedgefield Member of the Tabb Frm (Soller and Mills 1991); correlated with the Flanner Beach Frm (Harris 1996; Dockal 1996; Soller and Mills 1991).		
	Ladson			**~0.45-0.40**	McCartan et al (1990)	Named by Malde (1959) in the Charleston area; may be equivalent to the Canepatch Frm of the Myrtle Beach area of DuBar (1971), but the "Ladson" name is older and thus retained (Weems et al 1994). The unit is interpreted as a fluvial/deltaic deposit (Wehmiller et al 1988). Like the Canepatch Frm, the unit is also referred to as unit Q4 (Weems et al 1994; Bowen 2009).		Equivalent to the upper Talbot terrace of Colquhoun (1974) (Wehmiller et al 1988); considered a Charleston-area equivalent of the Canepatch Frm of Myrtle Beach (Corrado et al 1986; Weems et al 1994; Bowen 2009).		
	Waccamaw equivalent			**~2.1-1.7**	See references for Waccamaw Frm	The Waccamaw Frm or an equivalent unit is noted here by McCartan et al (1982), Weems and Lemon (1984, 1989), and Corrado et al (1986).		Correlative to the Waccamaw Frm.		

Table S2.2.2: Part 19. Southeast and central South Carolina

Region	Formation	Member	Unit	Age (Ma)	Supporting References	Notes	Other age details or opinions	Correlation	Other opinions on correlations	General regional notes
Southeast & central South Carolina	**Pringletown beds**			**<3.1 & >2.1**	Weems et al (1994) indicated a late Pliocene and early Pleistocene age; the age cited here was determined via stratigraphic position and based on ages of other units.	Informal unit named by Weems et al (1994) for sediments near Charleston; considered an estuarine to lagoon deposit.		The unit may underlie the Waccamaw? Frm and overlie the Raysor Frm (Weems et al 1994).		
	Raysor			**3.8-3.1**	Ward and Huddlestun (1988); Markewich et al (1992); Campbell and Campbell (1995); Campbell (pers comm 2013) [for lower date]	Cooke (1936) originally named the Raysor Marl for deposits in SC that are older than the Duplin Marl (he considered them to be upper Miocene in age). Raysor deposits were left behind from eroding Miocene shorelines and are spotty in Georgia (Huddlestun, pers comm 2013); these are also referred to as the Duplin Frm (equivalent) (Markewich, pers comm 2013); Weems et al (1982) indicated the Raysor Marl sediments (neostratotype) designated by Blackwelder and Ward (1979) are lithologically similar to the Goose Creek Limestone and should be abandoned. Campbell (1992) rejected the Raysor Frm on the basis that the only known locality that matches the original type description is hidden by a slump, but this rejection is not in use even 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 Raysor sands, and Raysor-equivalent strata to the east are referred to as "upper Goose Creek Limestone", which include the "Bear Bluff" deposits.	The Raysor Frm is thought to be within zone PL3 of Berggren or N20 (Huddlestun 1988; Cronin 1991).	Correlated with the Duplin Frm and Rushmere Member of the Yorktown Frm (Cronin et al 1984; Ward and Huddlestun 1988) and to the Jackson Bluff Frm (Huddlestun 1988); the Raysor Frm interfingers with the correlative Duplin Frm in SC and extends southward into GA (Ward et al 1991); correlated with the lower Pinecrest Beds, Jackson Bluff, Duplin and Raysor Frms and the Rushmere and Morgarts Beach Members of the Yorktown Frm (Cronin 1991; Allmon et al 1996a); correlated with the Yorktown and Duplin Frms on the basis of forams (Dowsett and Wiggs 1992); the Raysor Frm was placed below the Duplin Frm in Weems and Lewis (2002); Campbell and Campbell (1995) argued that the Goose Creek and Raysor Frms are older than the Duplin Frm at the Natural Well stratotype section. The Raysor Frm is equivalent to the upper Goose Creek Frm and overlies the lower Goose Creek Frm. In Ward and Huddlestun (1988), the Raysor Frm is depicted as below the Goose Creek Frm (but the authors later reversed their opinions, pers comm); the Raysor, Duplin and Jackson Bluff Frms are correlated (Huddlestun pers com 2013).	Krantz (1991) correlated the lower Duplin Frm with the Raysor Frm, but here the Duplin Frm is correlated with the upper Raysor Frm; Ward (2008) placed the Duplin and Raysor Frms as correlative with the Yorktown Frm, but with the Yorktown Frm younger than the Duplin and Raysor Frms; however, in this compilation, the Duplin and Raysor Frms correlate with the upper part of the Yorktown Frm.	

Table S2.2.2: Part 20. Southeast and central South Carolina

Region	Formation	Member	Unit	Age (Ma)	Supporting References	Notes	Other age details or opinions	Correlation	Other opinions on correlations	General regional notes
	Goose Creek Limestone	upper		**3.75-3.55**	Campbell and Campbell (1995); Ward and Huddlestun (1988)	The unit was originally mapped from Charleston, SC (Toumey 1848; Weems 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 Raysor Marl unconformably overlies the Goose Creek Limestone, which is a reversed relationship from previous publications. According to Campbell and Campbell (1995), the Raysor Frm and upper Goose Creek Limestone Frm appear to be coeval lithofacies distinct from and older than the Duplin Frm at the Natural Well stratotype. L. Campbell (pers comm 2013) indicated the lower Goose Creek limestone as found at the type section lies stratigraphically under the Raysor sands, and Raysor-equivalent strata to the east are referred to as "upper Goose Creek Limestone" and include the "Bear Bluff" deposits. Ward (pers comm 2012) does not support the name Goose Creek.	The unit is considered as 3.9-3.2 Ma or within zone NN 15 to mid-NN 14 (Bybell 1990).	According to Campbell and Campbell (1995), the upper Goose Creek Limestone Frm and the Raysor Frm appear to be laterally equivalent, coeval lithofacies, and both are older than the Duplin Frm. Here, the Duplin Frm is wholly equivalent to the Raysor Frm. Ward and Huddlestun (1988) placed the Goose Creek Frm above the Raysor Frm in their stratigraphic chart, which Huddlestun (pers comm 2013) indicated was incorrect and was reversed in a later publications by these authors.	The Bear Bluff is congruent with the upper Goose Creek Limestone Frm (Campbell and Campbell 1995); this relationship is not supported in this compilation, with the Bear Bluff Frm younger than the Goose Creek Frm here.	Plio-Pleistocene stratigraphy in S Carolina 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/elevation 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, Doar (2009) indicated the following formations for the Plio-Pleistocene of SC and SE VA: Wicomico, Penholoway, Ladson, Ten Mile Hill Beds, Pamlico, Princess Anne and Silver Bluff.
		lower		**4.0-3.8**	Ward and Huddlestun (1988); Campbell and Campbell (1995)			According to Campbell and Campbell (1995), the Raysor Marl unconformably overlies the lower Goose Creek Limestone, a reversal of the inferred stratigraphic sequence presented in other reports.		
	Wabasso Beds			**~5.5-4.3**	Huddlestun (1988); Markewich et al (1992); Campbell and Campbell (1995)	The Wabasso Beds is an informal name applied to lower Pliocene, 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 (Huddlestun 1988); Scott (2001) indicated the Wabasso Beds are also in the Peace River Frm in S Florida, but that they do not outcrop at the surface. The Wabasso Beds were treated as formational rank by Krantz (1991), but there seems to be no evidence for this, although Huddlestun (pers comm 2013) would like to see them formalized.	The unit is included within zone PL1 or N-18 (Huddlestun 1988); the unit is considered no older than 5.7 Ma and no younger than 4.2-4.0 Ma (Markewich et al 1992).	The unit is probably time equivalent to the Sunken Meadow Member of the Yorktown Frm in SE VA and NE NC.	Krantz (1991) indicated the lower Duplin Frm is time equivalent to the Sunken Meadow Member of the Yorktown Frm and Wabasso Beds, but this relationship was not supported in this compilation; here, the Duplin Frm is younger than the Wabasso Beds and the Sunken Meadow Member.	

Table S2.2.2: Part 21. Central/northeast SC & southeast North Carolina

Region	Formation	Member	Unit	Age (Ma)	Supporting References	Notes	Other age details or opinions	Correlation	Other opinions on correlations	General regional notes
	Waiter Island/Ocean Forest Peat/Qu			<0.1						
	Neuse/Socastee/ Flanner Beach			~0.2-0.1*	Wehmiller et al (1988); Wehmiller et al (1995)	Strata of this age are referred to by various names in the region; the Neuse Frm of Fallaw and Wheeler (1969) replaced the Flanner Beach Frm for just the fossiliferous Pleistocene deposits in NC. However, Mixon and Pilkey (1976) indicated Fallaw and Wheeler (1969)'s unit contained many different lithologies and was not used by these authors, with the type section re-defined as the Flanner Beach Frm. Blackwelder (1981b) also included sediments assigned to the Neuse Frm in the Flanner Beach Frm and abandoned the Neuse Frm. Dockal (1996) indicated the name Neuse Frm, which includes the Cape Fear Coquina, has priority over the Socastee Frm and should be in use. The Neuse Frm is still used in publications for sediments in NC, while others refer to these sediments as the Flanner Beach Frm or even the Socastee Frm.	*Age unclear in spite of years of study (see Muhs et al 2003). Wehmiller et al (1988) using amino acid racemization found an age for Snow Cut material of ~220 Ka or even older, with a further study (Wehmiller et al 1995) indicating an age of ~330-130 Ka. Prosser (1993) performed U-series dating on shell hash at Snows Cut and obtained an age of 62 Ka. Dockal (1996) did radiocarbon evaluation of Snows Cut material and found an age of 29-24 Ka (Dockal 1992, 1995), but these dates are probably too young according to the author, with an actual age closer to 75-55 Ka. Hollin and Hearty (1990) analyzed the Socastee Frm in SC and indicated an age younger than typically assigned, around 80 Ka. Muhs et al (2003) indicate the dates of Hollin and Hearty (1990) would be consistent with aminostratigraphic comparison with the Sea Islands VLPG data.	Correlative with the Great Bridge Frm of SE VA [now Acredale Frm] and with the Socastee Frm of SE NC and NE SC (Miller 1985) [the Acredale Frm, however, appears younger than the Socastee and Flanner Beach Frms, although the age is debated].		
	Canepatch			~0.42-0.3*	Cronin et al (1981); McCartan et al (1982); Szabo (1985)	Named for deposits near Horry County. The unit lies seaward of the Penholoway Terrace (Soller and Mills 1991). The Canepatch was restricted to one subsurface locality along the Intracoastal by Owens (1989), and thus was not used by Harris (1996); however, the Frm is still in use by others. Outcrops of the Canepatch are referred to as Q4 or the Talbot Frm by McCartan et al (1984) and Colquhoun (1986) (Soller and Mills 1991); according to Soller and Mills (1991), the unit outcrops in C and S SC; Huddlestun (pers comm 2013) indicated the Canepatch Frm also refers to a terrace deposit and, as such, is not in favor of the name.	*"In spite of many years of study, serious ambiguities about the relation between racemization, U-series, and stratigraphic interpretations of the Socastee and Canepatch deposits remain unresolved" (Muhs et al 2003, p. 171). Typically, the age was cited as around the middle Pleistocene (DuBar 1974) or ~ 400 Ka, e.g., McCartan et al (1982) 580-300 Ka, Cronin et al (1981) 450 Ka, Szabo (1985) ~460,000 +/- 100,000 Ka. However, Hollin and Hearty (1990) indicated the older U-series ages are too old, and they found ages matching isotope stage 5e using amino acid ratio correlations. These authors indicated that McCartan et al (1982) lumped DuBar's Socastee and Canepatch Frms together under the name "Socastee" and assigned the older "Canepatch" to deposits of an older unit. Muhs et al (2003) indicated the dates of Hollin and Hearty (1990) would be consistent with aminostratigraphic comparison with the Sea Islands VLPG data.	The unit unconformably overlies the Bear Bluff or Waccamaw Frms, and unconformably underlies the Socastee Frm (DuBar 1974); the unit is correlative with the Ladson Frm near Charleston; Lyons (1991) indicated that the Ft. Thompson Frm (exclusive of the Coffee Mill Hammock unit) seems to be the only Florida marine depositional unit available for correlation with the Canepatch Frm, which is congruent with this compilation.		

Table S2.2.2: Part 22. Central/northeast SC & southeast North Carolina

Region	Formation	Member	Unit	Age (Ma)	Supporting References	Notes	Other age details or opinions	Correlation	Other opinions on correlations	General regional notes
lina & southeast North Carolina	Waccamaw	upper		1.7-1.5	Graybill et al (2009); Badyrka et al (2010)	The youngest change in polarity (Matuyama Reverse Chron to Brunhes Normal Chron at about 0.78 Ma) occurs between the Waccamaw (Reverse) and Canepatch (Normal) formations near Myrtle Beach, SC (Liddicoat 2012).	Bybell (1990) indicated an age range of 1.8-1.0 Ma, which is close to that cited here; same for Akers (1972) of 1.6-0.7 Ma, which is younger, and Blackwelder (1981a,b, and unpub data cited within Lyons 1991) of 1.6-1.1 Ma; Campbell (1993) and Campbell and Campbell (1995) indicated an older age for both the lower and upper Waccamaw Frm (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. Mabry and Thayer (2001) indicated a late Pleistocene age of ~130-10 Ka.	The unit underlies the Canepatch Frm, overlies the Bear Bluff Frm, and correlates with the James City Frm (Ward et al 1991; Blackwelder and Ward 1979); correlative with the Caloosahatchee Frm based on faunal similarity (Lyons 1991), Campbell and Campbell (1995) agreed that the upper Waccamaw Frm correlates with the Caloosahatchee Frm; the Waccamaw Frm is correlated with the James City and Caloosahatchee Frms (Allmon et al 1996a); the James City Frm is a correlate (Harris 1996).	Campbell (1992) indicated the unit is laterally equivalent with the Cypresshead Frm, which is not supported in this report, as the Cypresshead is older here.	
		lower		2.1-1.7	Graybill et al (2009); Badyrka et al (2010); McGregor et al (2011)	The Waccamaw is divided into a lower and upper unit by an unconformity (Krantz 1991; Akers 1972; Ward et al 1991; Campbell and Campbell 1995).	Graybill et al (2009) is listed in support, but these authors found a slightly younger age for the lower Waccamaw Frm 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 Frm (2.5 or 2.4 Ma for the lower), but this is contrary to the recent dating work done and is not used here. Akers (1972) and Krantz (1991) indicated an age of 1.9-1.7 Ma, which is similar to the age cited here.	The lower Waccamaw Frm is correlated with the Bacons Castle Frm (Krantz 1991).		

Table S2.2.2: Part 23. Central/northeast SC & southeast North Carolina

Region	Formation	Member	Unit	Age (Ma)	Supporting References	Notes	Other age details or opinions	Correlation	Other opinions on correlations	General regional notes
Central/northeast South Caro	**Bear Bluff**			**2.6-2.1**	McCartan et al (1982); Krantz (1991); Markewich et al (1992); Campbell (1993)	The Bear Bluff Frm of southeastern NC and northeastern SC lies above the Duplin Frm (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 Frm be abandoned (the authors argued that the unit is actually part of the upper Goose Creek Limestone at the stratotype of the Bear Bluff Frm), but the Bear Bluff Frm is still in use by the USGS. Campbell and Campbell (1995) similarly argued that the Bear Bluff stratotype is pre-Natural Well Duplin Frm 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 faunally and lithologically dissimilar beds that in fact are much younger, after the 2.5 Ma boundary, equivalent to the Chowan River Frm [old Croatan Frm]. L. Campbell (pers comm 2013) indicated that the placement of the Bear Bluff Frm as younger than the Raysor Frm is based on Dubar including the lower Waccamaw Frm aragonitic 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 Raysor Frm.	All ages roughly point to about 2.5 Ma, with some minor differences: McCartan et al (1982) cited an age of 2.4-1.8 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; Markewich et al (1992) cited an age of PL5 (roughly equivalent to somewhere within 3.1-2.3 Ma); L. Campbell (pers comm 2013) indicated the Bear Bluff Frm is as old as 3.8 Ma or older and equivalent to the Raysor Frm.	Correlated with the Chowan River Frm (Ward et al 1991); correlated with the Chowan River Frm and Cypresshead Frm (Krantz 1991) [note that the Cypresshead Frm is older in this compilation, and thus not correlated with the Bear Bluff Frm here]; the Bear Bluff Frm is correlated with the Chowan River Frm and also potentially with the upper Pinecrest Beds of Florida (Allmon et al 1996a); Huddlestun (pers comm 2013) indicated the Bear Bluff Frm is younger than the Citronelle or Cypresshead Frms and not correlated with the Citronelle Frm.	Campbell (1993) indicated the molluscan fauna are younger than that of the Pinecrest Beds but older than that in the Caloosahatchee Frm, however, here the Pinecrest Beds are partially equivalent to the Bear Bluff Frm; Markewich et al (1992) indicated the unit lies above the Duplin Frm and is equivalent to the Cypresshead Frm (GA) and Nashua Frm of NE FL, but while partially time equivalent with the Nashua Frm, the unit is younger than the Cypresshead Frm in this compilation.	

Table S2.2.2: Part 24. Central/northeast SC & southeast North Carolina

Region	Formation	Member	Unit	Age (Ma)	Supporting References	Notes	Other age details or opinions	Correlation	Other opinions on correlations	General regional notes
	Duplin			**3.3-3.1**	Dowsett and Cronin (1990) indicated an age of 3.5-3.0 Ma; Campbell and Campbell (1995) cited an age of 3.2 Ma; Graybill et al (2009) found ages of 2.8, 2.4 and 2.3 Ma; McGregor et al (2011) found ages from 3.57 to 2.88 Ma, with the wide date range reflecting flattening of marine SR curve, time averaging or longer period of deposition; Liddicoat (2012), based on magnetostratigraphy, narrowed the range to the upper Gilbert Chron C2Ar (4.187-3.596 Ma), Mammoth Subchron C2An-2r (3.330-3.207 Ma), or Kaena Subchron C2An-1r (3.116-3.032 Ma). Based on the preceding information, the unit is assigned an age of 3.3-3.2 Ma.	Members of the Yorktown Frm 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 Duplin Frm (Ward 2001); Campbell and Campbell (1995) indicated that much confusion exists towards the Duplin Frm; for example, whether the unit should be interpreted narrowly and restricted to the stratotype section, or should be interpreted more broadly and include several transgressive-regressive sequences.	Krantz (1991) cited the lower Duplin Frm as 4.8-3.5 Ma; Campbell and Campbell (1995) indicated Dowsett and Cronin (1990) were dating the Duplin Frm from sites that yielded Raysor Frm index fossils.	Correlated with the lower Pinecrest Beds, the Raysor Frm, and the Rushmere and Morgarts Beach Members of the Yorktown Frm (Cronin 1991); age equivalent with the Yorktown Frm (Harris 1996); the lower Pinecrest Beds and Jackson Bluff Frm of W Florida are correlated with the Duplin Marl, Raysor Marl, Rushmere and Morgarts Beach Members of the Yorktown Frm (but not the Sunken Meadow Member) (Allmon et al 1996a); the Duplin Frm is slightly above the Raysor Frm (Weems and Lewis 2002); Markewich et al (1992) suggested that in SE GA, the fossils consistent with zone PL3 of Berggren are partially or wholly equivalent to the Duplin and Raysor Frms, to the Rushmere Member of the upper part of the Yorktown Frm in SE VA and NE NC, and to the Jackson Bluff Frm of extreme N Florida; Campbell and Campbell (1995) indicated that the Goose Creek and Raysor Frms are older than the Duplin Frm at the Natural Well stratotype and instead correlates with the middle Pinecrest Beds of Florida.	Krantz (1991) indicated the lower Duplin Frm is time equivalent with the Sunken Meadow Member of the Yorktown Frm and the Wabasso Beds, but this is not supported in this compilation; here, the Duplin Frm is younger than the Wabasso Beds and the Sunken Meadow Member of the Yorktown Frm. Ward (2008) placed the Duplin and Raysor Frms as correlative with the Yorktown Frm, but with the Yorktown Frm as younger than the Duplin and Raysor Frms; however, in this compilation, the Duplin and Raysor Frms correlate with the upper part of the Yorktown Frm.	The Penholoway Frm (Owens 1989), early Pleistocene in age (Soller and Mills 1991), was abandoned by Huddlestun (1988) but reinstated by Weems and Lemon (1989) and used by Soller and Mills (1991). The 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. Dating on the Penholoway Frm indicates the unit is not older than the

Table S2.2.2: Part 25. Central/northeast SC & southeast North Carolina

Region	Formation	Member	Unit	Age (Ma)	Supporting References	Notes	Other age details or opinions	Correlation	Other opinions on correlations	General regional notes
	Goose Creek Limestone	upper		**3.75-3.55**	Ward and Huddlestun (1988); Campbell and Campbell (1995)	The unit was originally mapped from Charleston, SC (Toumey 1848; Weems 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 Raysor Marl unconformably overlies the Goose Creek Limestone, which is a reversed relationship from previous publications. According to Campbell and Campbell (1995), the Raysor Frm and upper Goose Creek Limestone appear to be coeval lithofacies distinct from and older than the Duplin Frm at the Natural Well stratotype. L. Campbell (pers comm 2013) indicated the lower Goose Creek Limestone as found at the type section lies stratigraphically under the Raysor sands, and to the east, Raysor-equivalent strata are referred to as "upper Goose Creek Limestone" and include the "Bear Bluff" deposits.	Age cited at 3.9-3.2 Ma or zone NN 15 to mid-NN 14 (Bybell 1990).	According to Campbell and Campbell (1995), the upper Goose Creek Limestone and the Raysor Frm appear to be laterally equivalent, coeval lithofacies, and both are older than the Duplin Frm. The current compilation has the Duplin Frm wholly equivalent to the Raysor Frm. Ward and Huddlestun (1988) placed the Goose Creek above the Raysor Frm in their stratigraphic chart, which Huddlestun (pers comm 2013) indicated is incorrect and was reversed in later publications by these authors.	The Bear Bluff Frm is congruent with the upper Goose Creek Limestone (Campbell and Campbell 1995); however, this relationship is not supported in this compilation, as the Bear Bluff Frm is younger than the Goose Creek Limestone here.	upper part of Quaternary zone NN19 of Martini (1971) around 970 Ka (Weems et al 1994); equivalent beds in the Stallville Quadrangle yielded U-Th dis-equilibria ages of 700 Ka (Szabo 1985). The Penholoway is said to overlie the (lower) Waccamaw Frm and outcrops from Cape Fear River southward to Charleston, SC, and potentially correlates with the younger Waccamaw Frm and with unit Q5 of McCartan et al (1984) and Colquhoun (1986) (from Soller and Mills 1991). See overview of stratigraphic naming issues and associated problems of dating formations in Corrado et al (1986).
		lower		**4.0-3.8**	Ward and Huddlestun (1988); Campbell and Campbell (1995)			According to Campbell and Campbell (1995), the Raysor Marl unconformably overlies the lower Goose Creek Limestone, a reversal of the inferred stratigraphic sequence presented in other reports.		

Table S2.2.2: Part 26. Central and northeast North Carolina

Region	Formation	Member	Unit	Age (Ma)	Supporting References	Notes	Other age details or opinions	Correlation	Other opinions on correlations	General regional notes
	Core Creek Sand (informal unit) & Qu			**<0.080**						
	Flanner Beach			**~0.24-0.18**	McCartan et al (1982); Miller (1985); Krantz (1990); Denison et al (1993); Harris (1996)	Numerous names have been applied to middle and upper Pleistocene units between the Cape Fear and Neuse Rivers in NC, including the Socastee, Canepatch and Flanner Beach Frms (Harris 1996). DuBar and Solliday (1963) renamed the "Pamlico" deposits the Flanner Beach Frm and rejected the usage of the Pamlico Frm (Ward 2008). Fallaw and Wheeler (1969) rejected usage of the Flanner Beach Frm and indicated that the Flanner Beach Frm includes deposits of Horry Clay and Croatan Frm and is not a distinct lithological unit. Mixon and Pilkey (1976) adopted the Flanner Beach Frm for use by the USGS and restricted the unit to exclude the Minnesott Ridge sand and younger Pleistocene beds. Blackwelder (1981b) revised the Flanner Beach Frm to include sediments previously assigned to the Neuse Frm and abandoned usage of the Neuse Frm.	*The Flanner Beach Frm is typically assigned to the middle Pleistocene (Krantz 1990; Denison et al 1993; Harris 1996), with an age of 240-180 Ka (McCartan et al 1982; Miller 1985). However, younger dates for correlative sediments of the Socastee and Neuse Frms suggest that the age of the Flanner Beach Frm may be younger, around the Sangamon Interglacial (~125-75 Ka), which Phillips (1995) has cited as an age for the Frm. Denison et al (1993) cited a mid-Pleistocene age for lower Croatan sediments, but also indicated a possible age of 1.2-0.8 Ma; this older age could result from fact that the Croatan Frm = James City Frm, as the name has been in flux. Cronin et al (1981) found an age of >500 Ka for a coral from this Frm, but the coral may have been re-worked from lower units. Muhs et al (2003) discussed some of the ambiguities in dating Quaternary Frms in the Atlantic Coastal Plain.	Correlated with the Socastee, Norfolk [now Shirley, Tabb or Acredale Frms] and Omar Frms (McCartan et al 1982); correlated with the Great Bridge Frm of southeastern VA [now Acredale Frm] and with the Socastee Frm of southeastern NC and northeastern SC (Miller 1985); the Acredale Frm, however, appears younger than the Socastee and Flanner Beach Frms, although the age is debated; correlated with the Socastee Frm, Shirley Frm and the Sedgefield Member of the Tabb Frm (Soller and Mills 1991); Dockal (1996), Harris (1996), and Soller and Mills (1991) also correlated the unit with the Socastee Frm.	Miller (1985) indicated the Great Bridge Frm of southeastern VA [now Acredale Frm] is correlative, but the unit is younger than the Flanner Beach Frm in this compilation.	
	James City	upper*		**1.6-1.0***	Blackwelder (1981b); Wehmiller et al (1988); Krantz (1991)	The James City was initially called the Croatan Beds by Dall in 1892, and this name is probably still valid (Hazel 1983), but the "James City" name has predominated. Blackwelder (1981b) renamed the lower Croatan deposits as the Chowan River Frm and the upper Croatan deposits as the James City Frm. The Croatan name is still in use by some (e.g., Denison et al 1993). According to Ward et al (1991), correlative deposits are assigned to the Waccamaw Frm south of New River, and the James City Frm actually contains several beds of slightly different ages of similar lithology, but with different molluscan assemblages, all within the early Pleistocene; this was later echoed by Ward (2008), when he stated that the James City Frm is divided into two deposits, both of which are roughly equivalent to the two Waccamaw Frm deposits. *However, L. Campbell (pers comm 2013) indicated Ward and Blackwelder (1987) misapplied 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 Frm). Campbell also indicated the James City is not a Bermont Frm equivalent (~1.6-1.1 Ma), as is shown here, since none of the distinctive index fossils that mark the Bermont Frm have been found in the James City Frm; thus, the dates here may be too old for the upper or type James City Frm. The type James City equivalent beds in South Carolina are often called the Wicomico Frm (L. Campbell pers comm 2013).	Slightly younger ages are cited by Miller (1985) of 1-0.7 Ma, and by McCartan et al (1982) of 1.4-1.1 Ma.	The James City Frm unconformably overlies the Chowan River Frm in NC (Ward and Blackwelder 1987; Krantz 1991); the unit correlates with the Waccamaw Frm (Blackwelder and Ward 1979; Blackwelder 1981b). Campbell (1993) indicated the James City, upper Waccamaw, and upper Caloosahatchee faunas were victims of the same extinction event.	Campbell (pers comm 2013) indicated the James City and Bermont Frms are not equivalents and do not share characteristic index fossils, but here they are shown as time equivalent.	
		lower		**2.1-1.9**	Campbell (1993); Ward (2008)					

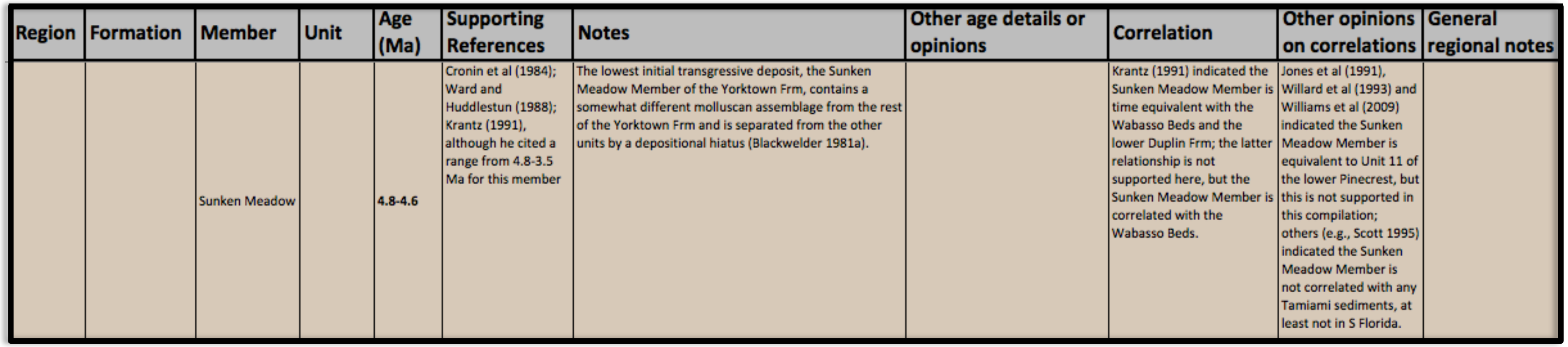
Table S2.2.2: Part 27. Central and northeast North Carolina

Region	Formation	Member	Unit	Age (Ma)	Supporting References	Notes	Other age details or opinions	Correlation	Other opinions on correlations	General regional notes
Central and northeast North Carolina	Bacons Castle			~2.1-2.0	Ramsey (1988, 1992); Groot 1991	Johnson and Berquist (1989) indicated age determination is difficult because there are no shell fossils or radiometrically datable material, but indicated a Pliocene age; Mixon et al (1989) and Radar and Evans (1993) both considered the unit to be of late Pliocene age.	Krantz (1991) indicated an age of 1.9-1.7 Ma, but dating was tentative; Ramsey (1992) indicated an age of 2.3-2.0 Ma.	The Bacons Castle Frm unconformably overlies the Yorktown and Chowan River Frms in eastern VA (Krantz 1991); the unit correlates with the upper Beaver Dam Frm (Ramsey 1992); correlative with the lower Waccamaw Frm (Krantz 1991).	The chart of Carter et al (2003) indicated the Bacons Castle Frm is equivalent with the Chowan River Frm, but Krantz (1991) indicated the unit overlies the Chowan River Frm.	Many of the Pleistocene units in North Carolina are non fossiliferous, either *a priori* or as a result of leaching, and thus correlation and dating on these units is difficult. The stratigraphy has been in flux, with many units having been named and re-named. Work is on-going in the region, and thus this particular compilation is sure to change in the future. The Talbot Frm, as mapped by Wentworth (1930) in southeastern Virginia, was abandoned by Huddlestun (1988) and is now called the Tabb Formation (Johnson and Berquest 1989); however, the unit name is still in use in NC by some (e.g., Denison et al 1993); see Wehmiller et al (2004a,b) and Wehmiller et al (2010, 2012) for further information on Quaternary units and dating issues in N Carolina.
	Chowan River	Colerain		2.6-2.1	Ages have been obtained anywhere from 3 to 1.9 Ma; see discussion in "Other age details or opinions" section.	The Chowan River Frm was named by Blackwelder (1981b) for sediments previously mapped as the Yorktown Frm and the Croatan Frm. Blackwelder (1981b) renamed the lower deposits as the Chowan River Frm and the upper deposits as the James City Frm. The Croatan Frm is still in use by some (e.g., Denison et al 1993). The Chowan River Frm unconformably overlies the Yorktown Frm and unconformably underlies the James City Frm (Ward et al 1991; Snyder and Riggs 1993). According to L. Campbell (pers comm 2013), Ward and Blackwelder (1987) misapplied the name "Chowan River" at Aurora because the fauna is not conformable with the fauna at the type section, but rather is equivalent to the lower Waccamaw Frm (with a cited older date for the lower Waccamaw of 2.4 Ma).	Ages have been obtained anywhere from 3 to 1.9 Ma. Ages have centered around 2.5 or 2.1 Ma, but have also been found as old as 2.8 or 3 Ma: 2.4-1.9 Ma (Bender unpublished data, from Blackwelder 1981a,b); N21 (~2.4-1.9 Ma) (Cronin et al 1984); 2.8 Ma (Groot 1991); 2.9-2.6 or 2.2-2.1 Ma (Krantz 1991); 2.5 Ma (Ramsey 1988, 1992); 2.5 Ma (Campbell 1993); 3.4-2 Ma from strat chart (Pazzaglia 1993); 3-2.8 Ma (Campbell and Campbell 1995); 2.40-1.9 Ma (Hobbs 2004).	Correlated with the Bear Bluff and Cypresshead Frms (Krantz 1991) [note that in this report, the Cypresshead and Bear Bluff Frms are not time equivalent]; correlated with deposits in SC known as the Bear Bluff Frm (Ward et al 1991); correlated with Pinecrest Beds 2 and 3 of the APAC Pit (Campbell 1993); the Chowan River fauna is older than the lower Waccamaw Frm, but younger than the Duplin Frm (Campbell and Campbell 1995); the upper Pinecrest Beds (units 4-2 *sensu* Allmon et al 1996a,b) are separated by a hiatus and may be equivalents of the Chowan River Frm of SE VA and NE Carolinas (Dowsett and Willard 1996; Jones et al 1991); the Bear Bluff (SC), Caloosahatchee (FL) and Chowan River Frms are equivalent (Blackwelder 1981a; Ward and Blackwelder 1987) [note that the Caloosahatchee Frm is younger than the Chowan River Frm in this report]; equivalent to the Bear Bluff Frm (Harris 1996).	Campbell (1993) correlated the unit in part with the Moore House Member of the Yorktown Frm of Krantz (1991) and Ward et al (1991), which is restricted to 3.5 Ma, but the Yorktown Frm (Moore House Member) is below the Chowan River Frm in this compilation. Ward and Gilinsky (1993) did not agree with Campbell (1993) in equating the Moore House Member of the Yorktown Frm with the Chowan River beds (Campbell and Campbell 1995). Evidence suggests that the Chowan River Frm is younger than 3.5 Ma.	
		Edenhouse								

Table S2.2.2: Part 28. Central and northeast North Carolina

Region	Formation	Member	Unit	Age (Ma)	Supporting References	Notes	Other age details or opinions	Correlation	Other opinions on correlations	General regional notes
	Yorktown	Morgarts Beach		4.6-3.1	Hazel (1983); Snyder et al (1983); Dowsett and Cronin (1990); Cronin (1991); Krantz (1991); Dowsett and Wiggs (1992)	Campbell (1993) indicated the members proposed by Ward and Blackwelder (1980) are not lithostratigraphic units and should not be in use; however, the units are still widely cited in the literature. The members of the Yorktown Frm are mapped as far south as the Neuse River in NC (Ward 2001, 2008). The Yorktown Frm is usually used for lower and lower upper Pliocene sediments that occur north of the Neuse Hing on the Albemarle Block, whereas the Duplin Frm is used for age-equivalent sediments that occur south of Neuse Hing on the Onslow Block (Ward et al 1991). The uppermost Moore House Member is restricted to southeastern Virginia (Ward et al 1991).	~4.8-2.8 Ma, with the upper limit near the middle of zone N21 (Cronin et al 1984; Lyons 1991); however, Ramsey (1992) indicated the dates may be closer to 4.5-3 Ma (following Krantz 1991); late zone N18 and zone N19 or PL1-PL3 (Akers 1972); upper zone N19 (Blackwelder 1981b); 4.5-3 Ma (Hazel 1983, Snyder et al 1983, Cronin 1991, Ramsey 1992); PL1b-PL3, authors favor younger dates in this range (Dowsett and Cronin 1990; Dowsett and Wiggs 1992); 3.2 Ma (Campbell 1993); 5.3-3.4 Ma (Pazzaglia 1993); 3.5-2.9 Ma (Willard 1994); 3.8 Ma (Campbell pers comm 2013); Denison et al (1993) suggested younger dates (age N21 or N22, ~2.1-1.4 Ma), but these may have resulted from differing definitions of stratigraphy: the authors placed the Yorktown Frm as immediately succeeded by the Croatan Frm, which is now the Flanner Beach, and thus they could have been sampling what is now the Chowan River Frm (in NC).	The Moore House Member is the youngest unit and does not seem to be correlated with any unit in SC or GA (Krantz 1991); the Yorktown Frm is the same age as the Duplin and Raysor Frms (Cronin et al 1984; Ward and Huddlestun 1988; Dowsett and Wiggs 1992) and the Jackson Bluff Frm (Huddlestun 1988; Allmon et al 1996a); Akers (1972) correlated the unit with the Jackson Bluff and Agurgurxquite Frms of Mexico; Cronin (1991) correlated the unit with the lower Pinecrest Beds and the Duplin and Raysor Frms of NC, SC and GA; Cronin and Dowsett (1996) indicated units 10-5 of the Pinecrest Beds are equivalent to these members of the Yorktown [only partially in this report].	Campbell (1993) correlated the Moore House Member of Ward et al (1991) and Krantz (1991) with the Chowan River Frm, which is restricted to 3.5 Ma, but the Yorktown Frm (Moore House Member) is below the Chowan River Frm in this compilation. Ward and Gilinsky (1993) did not agree with Campbell (1993) in equating the Moore House Member of the Yorktown Frm with the Chowan River beds (Campbell and Campbell 1995). Evidence suggests that the Chowan River Frm is younger than 3.5 Ma. Harris (1996) indicated the Rushmere and Morgarts Beach Members of the Yorktown Frm = Duplin Frm, but in this report, the Duplin Frm is only partially correlated with the upper part of the Yorktown Frm. Campbell et al (2011) indicated the lower Goose Creek Limestone of SC, Unit 3 of the Yorktown Frm, the Tamiami Limestone and lower Jackson Bluff Frm of Florida are all correlated by a *Leptopecten* unit (Early Pliocene), but while the Yorktown Frm seems to span all these units, the Jackson Bluff in this report overlies the Tamiami Limestone and is age-equivalent to the upper Goose Creek, not the lower.	
		Rushmere								

Table S2.2.2: Part 29. Central and northeast North Carolina

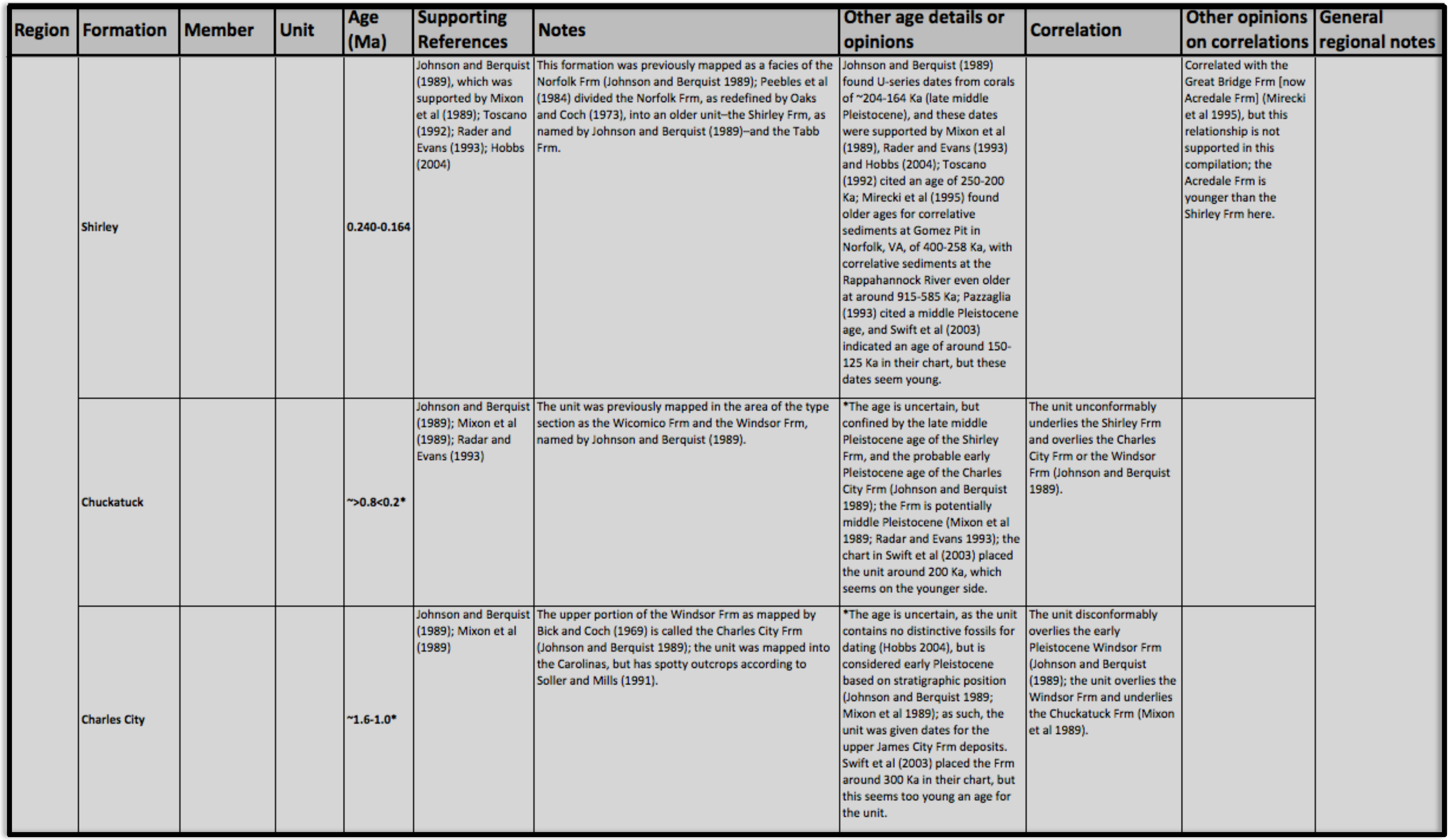


Region	Formation	Member	Unit	Age (Ma)	Supporting References	Notes	Other age details or opinions	Correlation	Other opinions on correlations	General regional notes
		Sunken Meadow		**4.8-4.6**	Cronin et al (1984); Ward and Huddlestun (1988); Krantz (1991), although he cited a range from 4.8-3.5 Ma for this member	The lowest initial transgressive deposit, the Sunken Meadow Member of the Yorktown Frm, contains a somewhat different molluscan assemblage from the rest of the Yorktown Frm and is separated from the other units by a depositional hiatus (Blackwelder 1981a).		Krantz (1991) indicated the Sunken Meadow Member is time equivalent with the Wabasso Beds and the lower Duplin Frm; the latter relationship is not supported here, but the Sunken Meadow Member is correlated with the Wabasso Beds.	Jones et al (1991), Willard et al (1993) and Williams et al (2009) indicated the Sunken Meadow Member is equivalent to Unit 11 of the lower Pinecrest, but this is not supported in this compilation; others (e.g., Scott 1995) indicated the Sunken Meadow Member is not correlated with any Tamiami sediments, at least not in S Florida.	

Table S2.2.2: Part 30. Southeastern Virginia

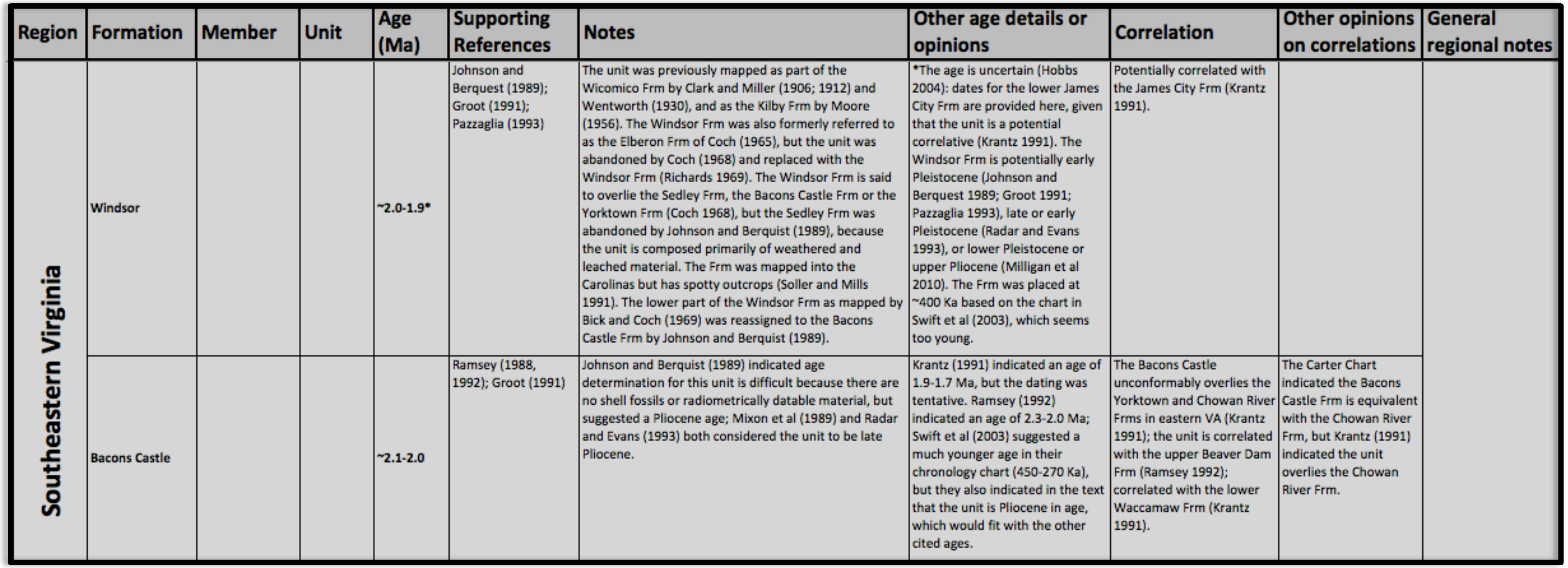
Region	Formation	Member	Unit	Age (Ma)	Supporting References	Notes	Other age details or opinions	Correlation	Other opinions on correlations	General regional notes
	Powells Crossroads			**<0.04**	Oaks and Coch (1963)	Little information could be found on this Frm, which is not used extensively in the literature. The unit outcrops at Virginia Beach and was named by Spencer and Campbell (1987); it now includes the Sand Bridge (at top) and London Bridge Frms, which were reduced to member rank.	The Sand Bridge Frm, now part of Powells Crossroads, had a radiocarbon age of 40 Ka (Oaks and Coch 1963); the Sand Bridge is Wisconsin in age (~85-10 Ka) (Coch 1965).			
	Acredale			**<0.04**	Oaks and Coch (1963); Spencer and Campbell (1987)	Little information could be found on this Frm, which is not used extensively in the literature; the Kempsville, Norfolk and Great Bridge Frms were reduced to member ranks and assigned to the Acredale Frm in the Virginia Beach area (Spencer and Campbell 1987).	Very few papers are available on this Frm; Oaks and Coch (1963) indicated a middle or late Pleistocene age for the Frm; Spencer and Campbell (1987) indicated a late Pleistocene age.	The unit overlies the Pliocene Croatan Frm [now either the James City or Chowan River Frms] (Spencer and Campbell 1987).		
	Tabb			**0.12-0.039**	Szabo (1985); Johnson and Berquist (1989); Johnson and Hobbs (1990); Mirecki et al (1995); Scott et al (2010)	The Talbot Frm, as mapped by Wentworth (1930) in southeastern VA, is now called the Tabb Frm (Johnson and Berquest 1989); the unit is also mapped as the Norfolk Frm by Bick and Coch (1969) and others (see Hobbs 2004).	Szabo (1985) found an age for the Norfolk Frm of 71 +/- 5 Ka [The Norfolk was divided into the Shirley and Tabb Frms]. Mixon et al (1982) thought the 72 Ka average for the Norfolk Frm was too young and resulted from loss of thorium due to burial in permeable, water-saturated detrital sediments; however, these dates may be appropriate for younger units (Tabb Frm), rather than the Shirley Frm; Mixon et al (1989), Pazzaglia (1993), and Rader and Evans (1993) cited a late Pleistocene age; Johnson and Berquist (1989) indicted Mixon (1982) dated sediments correlative with the Sedgefield Member at 75-120 Ka; correlative sediments at the Gomez Pit in Norfolk, VA, were dated to 125-80 Ka (Mirecki et al 1995); the majority of ages average around 76 Ka for the Sedgefield Member of the Tabb Frm (Scott et al 2010); Johnson and Hobbs (1990) suggested a 65 Ka for the Poquoson Member of the Tabb Frm; Scott et al (2010) found OSL dates of 39.6+/-6.6 Ka and 44.4+/-5.2 Ka for the Poquoson Member; overall, the Frm appears to have been deposited during MIS-3 or ~125-40 Ka (Swift et al 2003, Scott et al 2010).	The unit unconformably overlies the Norfolk Frm [now the Shirley, Tabb or Acredale Frms] or the Yorktown Frm and underlies Holocene sediments (Johnson 1976); the Tabb Frm is correlated with the Wachapreague and Nassawadox Frms (Toscano and York 1992).		

Table S2.2.2: Part 31. Southeastern Virginia



Region	Formation	Member	Unit	Age (Ma)	Supporting References	Notes	Other age details or opinions	Correlation	Other opinions on correlations	General regional notes
	Shirley			0.240-0.164	Johnson and Berquist (1989), which was supported by Mixon et al (1989); Toscano (1992); Rader and Evans (1993); Hobbs (2004)	This formation was previously mapped as a facies of the Norfolk Frm (Johnson and Berquist 1989); Peebles et al (1984) divided the Norfolk Frm, as redefined by Oaks and Coch (1973), into an older unit–the Shirley Frm, as named by Johnson and Berquist (1989)–and the Tabb Frm.	Johnson and Berquist (1989) found U-series dates from corals of ~204-164 Ka (late middle Pleistocene), and these dates were supported by Mixon et al (1989), Rader and Evans (1993) and Hobbs (2004); Toscano (1992) cited an age of 250-200 Ka; Mirecki et al (1995) found older ages for correlative sediments at Gomez Pit in Norfolk, VA, of 400-258 Ka, with correlative sediments at the Rappahannock River even older at around 915-585 Ka; Pazzaglia (1993) cited a middle Pleistocene age, and Swift et al (2003) indicated an age of around 150-125 Ka in their chart, but these dates seem young.		Correlated with the Great Bridge Frm [now Acredale Frm] (Mirecki et al 1995), but this relationship is not supported in this compilation; the Acredale Frm is younger than the Shirley Frm here.	
	Chuckatuck			~>0.8<0.2*	Johnson and Berquist (1989); Mixon et al (1989); Radar and Evans (1993)	The unit was previously mapped in the area of the type section as the Wicomico Frm and the Windsor Frm, named by Johnson and Berquist (1989).	*The age is uncertain, but confined by the late middle Pleistocene age of the Shirley Frm, and the probable early Pleistocene age of the Charles City Frm (Johnson and Berquist 1989); the Frm is potentially middle Pleistocene (Mixon et al 1989; Radar and Evans 1993); the chart in Swift et al (2003) placed the unit around 200 Ka, which seems on the younger side.	The unit unconformably underlies the Shirley Frm and overlies the Charles City Frm or the Windsor Frm (Johnson and Berquist 1989).		
	Charles City			~1.6-1.0*	Johnson and Berquist (1989); Mixon et al (1989)	The upper portion of the Windsor Frm as mapped by Bick and Coch (1969) is called the Charles City Frm (Johnson and Berquist 1989); the unit was mapped into the Carolinas, but has spotty outcrops according to Soller and Mills (1991).	*The age is uncertain, as the unit contains no distinctive fossils for dating (Hobbs 2004), but is considered early Pleistocene based on stratigraphic position (Johnson and Berquist 1989; Mixon et al 1989); as such, the unit was given dates for the upper James City Frm deposits. Swift et al (2003) placed the Frm around 300 Ka in their chart, but this seems too young an age for the unit.	The unit disconformably overlies the early Pleistocene Windsor Frm (Johnson and Berquist (1989); the unit overlies the Windsor Frm and underlies the Chuckatuck Frm (Mixon et al 1989).		

Table S2.2.2: Part 32. Southeastern Virginia



Region	Formation	Member	Unit	Age (Ma)	Supporting References	Notes	Other age details or opinions	Correlation	Other opinions on correlations	General regional notes
Southeastern Virginia	**Windsor**			**~2.0-1.9***	Johnson and Berquest (1989); Groot (1991); Pazzaglia (1993)	The unit was previously mapped as part of the Wicomico Frm by Clark and Miller (1906; 1912) and Wentworth (1930), and as the Kilby Frm by Moore (1956). The Windsor Frm was also formerly referred to as the Elberon Frm of Coch (1965), but the unit was abandoned by Coch (1968) and replaced with the Windsor Frm (Richards 1969). The Windsor Frm is said to overlie the Sedley Frm, the Bacons Castle Frm or the Yorktown Frm (Coch 1968), but the Sedley Frm was abandoned by Johnson and Berquist (1989), because the unit is composed primarily of weathered and leached material. The Frm was mapped into the Carolinas but has spotty outcrops (Soller and Mills 1991). The lower part of the Windsor Frm as mapped by Bick and Coch (1969) was reassigned to the Bacons Castle Frm by Johnson and Berquist (1989).	*The age is uncertain (Hobbs 2004): dates for the lower James City Frm are provided here, given that the unit is a potential correlative (Krantz 1991). The Windsor Frm is potentially early Pleistocene (Johnson and Berquest 1989; Groot 1991; Pazzaglia 1993), late or early Pleistocene (Radar and Evans 1993), or lower Pleistocene or upper Pliocene (Milligan et al 2010). The Frm was placed at ~400 Ka based on the chart in Swift et al (2003), which seems too young.	Potentially correlated with the James City Frm (Krantz 1991).		
	Bacons Castle			**~2.1-2.0**	Ramsey (1988, 1992); Groot (1991)	Johnson and Berquist (1989) indicated age determination for this unit is difficult because there are no shell fossils or radiometrically datable material, but suggested a Pliocene age; Mixon et al (1989) and Radar and Evans (1993) both considered the unit to be late Pliocene.	Krantz (1991) indicated an age of 1.9-1.7 Ma, but the dating was tentative. Ramsey (1992) indicated an age of 2.3-2.0 Ma; Swift et al (2003) suggested a much younger age in their chronology chart (450-270 Ka), but they also indicated in the text that the unit is Pliocene in age, which would fit with the other cited ages.	The Bacons Castle unconformably overlies the Yorktown and Chowan River Frms in eastern VA (Krantz 1991); the unit is correlated with the upper Beaver Dam Frm (Ramsey 1992); correlated with the lower Waccamaw Frm (Krantz 1991).	The Carter Chart indicated the Bacons Castle Frm is equivalent with the Chowan River Frm, but Krantz (1991) indicated the unit overlies the Chowan River Frm.	

Table S2.2.2: Part 33. Southeastern Virginia

Region	Formation	Member	Unit	Age (Ma)	Supporting References	Notes	Other age details or opinions	Correlation	Other opinions on correlations	General regional notes
	Chowan River	Colerain		2.6-2.1	Ages have been obtained anywhere from 3 to 1.9 Ma; see discussion in "Other age details or opinions" section.	The Chowan River Frm was named by Blackwelder (1981b) for sediments previously mapped as the Yorktown Frm and the Croatan Frm. The unit unconformably overlies the Yorktown Frm and unconformable underlies the James City Frm (Ward et al 1991; Snyder and Riggs 1993).	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); N21 (~2.4-1.9 Ma) (Cronin et al 1984); 2.8 Ma (Groot 1991); 2.9-2.6 or 2.2-2.1 Ma (Krantz 1991); 2.5 Ma (Ramsey 1988, 1992); 2.5 Ma (Campbell 1993); 3.4-2 Ma from their stratigraphic chart (Pazzaglia 1993); 3-2.8 Ma (Campbell and Campbell 1995); 2.40-1.9 Ma (Hobbs 2004).	Correlated with the Bear Bluff and Cypresshead Frms (Krantz 1991) [note that in this report, the Cypresshead and Bear Bluff Frms are not time equivalent]; correlated with deposits in SC known as the Bear Bluff Frm (Ward et al 1991); correlated with Pinecrest Beds 2 and 3 of the APAC Pit (Campbell 1993); the Chowan River fauna is older than the lower Waccamaw Frm, but younger than the Duplin Frm (Campbell and Campbell 1995); the upper Pinecrest Beds (units 4-2 sensu Allmon et al 1996a,b) are separated by a hiatus and may be equivalents of the Chowan River Frm of SE VA and NE Carolinas (Dowsett and Cronin 1996; Jones et al 1991); the Bear Bluff (SC), Caloosahatchee (FL) and Chowan River Frms are equivalent (Blackwelder 1981a; Ward and Blackwelder 1987) [note that the Caloosahatchee Frm is younger than the Chowan River Frm in this report]; equivalent to the Bear Bluff Frm (Harris 1996).	Campbell (1993) correlated the unit in part with the Moore House Member of the Yorktown Frm of Krantz (1991) and Ward et al (1991), which is restricted to 3.5 Ma, but the Yorktown Frm (Moore House Member) is below the Chowan River Frm in this compilation. Ward and Gilinsky (1993) did not agree with Campbell (1993) in equating the Moore House Member of the Yorktown Frm with the Chowan River beds (Campbell and Campbell 1995). Evidence suggests that the Chowan River Frm is younger than 3.5 Ma.	
		Edenhouse								

Table S2.2.2: Part 34. Southeastern Virginia

Region	Formation	Member	Unit	Age (Ma)	Supporting References	Notes	Other age details or opinions	Correlation	Other opinions on correlations	General regional notes
	Yorktown	Moore House		4.6-3.1	Hazel (1983); Snyder et al (1983); Cronin (1991); Dowsett and Cronin (1990); Krantz (1991); Dowsett and Wiggs (1992)	Campbell (1993) indicated the members proposed by Ward and Blackwelder (1980) are not lithostratigraphic units and should not be in use; however, the units are still widely cited in the literature. The members of the Yorktown Frm are mapped as far south as the Neuse River in NC (Ward 2001, 2008). The Yorktown Frm is usually used for lower and lower upper Pliocene sediments that occur north of the Neuse Hing on the Albemarle Block, whereas the Duplin Frm is used for age-equivalent sediments that occur south of Neuse Hing on the Onslow Block (Ward et al 1991). The uppermost Moore House Member is restricted to southeastern Virginia (Ward et al 1991).	~4.8-2.8 Ma, with the upper limit near the middle of zone N21 (Cronin et al 1984; Lyons 1991); however, Ramsey (1992) indicated the dates may be closer to 4.5-3 Ma (following Krantz 1991); late zone N18 and zone N19 or PL1-PL3 (Akers 1972); upper zone N19 (Blackwelder 1981b); 4.5-3 Ma (Hazel 1983; Snyder et al 1983; Cronin 1991; Ramsey 1992); PL1b-PL3, authors favor younger dates in this range (Dowsett and Cronin 1990; Dowsett and Wiggs 1992); 3.2 Ma (Campbell 1993); 5.3-3.4 Ma (Pazzaglia 1993); 3.5-2.9 Ma (Willard 1994); 3.8 Ma (Campbell pers comm 2013); Denison et al (1993) suggested younger dates (age N21 or N22, ~2.1-1.4 Ma), but these may have resulted from differing definitions of stratigraphy: the authors placed the Yorktown Frm as immediately succeeded by the Croatan Frm, which is now the Flanner Beach, and thus they could have been sampling what is now the Chowan River Frm (in NC).	The Moore House Member is the youngest unit and does not seem to be correlated with anything in SC or GA (Krantz 1991); the Yorktown Frm is the same age as the Duplin and Raysor Frms (Cronin et al 1984; Ward and Huddlestun 1988; Dowsett and Wiggs 1992) and the Jackson Bluff Frm (Huddlestun 1988; Allmon et al 1996a); Akers (1972) correlated the unit with the Jackson Bluff and Agurgurxquite Frms of Mexico; Cronin (1991) correlated the unit with the lower Pinecrest Beds and the Duplin and Raysor Frms of NC, SC and GA; Cronin and Dowsett (1996) indicated units 10-5 of the Pinecrest Beds are equivalent to these members of the Yorktown [only partially in this report].	Campbell (1993) correlated the Moore House Member of Ward et al (1991) and Krantz (1991) with the Chowan River Frm, which is restricted to 3.5 Ma, but the Yorktown Frm (Moore House Member) is below the Chowan River Frm in this compilation. Ward and Gilinsky (1993) did not agree with Campbell (1993) in equating the Moore House Member of the Yorktown Frm with the Chowan River beds (Campbell and Campbell 1995). Evidence suggests that the Chowan River Frm is younger than 3.5 Ma. Harris (1996) indicated the Rushmere and Morgarts Beach Members of the Yorktown Frm = Duplin Frm, but in this report, the Duplin Frm is only partially correlated with the upper part of the Yorktown Frm. Campbell et al (2011) indicated the lower Goose Creek Limestone of SC, Unit 3 of the Yorktown Frm, the Tamiami Limestone and lower Jackson Bluff Frm of Florida are all correlated by a Leptopecten unit (Early Pliocene), but while the Yorktown Frm seems to span all these units, the Jackson Bluff in this report overlies the Tamiami Limestone and is age-equivalent to the upper Goose Creek, not the lower.	
		Morgarts Beach								
		Rushmere								

Table S2.2.2: Part 35. Southeastern Virginia

Region	Formation	Member	Unit	Age (Ma)	Supporting References	Notes	Other age details or opinions	Correlation	Other opinions on correlations	General regional notes
		Sunken Meadow		**4.8-4.6**	Cronin et al (1984); Ward and Huddlestun (1988); Krantz (1991), although he cited a range from 4.8-3.5 Ma for this member	The lowest initial transgressive deposit, the Sunken Meadow Member of the Yorktown Frm, contains a somewhat different molluscan assemblage from the rest of the Yorktown Frm and is separated from the other units by a depositional hiatus (Blackwelder 1981a).		Krantz (1991) indicated the Sunken Meadow Member is time equivalent with the Wabasso Beds and the lower Duplin Frm; the latter relationship is not supported here, but the Sunken Meadow Member is correlated with the Wabasso Beds.	Jones et al (1991), Willard et al (1993) and Williams et al (2009) indicated the Sunken Meadow Member is equivalent to Unit 11 of the lower Pinecrest, but this is not supported in this compilation; others (e.g., Scott 1995) indicated the Sunken Meadow Member is not correlated with any Tamiami sediments, at least not in S Florida.	

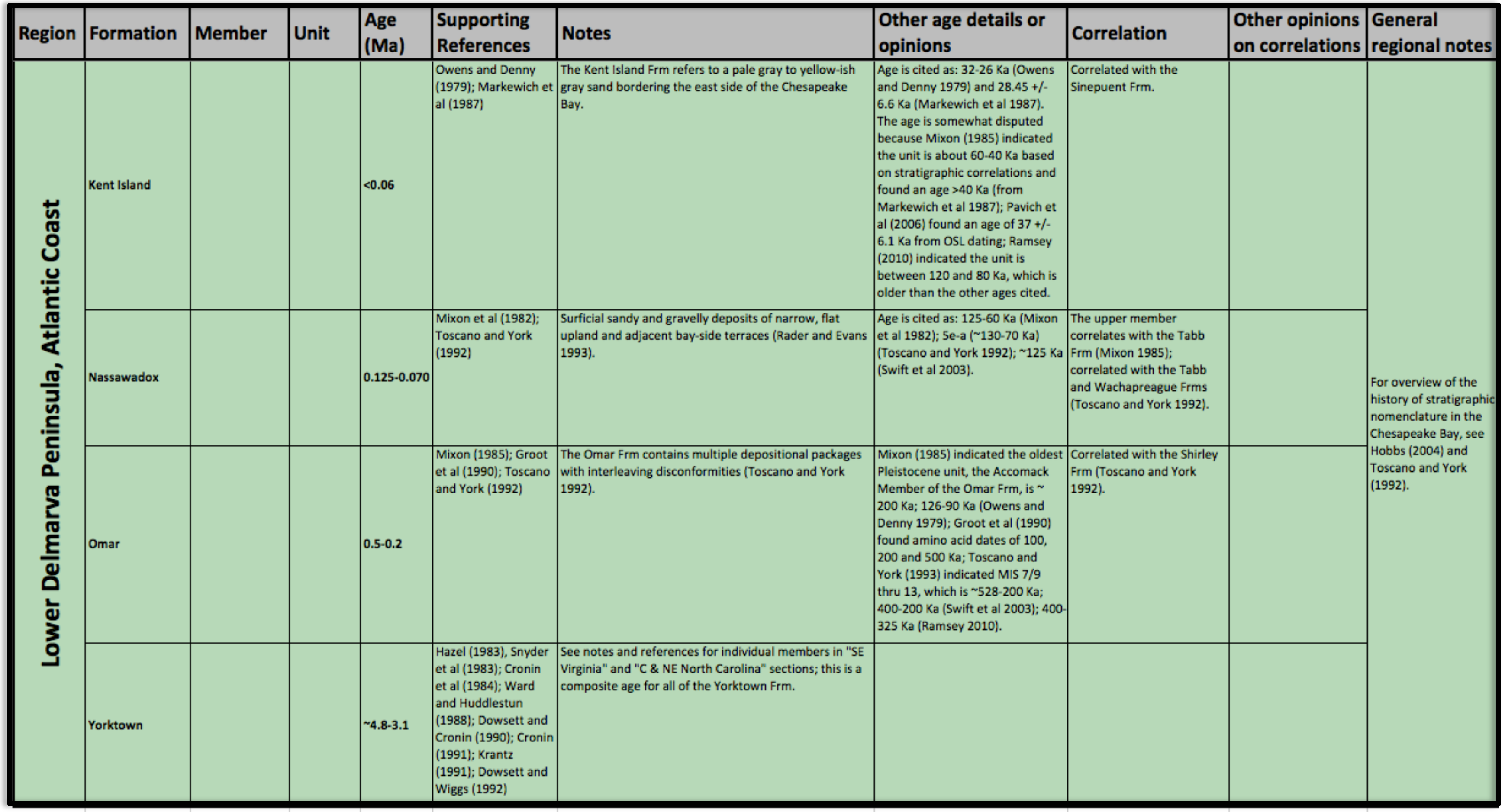
Table S2.2.2: Part 36. Lower Delmarva Peninsula, Chesapeake Bay Coast

Region	Formation	Member	Unit	Age (Ma)	Supporting References	Notes	Other age details or opinions	Correlation	Other opinions on correlations	General regional notes
marva Peninsula, Chesapeake Bay Coast	Wachapreague			0.06-0.02	Owens and Denny (1979); Shideler et al (1984); Finkelstein and Kearny (1988); Pavich et al (2006); Scott et al (2010)	The unit unconformably overlies the Yorktown Frm; in other places, it truncates and/or overlaps the Omar and Nassawadox Frms (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 128 Ka, and amino acid racemization dates of 82 Ka; according to Scott et al (2010), the 128 Ka is too old; Shideler et al (1984) obtained dates of 23,350 and 30,870, which according to Toscano and York (1992), suggested contamination; Finkelstein 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 as older in MIS-5 (specifically 5d-a), equivalent to ~115-84 Ka; Owens and Denny (1979) indicated dates of 30 +/- 1 Ka for the stratigraphic equivalent Kent Island Frm, and Pavich et al (2006) found dates of 37+/- 6.1 Ka from OSL dating for the Kent Island Frm; Scott et al (2010) found OSL ages of 46.9 +/- 6.9 and 38.9+/-5.5 Ka, and Swift et al (2003) placed the unit within MIS-3 (80-40 Ka).	Correlated with the upper member of the Sand Bridge Frm [now Powells Crossroads Frm] and potentially with the Sinepuxent Frm as discussed by Owens and Denny (1979) (Mixon 1985, Hobbs 2004); considered a stratigraphic equivalent to the Kent Island Frm (Scott et al 2010); correlated with the Tabb and Nassawadox Frms (Toscano and York 1992).		For an overview of the history of stratigraphic nomenclature in the Chesapeake Bay area, see Toscano and York (1992) and Hobbs (2004).
	Joynes Neck Sand			~0.07-0.06	Scott et al (2010)	The Joynes Neck Sand truncates and disconformably overlies the Accomack Member of the Omar Frm (Mixon 1985).	The age is uncertain (Hobbs 2004): Rader and Evans (1993) placed the unit as late Pleistocene; Toscano and York (1992) indicated the unit was deposited during isotope stage 5 d and e, which is ~130-105 Ka, while Scott et al (2010) indicated the unit was deposited after MIS-5 and before the middle of MIS-3.	The unit may be correlated with the upper lens of the Accomoack Member of the Omar Frm (Hobbs 2004).		

Table S2.2.2: Part 37. Lower Delmarva Peninsula, Chesapeake Bay Coast

Region	Formation	Member	Unit	Age (Ma)	Supporting References	Notes	Other age details or opinions	Correlation	Other opinions on correlations	General regional notes
Lower Del	Omar			0.5-0.2	Mixon (1985); Groot et al (1990); Toscano and York (1992)	The unit is composed of multiple depositional packages with disconformities in between (Toscano and York 1992).	Mixon (1985) indicated the oldest Pleistocene unit, the Accomack Member of the Omar Frm, is ~ 200 Ka; Owens and Denny (1979) indicated an age of 126-90 Ka; Groot et al (1990) found amino acid dates of 100, 200 and 500 Ka; Toscano and York (1993) indicated the unit placed within MIS 7/9 thru 13, which is ~528-200 Ka; Swift et al (2003) cited ages of 400-200 Ka; and Ramsey (2010) cited ages of 400-325 Ka.	Correlated with the Shirley Frm (Toscano and York 1992) [note that it is only partly correlated here].		
	Yorktown			~4.8-3.1	Hazel (1983); Snyder et al (1983); Cronin et al (1984); Ward and Huddlestun (1988); Dowsett and Cronin (1990); Cronin (1991); Krantz (1991); Dowsett and Wiggs (1992)	See notes and references for individual members in the "SE Virginia" and "C & NE North Carolina" sections; this is a composite age for all of the Yorktown Frm.				

Table S2.2.2: Part 38. Lower Delmarva Peninsula, Atlantic Coast



Region	Formation	Member	Unit	Age (Ma)	Supporting References	Notes	Other age details or opinions	Correlation	Other opinions on correlations	General regional notes
Lower Delmarva Peninsula, Atlantic Coast	Kent Island			<0.06	Owens and Denny (1979); Markewich et al (1987)	The Kent Island Frm refers to a pale gray to yellow-ish gray sand bordering the east side of the Chesapeake Bay.	Age is cited as: 32-26 Ka (Owens and Denny 1979) and 28.45 +/- 6.6 Ka (Markewich et al 1987). The age is somewhat disputed because Mixon (1985) indicated the unit is about 60-40 Ka based on stratigraphic correlations and found an age >40 Ka (from Markewich et al 1987); Pavich et al (2006) found an age of 37 +/- 6.1 Ka from OSL dating; Ramsey (2010) indicated the unit is between 120 and 80 Ka, which is older than the other ages cited.	Correlated with the Sinepuent Frm.		For overview of the history of stratigraphic nomenclature in the Chesapeake Bay, see Hobbs (2004) and Toscano and York (1992).
	Nassawadox			0.125-0.070	Mixon et al (1982); Toscano and York (1992)	Surficial sandy and gravelly deposits of narrow, flat upland and adjacent bay-side terraces (Rader and Evans 1993).	Age is cited as: 125-60 Ka (Mixon et al 1982); 5e-a (~130-70 Ka) (Toscano and York 1992); ~125 Ka (Swift et al 2003).	The upper member correlates with the Tabb Frm (Mixon 1985); correlated with the Tabb and Wachapreague Frms (Toscano and York 1992).		
	Omar			0.5-0.2	Mixon (1985); Groot et al (1990); Toscano and York (1992)	The Omar Frm contains multiple depositional packages with interleaving disconformities (Toscano and York 1992).	Mixon (1985) indicated the oldest Pleistocene unit, the Accomack Member of the Omar Frm, is ~ 200 Ka; 126-90 Ka (Owens and Denny 1979); Groot et al (1990) found amino acid dates of 100, 200 and 500 Ka; Toscano and York (1993) indicated MIS 7/9 thru 13, which is ~528-200 Ka; 400-200 Ka (Swift et al 2003); 400-325 Ka (Ramsey 2010).	Correlated with the Shirley Frm (Toscano and York 1992).		
	Yorktown			~4.8-3.1	Hazel (1983), Snyder et al (1983); Cronin et al (1984); Ward and Huddlestun (1988); Dowsett and Cronin (1990); Cronin (1991); Krantz (1991); Dowsett and Wiggs (1992)	See notes and references for individual members in "SE Virginia" and "C & NE North Carolina" sections; this is a composite age for all of the Yorktown Frm.				

References

Akers, H.W. (1972) Planktonic foraminifera and biostratigraphy of some Neogene formations, northern Florida and Atlantic Coastal Plain. *Tulane Studies in Geology and Paleontology*, **9**, 1–139.

Alber, M., Alexander, C., Blanton, J., Chalmers, A. & Gates, K. (2003) The Satilla River estuarine system: the current state of knowledge. *A report submitted to The Georgia Sea Grant College Program and The South Carolina Sea Grant Consortium*, 55 pp.

Allmon, W.D., Emslie, S.D., Jones, D.S. & Morgan, G.S. (1996a) Late Neogene oceanographic change along Florida's west coast: evidence and mechanisms. *The Journal of Geology*, **104**, 143–162.

Allmon, W.D., Rosenberg, G., Portell, R.W. & Schindler, K.S. (1996b) Diversity of Pliocene-Recent mollusks in the Western Atlantic: extinction, origination, and environmental change. *Evolution and Environment in Tropical America* (ed. by J.B.C. Jackson, A.G. Coates and A.F. Budd). University of Chicago Press, Chicago.

Andrus, R.D., Hayati, H. & Mohanan, N.P. (2009) Correcting liquefaction resistance for aged sands using measured to estimated velocity ratio. *Journal of Geotechnical and Geoenvironmental Engineering* **135**, 735–744.

Badyrka, K.A., Kelley, P.H., Harris, W. & Dietl, G.P. (2010) Paleontologic and strontium isotopic age analysis of the Waccamaw Formation, Waccamaw River and Intracoastal Waterway, Horry County, South Carolina. *Geological Society of America Abstracts with Programs*, **42**, 187.

Banks, K.W., Riegl, B.M., Shinn, E.A., Piller, W.E. & Dodge, R.E. (2007) Geomorphology of the southeast Florida continental reef tract (Miami-Dade, Broward, and Palm Beach Counties, USA). *Coral Reefs* **26**, 617–633.

Bender, M.L. (1972) Notes on the fauna of the Chipola Formation. XI. Helium-uranium dating studies of corals. *Tulane Studies in Geology and Paleontology*, **10**, 51–52.

Bender, M.L. (1973) Helium-uranium dating of corals. *Geochimica et Cosmochimia Acta* **37**, 1229–1247.

Bick, K.F. & Coch, N.K. (1969) Geology of the Williamsburg, Hog Island, and Bacons Castle Quadrangles, Virginia. Department of Conservation and Economic Development, Commonwealth of Virginia.

Blackwelder, B.W. (1981a) Late Cenozoic marine deposition in the United States Atlantic Coastal Plain related to tectonism and global climate. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **34**, 87–114.

Blackwelder, B.W. (1981b) Stratigraphy of upper Pliocene and lower Pleistocene marine and estuarine deposits of northeastern North Carolina and southeastern Virginia. *Contributions to Stratigraphy: US Geological Survey Bulletin*, **102-B**, B1–B16.

Blackwelder, B.W. & Ward, L.W. (1979) Stratigraphic revision of the Pliocene deposits of North Carolina and South Carolina. *South Carolina Division of Geology, Geological Notes*, **23**, 33–43.

Bowen, D.Q. (2009) Sea level ~400 000 years ago (MIS 11): analogue for present and future sea-level? *Climate of the Past*, **6**, 19–29.

Broecker, W.S. & Thurber, D.L. (1965) Uranium-series dating of corals and oolites from Bahaman and Florida Key limestones. *Science*, **149**, 58–60.

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*

Florida-a reappraisal, with additional notes on Sunoco-Felda and Sunniland oil fields. Guidebook, Second Annual Field Trip, Feb 1968. (ed. by R.D. Perkins), pp. 3–42. Miami Geological Society, Miami.

Brooks, H.K. (1974) Lake Okeechobe. *Environments of south Florida: present and past* (ed. by P.J. Gleason), pp. 256–286. Miami Geological Society Memoir, Miami.

Burdette, K.E. (2010) *Pleistocene stratigraphy and optical dating of surficial sands in Florida's Coastal Plain and Central Highlands: implications for sea-level and shoreline ages*. PhD (McMaster University, Ann Arbor).

Burdette, K.E., Rink, W.J., Means, G.H. & Portell, R.W. (2009) Optical dating of the Anastasia Formation, Northeastern Florida, USA. *Southeastern Geology*, **46**, 173–185.

Bybell, L.M. (1990) Calcareous nannofossils from Pliocene and Pleistocene deposits in South Carolina. *Studies related to the Charleston, South Carolina, Earthquake of 1886 - Neogene and Quaternary lithostratigraphy and biostratigraphy*, U.S. Geological Survey Professional Paper, **1367**, B1–B9.

Campbell, L., Campbell, M.R. & Campbell, S.C. (2011) Biodiversity and stratigraphy of the basal Yorktown Formation at Kings Mill, James City County, Virginia, USA. *Geological Society of America Abstracts with Programs*, **43**, 85.

Campbell, L.D. (1993) Age and correlation of the Pliocene Chowan River Formation of Virginia and northeastern North Carolina. *Geological Society of America Abstracts with Programs*, **25**, 4.

Campbell, M.R. (1992) Molluscan biostratigraphy of the Pliocene beds of eastern South Carolina and southeastern North Carolina. *Geologic field guides to North Carolina and vicinity: University of North Carolina-Chapel Hill, Department of Geology Geologic Guidebook, Joint Annual Meeting of Geological Society of America* (ed. by J.M. Dennison and K.G. Stewart), pp. 145–151. Southeastern section, Society of Economic Paleontologists and Mineralogists, Eastern Section, and Paleontological Society, Southeastern Section, Winston-Salem.

Campbell, M.R. & Campbell, L.D. (1995) Preliminary biostratigraphy and molluscan fauna of the Goose Creek Limestone of eastern South Carolina. *Tulane Studies in Geology and Paleontology*, **27**, 53–100.

Carter, J.G., Rossbach, T.J., Mateo, Z.P. & Badiali, M.J. (2003) Summary of lithostratigraphy and biostratigraphy for the Coastal Plain of the Southeastern United States. *Biostratigraphy Newsletter* 4.

Clark, M.W. & Wright, R.C. (1979) Subsurface Neogene stratigraphy of Bay County, Florida. *AAPG Bulletin*, **63**, 1599.

Clark, W.B. & Miller, B.L. (1906) Geology of the Virginia Coastal Plain. In: The Clay Deposits of the Virginia Coastal Plain. *Virginia Geological Survey Bulletin*, **2**, 11–24.

Clark, W.B. & Miller, B.L. (1912) The physiography and geology of the coastal plain province of Virginia. *Virginia Geological Survey Bulletin*, **4**, 222 pp.

Coch, N.K. (1960) Post-Miocene stratigraphy and morphology, inner coastal plain, southeastern Virginia. In: *Geography Branch Technical Report*, 97 pp, Office of Naval Research.

Coch, N.K. (1968) Geology of the Benns Church, Smithfield, Windsor, and Chuckatuck quadrangles, Virginia. *Virginia Division of Mineral Resources Report of Investigations*, **17**, 1039.

Colquohoun, D.J. (1986) The geology and physiography of the Orangeburg Scarp. *Geological Society of America Centennial Field Guide, Southeastern Section*, **6**, 321–322.

Cooke, C.W. (1936) Geology of the coastal plain of South Carolina. *U.S. Geological Survey Bulletin*, **867**, 196 pp.

Cooke, C.W. (1943) Geology of the Coastal Plain of Georgia. *U.S. Geological Survey Bulletin*, **941**, 100–113.

Cooke, C.W. & Mossom, D. (1929) Geology of Florida. In: *Florida Geological Survey Annual Report*, pp. 29–277

Corrado, J.C., Weems, R.E., Hare, P.E. & Bambach, R.K. (1986) Capabilities and limitations of applied aminostratigraphy, as illustrated by analyses of *Mulinia lateralis* from the late Cenozoic marine beds near Charleston, South Carolina. *South Carolina Geology*, **30**, 19–46.

Cronin, T.M. (1991) Pliocene shallow water paleoceanography of the North Atlantic Ocean based on marine ostracodes. *Quaternary Science*, **10**, 175–188.

Cronin, T.M. & Dowsett, J.H. (1996) Biotic and oceanographic response to the Pliocene closing of the Central American Isthmus. *Evolution and Environment in Tropical America* (ed. by J.B.C. Jackson, A.F. Budd and A.G. Coates), pp. 76–104. University of Chicago Press, Chicago.

Cronin, T.M., Szabo, B.J., Ager, T.A., Hazel, J.E. & Owens, J.P. (1981) Quaternary climates and sea levels of the U.S. Atlantic Coastal Plain. *Science*, **211**, 233–240.

Cronin, T.M., Bybell, L.M., Poore, R.Z., Blackwelder, B.W., Liddicoat, J.C. & E, H.J. (1984) Age and correlation of emerged Pliocene and Pleistocene deposits, U.S. Atlantic Coastal Plain. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **47**, 21–51.

Cunningham, K.J., Locker, S.D., Hine, A.C., Bukry, D. & Guertin, L.A. (2003) Interplay of Late Cenozoic siliciclastic supplyand carbonate response on the southeast Florida Platform. *Journal of Sedimentary Research*, **73**, 31–46.

Cunningham, K.J., McNeill, D.F., Guertin, L.A., Ciesielski, P.F., Scott, T.M. & de Verteuil, L. (1998) New Tertiary stratigraphy for the Florida Keys and southern peninsula of Florida. *GSA Bulletin*, **110**, 231–258.

Cunningham, K.J., Bukry, D., Sato, T., Barron, J.A., Guertin, L.A. & Reese, R.S. (2001) Sequence stratigraphy of a south Florida carbonate ramp and bounding siliciclastics (Late Miocene-Pliocene). *Geology and Hydrology of Lee County, Florida, Durward H. Boggess Memorial Symposium, Florida Geological Survey Special Publication*, **49**, 1–6.

Denison, R.E., Hetherington, E.A., Bishop, B.A., Dahl, D.A. & Koepnick, R.B. (1993) The use of strontium isotopes in stratigraphic studies: an example from North Carolina. *Southeastern Geology*, **33**, 53–69.

Doar, W.R.I. (2009) The Late Pliocene and Pleistocene marine stratigraphies of South Carolina and southeastern Virginia. *Geological Society of America Abstracts with Programs*, **41**, 53.

Dockal, J.A. (1992) Radiocarbon dating of late Pleistocene marine deposits, New Hanover County, North Carolina. *Geological Society of America Abstracts with Programs*, **24**, 12.

Dockal, J.A. (1995) Documentation and evaluation of radiocarbon dates from the "Cape Fear Coquina" (Late Pleistocene) of Snows Cut, New Hanover County, North Carolina. *Southeastern Geology*, **35**, 169–186.

Dockal, J.A. (1996) The coquinas of the Neuse Formation, New Hanover County, North Carolina. In Environmental Coastal Geology: Cape Lookout to Cape Fear, NC. *Carolina Geological Society Fieldtrip Guidebook, Nov. 8-10* (ed. by W.J. Cleary), pp. 11–21.

Donoghue, J.F. (1992) Late Quaternary coastal and inner shelf stratigraphy, Apalachicola Delta region, Florida. *Sedimentary Geology*, **80**, 293–304.

Dowsett, H.J. & Cronin, T.M. (1990) High eustatic sea level during the middle Pliocene: evidence from the southeastern U.S. Atlantic Coastal Plain. *Geology*, **18**, 35–438.

Dowsett, H.J. & Wiggs, L.B. (1992) Planktonic foraminiferal assemblage of the Yorktown Formation, Virginia, USA. *Micropaleontology*, **38**, 75–86.

Dowsett, H.J. & Willard, D. (1996) Southeast Atlantic marine and terrestrial response to middle Pliocene climate change. *Marine Micropaleontology*, **27**, 181–193.

DuBar, J.R. (1971) Neogene stratigraphy of the lower Coastal Plain of the Carolinas. *Atlantic coastal Plain Geological Association 12th Annual Field Conference Guidebook, Oct 23-24*, 128 pp.

DuBar, J.R. (1974) Summary of the Neogene stratigraphy of the late Neogene strata of the Caloosahatchee River area of southern Florida. *Post-Miocene Stratigraphy, Central and Southern Atlantic Coastal Plain* (ed. by R.Q. Oakes and J.R. Dubar), pp. 206–231. Utah State University Press, Logan.

DuBar, J.R. (1991) Florida Peninsula. *Quaternary nonglacial geology; conterminous United States: Geological Society of America, The Geology of North America, The Decade of North American Geology* (ed. by R.B. Morrison), pp. 595–604. Geological Society of America, Boulder.

DuBar, J.R. & Solliday, J.R. (1963) Stratigraphy of the Neogene deposits, lower Neuse Estuary, North Carolina. *Southeastern Geology*, **4**, 213–233.

Emslie, S.D. & Morgan, G.S. (1994) A catastrophic death assemblage and paleoclimatic implications of Pliocene seabirds of Florida. *Science*, **264**, 684–685.

Fallaw, W. & Wheeler, W.H. (1969) Marine fossiliferous Pleistocene deposits in southeastern North Carolina. *Southeastern Geology*, **10**, 35–54.

Finkelstein, K.L. & Kearny, M.S. (1988) Late Pleistocene barrier island sequence along the southern Delmarva Peninsula: implications for middle Wisconsin sea levels. *Geology*, **16**, 41–45.

Finkle, C.W., Becerra, J.E., Achatz, V. & Andrews, J.L. (2008) Geomorphological mapping along the upper southeast Florida Atlantic Continental Platform; 1: Mapping units, symbolization and geographic information system presentation of interpreted seafloor topography. *Journal of Coastal Research* **24**, 1388–1417.

Fountain, K.B. (2010) *Origin and stratigraphic significance of kaolinitic sediments from the Cypresshead Formation: a sedimentological, mineralogical and geochemical investigation*. PhD (University of Florida, Gainesville).

Fruijtier, C., Elliott, T. & Schlagr, W. (2000) Mass-spectrometric 234U-230Th ages from the Key Largo Formation, Florida Keys, United States: constraints on diagenetic age disturbance. *GSA Bulletin* **112**, 267–277.

Graybill, E.A., Harris, W.B., Kelley, P., Dietl, G. & Visaggi, C. (2009) Age of Duplin and Waccamaw Formations, Cape Fear River Basin, North Carolina. *Geological Society of America Abstracts with Programs*, **41**, 45.

Groot, J.J. (1991) Palynological evidence for late Miocene to early Pleistocene climate changes in the middle Atlantic Coastal Plain. *Quaternary Science Reviews*, **10**, 146–162.

Groot, J.J., Ramsey, K.W. & Wehmiller, J.F. (1990) Ages of the Bethany, Beaverdam, and Omar Formations of southern Delaware. *Delaware Geological Survey Report of Investigations*, **47**, 1–19.

Guertin, L.A. (1998) *A Late Cenozoic mixed carbonate/siliciclastic system, south Florida: lithostratigraphy, chronostratigraphy, and sea-level record*. PhD (University of Miami).

Guertin, L.A., Missimer, T.M. & McNeill, D.F. (2000) Hiatal duration of correlative sequence boundaries from Oligocene-Pliocene mixed carbonate/siliciclastic sediments of the south Florida Platform. *Sedimentary Geology*, **134**, 1–26.

Guertin, L.A., McNeill, D.F., Lidz, B.H. & Cunningham, K.J. (1999) Chronologic model and transgressive-regressive signatures in the Late Neogene siliciclastic foundation (Long Key Formation) of the Florida Keys. *Journal of Sedimentary Research*, **69**, 653–666.

Hails, J.R. & Hoyte, J.H. (1969) The significance and limitations of statistical parameters for distinguishing ancient and modern sedimentary environments of the lower Georgia Coastal Plain. *Journal of Sedimentary Research*, **39**, 559–580.

Harmon, R.S., Ku, T.L., Matthews, R.K. & Smart, P.L. (1979) Limits of U-series analysis: Phase 1 of the uranium-series intercomparison project. *Geology*, **7**, 405–409.

Harris, M.S. (2000) *Influence of a complex geologic framework on Quaternary coastal evolution: an example from Charleston, South Carolina*. PhD (University of Delaware).

Harris, W.B. (1996) An overview of the marine Tertiary and Quaternary deposits between Cape Fear and Cape Lookout, North Carolina. *Environmental Coastal Geology: Cape Lookout to Cape Fear, NC. Carolina Geological Society Fieldtrip Guidebook for 1996 Annual Meeting* (ed. by W.J. Cleary), pp. 1–8.

Hazel, J.E. (1983) Age and correlation of the Yorktown (Pliocene) and Croatan (Pliocene and Pleistocene) formations at the Lee Creek Mine. *Smithsonian Contributions to Paleobiology*, **53**, 81–199.

Henderson, G.M. & Slowey, N.C. (2000) Evidence from U-Th dating against Northern Hemisphere forcing of the penultimate deglaciation. *Nature*, **404**, 61–66.

Hickey, T.D., Hine, A.C., Shinn, E.A., Kruse, S.E. & Poore, R.Z. (2010) Pleistocene carbonate stratigraphy of South Florida: evidence for high-frequency sea-level cyclicity. *Journal of Coastal Research*, **26**, 605–614.

Hobbs, C.H.I. (2004) Geological history of Chesapeake Bay, USA. *Quaternary Science Reviews*, **23**, 641–661.

Hollin, J.T. & Hearty, P.J. (1990) South Carolina interglacial sites and Stage 5 sea levels. *Quaternary Research*, **33**, 1–17.

Hoyte, J.H. & Hails, J.R. (1974) Pleistocene stratigraphy of south-eastern Georgia. *Post-Miocene stratigraphy, central and southern Atlantic coastal plain* (ed. by R.Q. Oaks and J.R. Dubar), pp. 191–205. Utah State University Press, Logan.

Huddlestun, P.F. (1988) A revision of the lithostratigraphic units of the coastal plain of Georgia, the Miocene through Holocene. *Georgia Geological Survey Bulletin*, **104**, 162 pp.

Hulbert, R.C.J. & Morgan, G.S. (1989) Stratigraphy, paleoecology, and vertebrate fauna of the Leisey Shell Pit local fauna, early Pleistocene (Irvingtonian) of southwestern Florida. *Papers in Florida Paleontology*, **2**, 1–19.

Hunter, M.E. (1968) Molluscan guide fossils in late Miocene sediments of southern Florida. *Transactions of the Gulf Coast Association of Geological Societies*, **18**, 439–450.

Johnson, G.H. (1976) Geology of the Mulberry Island, Newport, News North, and Hampton quadrangles, Virginia. *Virginia Division of Mineral Resources Report of Investigations*, **41**, 72 pp.

Johnson, G.H. & Peebles, P.C. (1986) Quaternary geologic map of the Hatteras 4°x6° quadrangle, United States. *Quaternary Atlas of the United States, U.S. Geologic Survey Miscellaneous Map 1-1420 (NJ-18)* (ed. by G.M. Richmond, D.S. Fullerton and D.L. Weikle).

Johnson, G.H. & Berquist, C.R.J. (1989) Geology and mineral resources of the Brandon and Norge quadrangles, Virginia. *Virginia Division of Mineral Resources Publication*, **87**, 28 pp.

Johnson, G.H. & Hobbs, C.H.I. (1990) Pliocene and Pleistocene depositional environments on the York–James Peninsula, Virginia: a field guidebook for Field Trip 2, Geologic History of the Lower Chesapeake Bay, American Society of Limnology and Oceanography, 1990 Annual Meeting, College of William & Mary. *Virginia Institute of Marine Science*, 39 pp.

Jones, D.S., MacFadden, B.J., Webb, S.D., Mueller, P.A., Hodell, D.A. & Cronin, T.M. (1991) Integrated geochronology of a classic Pliocene fossil site in Florida: linking marine and terrestrial biochronologies. *The Journal of Geology*, **99**, 637–648.

Karrow, P.F., Morgan, G.S., Portell, R.W., Simmon, E. & Auffenberg, K. (1996) Middle Pleistocene (early Rancholabrean) vertebrates and associated marine and non-marine invertebrates from Oldsmar, Pinellas County, Florida. *Palaeoecology and palaeoenvironments of Late Cenozoic mammals: tributes to the career of C.S. (Rufus) Churcher* (ed. by K.M. Stewart and K.L. Seymour), pp. 97–133. University of Toronto Press, Toronto.

Kittle, B.A. & Portell, R.W. (2010) Mollusca: Fort Thompson Formation (Late Pleistocene). *Florida Fossil Invertebrates*, **12**, 32 pp.

Knorr, P.O. & Harries, P.J. (2007) High order, Pleistocene sea-level fluctuations in southwest Florida. *Geological Society of America Meeting Southeastern Section*, **39**, 23.

Knowles, T., Taylor, P.D., Williams, M., Haywood, A.M. & Okamura, B. (2009) Pliocene seasonality across the North Atlantic from cheilostome bryozoans. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **227**, 226–235.

Kolbe, S.E., Lockwood, R. & Hunt, G. (2011) Does morphological variation buffer against extinction? A test using veneroid bivalves from the Plio-Pleistocene of Florida. *Paleobiology*, **37**, 355–368.

Krantz, D.E. (1991) A chronology of Pliocene sea-level fluctuations: the U.S. Middle Atlantic Coastal Plain record. *Quaternary Science Reviews*, **10**, 163–174.

Liddicoat, J.C. (2012) Magnetostratigraphy of Atlantic Coastal Plain and Continental Shelf sediments for portions of the geologic record since the Late Cretaceous. *Geological Society of America Abstracts with Programs*, **44**, 195.

Locker, S.D. & Doyle, L.J. (1992) Neogene to Recent stratigraphy and depositional regimes of the northwest Florida inner continental shelf. *Marine Geology*, **104**, 123–138.

Lyons, W.G. (1991) Post-Miocene species of *Latirus* Montfort, 1810 (Mollusca: Fasiolariidae) of southern Florida, with a review of regional marine biostratigraphy. *Bulletin of the Florida Museum of Natural History*, **35**, 131–208.

Mabry, M.Y. & Thayer, P.A. (2001) Sedimentology of Pleistocene Waccamaw and Canepatch Formations, Todd Pit, Brunswick County, North Carolina. *Geological Society of America Meeting Southeast Abstracts with Programs*, **19**, 29.

Malde, H.E. (1959) Geology of the Charleston phosphate area, South Carolina. *Geological Survey Bulletin*, **1079**, 105 pp.

Markewich, H.W., Hacke, C.M. & Huddlestun, P.F. (1992) Emergent Pliocene and Pleistocene sediments of southeastern Georgia: an anomalous, fossil-poor, clastic section. *Quaternary Coasts of the United States Marine and Lacustrine System SEPM Special Publication*, **48**, 173–189.

Markewich, H.W., Pavich, M.J., Mausbach, M.J., Hall, R.L., Johnson, R.G. & Hearn, P.P. (1987) Age relations between soils and geology in the coastal plain of Maryland and Virginia, Chapter A. *U.S. Geological Survey Bulletin*, **1589-A**, 34 pp.

Markewich, H.W., Pavich, M.J., Schultz, A.P., Mahan, S.A., Aleman-Gonzalez, W.B. & Bierman, P.R. (2013) Geochronologic evidence for a possible MIS-11 emergent barrier/beach-ridge in southeastern Georgia, USA. *Quaternary Science Reviews*, **60**, 49–75.

Martini, E. (1971) Standard Tertiary and Quaternary calcareous nannoplankton zonation. *Proceedings of the Second Planktonic Conference, Roma* (ed by A. Farinacci), pp. 739–777. Rome, Edizioni Tecnoscienza.

Mateo, Z.R. (2005) *Fluvial response to climate and sea-level change: Prairie Complex, Lower Mississippi Valley*. PhD (University of Chicago).

Matson, G.C. & Clapp, F.G. (1909) A preliminary report on the geology of Florida with special reference to stratigraphy. *Florida State Geological Survey 17th Annual Report*, 169–268.

McCartan, L., Weems, R.E. & Lemon, E.M.J. (1980) The Wando Formation (Upper Pleistocene) in the Charleston, South Carolina, area. *Geological Survey Bulletin*, **1502-A**, A110–A116.

McCartan, L., Lemon, E.M.J. & Weems, R.E. (1984) Geologic map of the area between Charleston and Orangeburg, South Carolina. *U.S. Geological Survey Miscellaneous Investigations Series, Map 1-1472, scale 1:250,000.*

McCartan, L., Weems, R.E. & Lemon, E.M.J. (1990) Quaternary stratigraphy in the vicinity of Charleston, South Carolina, and its relation to local seismicity and regional tectonism. *Studies related to the Charleston, South Carolina, Earthquake of 1886 – Neogene and Quaternary Lithostratigraphy and Biostratigraphy*, U.S. Geological Survey Professional Paper, **1367-A**, A1–A39.

McCartan, L., Owens, J.P., Blackwelder, B.W., Szabo, B.J., Belknap, D.F., Kriausakul, N., Mitterer, M. & Wehmiller, J.F. (1982) Comparison of amino acid racemization geochronometry with lithostratigraphy, biostratigraphy, Uranium-Series Coral Dating, and magnetostratigraphy in the Atlantic Coastal Plain of the Southeastern United States. *Quaternary Research*, **18**, 337–359.

McCartan, L., Weedman, S.D., Wingard, G.L., Edwards, L.E., Sugerman, P.J., Feigenson, M.D., Buursink, M.L. & Libarkin, J.C. (1995) Age and diagenesis of the Upper Floridan Aquifer and the intermediate aquifer system in southwestern Florida. *USGS Bulletin*, **2122,** 26 pp.

McGregor, D.A., Harris, W.B., Dietl, G.P. & Kelley, P.H. (2011) Strontium isotopic dating of the Waccamaw Formation at ACME, NC, and the Duplin Formation at Tar Heel, NC: a Plio-Pleistocene research progress report. *Geological Society of America Abstracts with Programs*, **43**, 4.

McNeil, D.F. (1985) Coastal geology and the occurrence of beach-rock: Central Florida Atlantic Coast, Part 1. *Geological Society of America Annual Meeting Guidebook, Field Trip 4*, 27 pp.

Means, G.H. (2009) *A marine-influenced siliciclastic unit (Citronelle Formation) in Western Panhandle Florida*. MSc (Florida State University).

Meeder, J.F. (1987) *The paleoecology, petrology, and depositional model of the Pliocene Tamiami Formation, southwest Florida [with special reference to corals and reef development*. PhD (University of Miami).

Miller, W.I. (1985) The Flanner Beach Formation (middle Pleistocene) in eastern North Carolina. *Tulane Studies in Geology and Paleontology*, **18**, 93–122.

Milligan, D.A., O'Brian, K.P., Wilcox, C. & Hardaway, C.S.J. (2010) Shoreline evolution: York County, Virginia York River, Chesapeake Bay and Poquoson River Shorelines. In: *Data Report Shoreline Studies Program*, Virginia Institute of Marine Science, College of Wlliam and Mary, 19 pp.

Mirecki, J.E., Wehmiller, J.F. & Skinner, A.F. (1995) Geochronology of Quaternary coastal plain deposits, southeastern Virginia, USA. *Journal of Coastal Research*, **11**, 1135–1144.

Missimer, T.M. (1984) The geology of South Florida. *Environments of South Florida. Present and Past* (ed. by P. Gleason), pp. 385–404. Miami Geological Society, Coral Gables.

Missimer, T.M. (1990) Stratigraphic correlation of sediment facies within the Tamiami Formation of southwest Florida. *Plio-Pleistocene stratigraphy and paleontology of South Florida: Southeastern Geological Society Field Trip Guidebook, 1990 Field Excursion, Dec 7-8* (ed. by W.D. Allmon and T.M. Scott), 12 pp.

Missimer, T.M. (1992) Stratigraphic relationships of sediment facies within the Tamiami Formation of southwest Florida: proposed intraformational correlations. *Florida Geological Survey Special Publication*, **36**, 63–73.

Missimer, T.M. (1993) Pliocene stratigraphy of southern Florida: unresolved issues of facies correlation in time. *Florida Geological Society Special Publication*, **37**, 33–42.

Missimer, T.M. (1997) *Late Oligocene to Pliocene evolution of the central portion of the South Florida Platform: mixing of siliciclastic and carbonate sediments*. PhD (University of Miami).

Missimer, T.M. (1999) Sequence stratigraphy of the Late Miocene-Early Pliocene Peace River Formation, southwestern Florida. *Gulf Coast Association of Geological Societies Transactions*, **49**, 358–368.

Missimer, T.M. (2000) Anatomy of a nearshore mixed siliciclastic-carbonate deposit, the Plio-Pleistocene of southern Broward County, Florida. *Gulf Coast Association of Geological Societies Transactions*, **50**, 11–128.

Missimer, T.M. (2001a) Late Neogene geology of northwestern Lee County, Florida. *Geology and Hydrology of Lee County, Florida: Durward H. Boggess Memorial Symposium*, pp. 21–34, Florida Geological Survey Special Publication.

Missimer, T.M. (2001b) Late Paleogene and Neogene chronostratigraphy of Lee County, Florida. *Geology and hydrology of Lee County, Florida (Durward H. Boggess Memorial Symposium)* (ed. by T.M. Missimer and T.M. Scott), pp. 57–90, Florida Geological Survey Special Publication.

Missimer, T.M. & Wise, S.W. (2012) Ages of Plio-Pleistocene formations in South Florida based on the revised IUGS boundary age of the Lower Pleistocene. *Geological Society of America Abstracts with Programs*, **44**, 607.

Missimer, T.M., Maliva, R.G., Walker, C.W. & Owosina, E. (2000) Anatomy of a nearshore mixed siliciclastic-carbonate deposit, the Plio-Pleistocene of southern Broward County, Florida. *Gulf Coast Association of Geological Societies Transactions*, **L**, 11–128.

Mitterer, R.M. (1974) Pleistocene stratigraphy in southern Florida based on amino acid diagensis in fossil Mercenaria. *Geology*, **2**, 425–428.

Mitterer, R.M. (1975) Ages and diagenetic temperatures of Pleistocene deposits of Florida based on isoleucine epimerization in Mercenaria. *Earth and Planetary Science Letters*, **28**, 275–282.

Mixon, R.B. (1985) Stratigraphic and geomorphic framework of Upper Cenozoic deposits in the southern Delmarva Peninsula, Virginia and Maryland. *U.S. Geological Survey Professional Paper*, **1067-G**, 60 pp.

Mixon, R.B. & Pilkey, O.H. (1976) Reconnaissance geology of the submerged and emerged Coastal Plain province, Cape Lookout area, North Carolina. *U.S. Geological Survey Professional Paper*, **859**, 1–45.

Mixon, R.B., Szabo, B.J. & Owens, J.P. (1982) Uranium-series dating of the mollusks and corals, and age of Pleistocene deposits, Chesapeake Bay area, Virginia and Maryland. *U.S. Geological Survey Professional Paper*, **1067-E**, 18 pp.

Mixon, R.B., Berquist, C.R.J., Newell, W.L., Johnson, G.H., Powars, D.S., Schindler, J.S. & Rader, E.K. (1989) Geologic map and generalized cross sections of the coastal plain and adjacent parts of the Piedmont, Virginia. U.S. *Geological Survey Miscellaneous Investigations Series Map, I-2033, 2 sheets, scale 1:250,000.*

Moore, W.E. (1956) Pleistocene terraces south of the James River, Virginia. *Virginia Academy of Science Geology Section Guidebook, May 1956*, 16 pp.

Muhs, D.R., Wehmiller, J.F., Simmons, K.R. & York, L.L. (2003) Quaternary sea-level history of the United States. *Development in Quaternary Science*, **1**, 147–183.

Muhs, D.R., Szabo, B.J., McArtan, L., Maat, P.B., Bush, C.A. & Halley, R.B. (1992) Uranium-series age estimates of corals from Quaternary marine sediments of southern Florida. *Plio-Pleistocene stratigraphy and paleontology of southern Florida: Florida Geological Survey Special Publication* (ed. by T.M. Scott and W.D. Allmon), pp. 41–49.

Multer, H.G., Gischler, E., Lundberg, J., Simmons, K.R. & Shinn, E.A. (2002) Key Largo Limestone revisited: Pleistocene shelf-edge facies, Florida Keys, USA. *Facies*, **46**, 229–272.

Murphy, J.M. (1973) *Holocene diagenesis of the Anastasia Formation*. Msc (Duke University).

Neal, A., Grasmueck, M., McNeill, D.F., Viggiano, D.A. & Eberli, G.P. (2008) Full-resolution 3D radar stratigraphy of complex oolitic sedimentary architecture: Miami Limestone, Florida, USA. *Journal of Sedimentary Research*, **78**, 638–653.

Oaks, R.Q. & Coch, N.K. (1963) Pleistocene sea levels, southeastern Virginia. *Science*, **140**, 979–983.

Oaks, R.Q. & Coch, N.K. (1973) Post-Miocene stratigraphy and morphology, southeastern Virginia. In: *Commonwealth of Virginia, Division of Mineral Resources*, 135 pp.

Osmond, J.K., Carpenter, J.R. & Windom, H.L. (1965) Th230/U234 age of Pleistocene corals and oolites of Florida. *Journal of Geophysical Research*, **70**, 1843–1847.

Osmond, J.K., May, J.P. & Tanner, W.P. (1970) Age of the Cape Kennedy Barrier and lagoon complex. *Journal of Geophysical Research*, **75**, 468–479.

Otvos, E.G. (1988) Pliocene age of coastal units, northeastern Gulf of Mexico. *Transactions of the Gulf Coast Association of Geological Societies*, **38**, 485–494.

Otvos, E.G. (1992) Quaternary evolution of the Apalachicola Coast, northeastern Gulf of Mexico. *Quaternary Coasts of the United States Marine and Lacustrine Systems SEPM Special Publication*, **48**, 221–232.

Otvos, E.G. (1995) Multiple Pliocene-Quaternary marine highstands, northeast Gulf Coastal Plain--fallacies and facts. *Journal of Coastal Research*, **11**, 984–1002.

Otvos, E.G. (1998) Citronelle Formation, Northeastern Gulf Coastal Plain: Pliocene stratigraphic framework and age issues. *Gulf Coast Association of Geological Societies Transactions*, **48**, 321–334.

Otvos, E.G. (2004) Lithofacies and depositional environments of the Pliocene Citronelle Formation, Gulf of Mexico Coastal Plain. *Southeastern Geology*, **43**, 1–20.

Otvos, E.G. (2005) Numerical chronology of Pleistocene coastal plain and valley development; extensive aggradation during glacial low sea-levels. *Quaternary International*, **135**, 91–113.

Otvos, E.G. (2009) Pleistocene Gulf Coastal Plain: Regional stratigraphic and geomorphic contrasts. Intensive erosion related to sea-level decline and hinterland uplift. *Gulf Coast Association of Geological Societies Transactions*, **59**, 585–600.

Otvos, E.G. (2013) Discussion: "Geological investigation and optical dating of Quaternary siliciclastic sediments near Apalachicola, North-west Florida, USA" by Burdette et al. (2012). *Sedimentology*, **59**, 1836–1849.

Owens, J.P. (1989) Geologic map of the Cape Fear region, Florence 10 X 20 Quadrangle and northern half of the Georgetown 10 x 20 Quadrangle, North Carolina and South Carolina. *U.S. Geological Survey, Miscellaneous Investigations Map 1-1948-A*.

Owens, J.P. & Denny, C.S. (1979) Upper Cenozoic deposits of the Central Delmarva Peninsula, Maryland and Delaware. *U.S. Geological Survey Professional Paper 1067-A*, 28 pp.

Parker, G.G. & Cooke, C.W. (1944) Late Cenozoic geology of southern Florida, with a discussion of the groundwater. *Florida Geological Survey Bulletin*, **27**, 119 pp.

Pavich, M.J., Markewich, H.W. & Brook, G.A. (2006) Significance of Kent Island Formation to Geomorphic History of the mid-Atlantic Region. *Geological Society of America Abstracts with Programs*, **38**, 226.

Pazzaglia, F.J. (1993) Stratigraphy, petrography, and correlation of late Cenozoic middle Atlantic Coastal Plain deposits: implications for late-stage passive-margin geologic evolution. *Geological Society of America Bulletin*, **105**, 1617√1634.

Peebles, P.C., Johnson, G.H. & Berquist, C.R. (1984) The Middle and Late Pleistocene stratigraphy of the outer coastal plain, southeastern Virginia. *Virginia Minerals*, **30**, 13–22.

Petuch, E.J. (1982) Notes on the molluscan paleoecology of the Pinecrest Beds at Sarasota, Florida with the description of *Pyruella*, a stratigraphically important new genus (Gastropoda: Melongenidae). *Proceedings of the Academy of Natural Sciences of Philadelphia*, **134**, 12–30.

Petuch, E.J. & Roberts, C.E. (2007) *The Geology of the Everglades and Adjacent Areas*. CRC Press, Boca Raton, 168 pp.

Petuch, E.J. & Drolshagen, M. (2010) *Molluscan Paleontology of the Chesapeake Miocene*. CRC Press, Boca Rotan, 240 pp.

Phillips, J.D. (1995) Biogeography and landscape evolution: the problem of scale. *Geomorphology*, **13**, 337–347.

Portell, R.W., Turner, R.L. & Beerensson, J.L. (2003) Occurrence of the Atlantic ghost crab *Ocypode quadrata* from the Upper Pleistocene to Holocene Anastasia Formation of Florida. *Journal of Crustacean Biology*, **23**, 712–722.

Portell, R.W., Means, G.H. & Hulbert, R.C.J. (2012) SMR Aggregates, Inc. Sarasota, Florida. *Southeastern Geological Society Field Trip Guidebook*, **56**, 26 pp.

Prosser, J.F. (1993) *Apparent uranium-series dates for mollusks from Snow's Cut, North Carolina: implications for Late Pleistocene chronology, sea-level, and tectonics along the Coastal Plain of Southeastern North Carolina*. PhD (University of North Carolina at Chapel Hill, Chapel Hill).

Puri, H.S. & Vanstrum, V.V. (1969) Geologic history of the Miocene and younger sediments in south Florida. *Late Cenozoic stratigraphy of southwestern Florida* (ed. by J.R. Dubar and S.S. Dubar), pp. 70–86. Gulf Coast Association of Geological Societies, Society of

Economic Mineralogists and Paleontologists, Miami Beach, Guidebook Field Trip, Miami.

Rader, E.K. & Evans, N.H. (1993) Geologic map of Virginia; expanded explanation. In: *Virginia Division of Mineral Resources*, 80 pp.

Ramsey, K.W. (1988) *Stratigraphy and sedimentology of a late Pliocene intertidal to fluvial transgressive deposit: Bacons Castle Formation, Upper York-James Peninsula, Virginia*. PhD (University of Delaware).

Ramsey, K.W. (1992) Coastal response to Late Pliocene climate change: Middle Atlantic Coastal Plain, Virginia and Delaware. *Quaternary Coasts of the United States: Marine and Lacustrine Systems, SEPM Special Publication*, **48**, 121–127.

Ramsey, K.W. (2010) Stratigraphy, correlation, and depositional environments of the Middle to Late Pleistocene Interglacial deposits of southern Delaware. *Report of Investigations State of Delaware*, **76**, 50 pp.

Richards, H.G. (1969) A Review of Recent Studies on the Marine Pleistocene of the Atlantic Coastal Plain--New Jersey to Georgia. *Gulf Coast Association of Geological Societies Transactions*, **19**, 601–609.

Rupert, F.R. (1990) Geology of Gadson County, Florida. *Florida Geological Survey Bulletin*, **62**, 61 pp.

Schmidt, W. & Clark, M.W. (1980) Geology of Bay County, Florida. *Florida Geological Survey Bulletin*, **57**, 96 pp.

Scott, T.M. (1988) The lithostratigraphy of the Hawthorn Group (Miocene) of Florida. *Florida Geological Survey Bulletin*, **59**, 1–148.

Scott, T.M. (1992) A geological overview of Florida. *Florida Geological Survey Open File Report*, **50**, 1–78.

Scott, T.M. (1995) Stratigraphy and paleontology of the Plio-Pleistocene shell beds: Leisey Shell Pit, Hillsborough Co., Quality Aggregates Mine, Sarasota Co. *Southeastern Geological Society Guidebook*, **35.**

Scott, T.M. (2011) Geology of the Florida Platform: Pre-Mesozoic to Recent. *Gulf of Mexico Origin, Waters, and Biota: Volume 3, Geology* (ed. by N.A. Buster and C.W. Holmes), pp. 17–31. Texas A&M Press, College Station.

Scott, T.W., Swift, D.J.P., Whittecar, G.R. & Brook, G.A. (2010) Glacioisostatic influences on Virginia's late Pleistocene coastal plain deposits. *Geomorphology*, **116**, 175–188.

Shen, Z., Törnqvist, T.E. & Mauz, B. (2008) Optical chronology of Late Pleistocene strata in the Lower Mississippi Valley: implications for fluvial response to relative sea-level change. *Geological Society of America and American Soil Abstract* **206**, 3.

Shideler, G.L., Ludwick, J.C., Oertel, G.F. & Finkelstein, K.L. (1984) Quaternary stratigraphic evolution of the southern Delmarva Peninsula coastal zone, Cape Charles, Virginia. *Geological Society of America Bulletin*, **95**, 489–502.

Shin, E.A. (2001) Coral reefs and shoreline dipsticks. *Geological perspectives of global climate change* (ed. by L.C. Gerhard, W.E. Harrison and B.M. Hanson), pp. 251–264. AAPG Studies in Geology.

Snyder, S.W. & Riggs, S.R. (1993) Geological overview of Lee Creek Mine and vicinity, North Carolina coastal plain. *The Compass, Sigma Gamma Epsilon Journal of Earth Sciences*, **70**, 13–35.

Snyder, S.W., Mauger, L.L. & Akers, W.H. (1983) Planktonic foraminifera and biostratigraphy of the Yorktown Formation, Lee Creek Mine. *Geology and Paleontology of the Lee*

Creek Mine, North Carolina (ed. by C.E. Rays), pp. 455–482. Smithsonian Contributions to Paleobiology.

Soller, D.R. & Mills, H.H. (1991) Surficial geology and geomorphology. *The Geology of the Carolinas* (ed. by J.W.J. Horton and V.A. Zullo), pp. 280–308. Carolina Geological Society 50th Anniversary Volume.

Spencer, R.S. & Campbell, L.D. (1987) The fauna and paleoecology of the late Pleistocene marine sediments of southeastern Virginia. *Bulletins of American Paleontology*, **92**, 124 pp.

Stringfield, V.T. & LaMoreaux, P.E. (1957) Age of Citronelle Formation in Gulf Coastal Plain. *Bulletin of the American Association of Petroleum Geologists*, **41**, 742–757.

Swift, D.J.P., Parsons, B.S., Foyle, A. & Oertel, G.F. (2003) Between beds and sequences: stratigraphic organization at intermediate scales in the Quaternary of the Virginia coast, USA. *Sedimentology*, **50**, 81–111.

Szabo, B.J. (1985) Uranium-series dating of fossil corals from marine sediments of southeastern United States Atlantic Coastal Plain. *Geological Society of America Bulletin*, **96**, 398–406.

Szabo, B.J. & Halley, R.B. (1988) 230Th/234U ages of aragonitic corals from the Key Largo limestone of south Florida. *American Quaternary Association, Program and Abstracts of the Tenth Biennial Meeting*, 154.

Toscano, M.A. (1992) Record of oxygen-isotope stage 5 on the Maryland inner shelf and Atlantic Coastal Plain -- Post-transgressive-highstand regime. *Quaternary Coasts of the United States: Marine and Lacustrine Systems, SEPM Special Publication* (ed. by C.H.I. Fletcher and J.F. Wehmiller), pp. 89–99.

Toscano, M.A. & York, L.L. (1992) Quaternary stratigraphy and sea-level history of the U.S. Middle Atlantic Coastal Plain. *Quaternary Science Reviews*, **11**, 301–328.

Toumey, M. (1848) Report on the geology of South Carolina. (Printed and published for the State, Columbia), 293 pp.

Wade, B.S., Pearson, P.N., Berggren, W.A. & Pälike, H. (2011) Review and revision of Cenozoic tropical planktonic foraminiferal biostratigraphy and calibration to the geomagnetic polarity and astronomical time scale. *Earth-Science Reviews*, **104**, 111–142.

Waldrup, J.S. & Wilson, D. (1990) Late Cenozoic stratigraphy of the Sarasota area. *Southeastern Geological Society Annual 1990 Field Excursion: Plio-Pleistocene stratigraphy and paleontology of South Florida, Guidebook Dec. 7-8* (ed. by W.D. Allmon and T.M. Scott). Southeastern Geological Society, Tallahassee.

Waller, T.R. (1996) Bridging the gap between the eastern Atlantic and eastern Pacific: a new species of *Crassadoma* (Bivalvia: Pectinidae) in the Pliocene of Florida. *Journal of Paleontology*, **70**, 941–946.

Ward, L.W. (2001) A retrospective of Miocene and Pliocene stratigraphy of the Virginia Coastal Plain. *Southeastern Section - 50th Annual Meeting Session 37.*

Ward, L.W. (2008) Synthesis of paleontological and stratigraphic investigations at the Lee Creek Mine, Aurora, N.C. (1958-2007). *Geology and Paleontology of the Lee Creek Mine, North Carolina, IV* (ed. by C.E. Ray, D.J. Bohaska, I.A. Koretsky, L.W. Ward and L.G. Barnes), pp. 325–436. Virginia Museum of Natural History Special Publication.

Ward, L.W. & Blackwelder, B.W. (1980) Stratigraphic revision of upper Miocene and lower Pliocene beds of the Chesapeake Group, middle Atlantic Coastal Plain. *US Geological Survey Bulletin*, **1482-D**, 60 pp.

Ward, L.W. & Blackwelder, B.W. (1987) Late Pliocene and Early Pleistocene mollusca from the James City and Chowan River Formations at the Lee Creek Mine. *Geology and Paleontology of the Lee Creek Mine, North Carolina, II* (ed. by C.E. Ray), pp. 113–283. Smithsonian Contributions to Paleobiology.

Ward, L.W. & Huddlestun, P.F. (1988) Age and stratigraphic correlation of the Raysor Formation, Late Pliocene, South Carolina. *Tulane Studies in Geology and Paleontology* **21**, 59–75.

Ward, L.W. & Gilinsky, N.L. (1993) Molluscan assemblages of the Chowan River Formation. Part A, Biostratigraphic analysis of the Chowan River Formation (Upper Pliocene) and adjoining units, the Moore House Member of the Yorktown Formation (Upper Pliocene) and the James City Formation (Lower Pleistocene). *Virginia Museum of Natural History Memoir*, **3**, 32 pp.

Ward, L.W., Bailey, R.H. & Carter, J.G. (1991) Pliocene and Early Pleistocene stratigraphy, depositional history, and molluscan paleobiogeography of the Coastal Plain. *The Geology of the Carolinas* (ed. by J.W. Horton and V.A. Zullo), pp. 274–289. University of Tennessee Press, Knoxville.

Warzeski, E.R., Cunningham, K.J., Ginsburg, R.N., Anderson, J.B. & Ding, Z.-D. (1996) A Neogene mixed siliciclastic and carbonate foundation for the Quaternary carbonate shelf, Florida Keys. *Journal of Sedimentary Research*, **66**, 788–800.

Webb, S.D., Morgan, G.S., Hulbert, R.C.J., Jones, D.S., MacFadden, B.J. & Mueller, P.A. (1989) Geochronology of a rich Early Pleistocene vertebrate fauna, Leisey Shell Pit, Tampa Bay, Florida. *Quaternary Research*, **32**, 96–110.

Weems, R.E. & Lemon, E.M.J. (1984) Geologic map of the Stallville quadrangle, Charleston and Dorchester Counties, South Carolina, with text. *U.S. Geological Survey Map G Q-1581, scale 1:24,000.*

Weems, R.E. & Lemon, E.M.J. (1989) Geology of the Bethera, Cordesville, Huger, and Kittredge quadrangles Berkley County, South Carolina. *U.S. Geological Survey Miscellaneous Investigations Series Map, I-1854, 1 sheet, scale 1:24,000.*

Weems, R.E. & Lewis, W.C. (2002) Structural and tectonic setting of the Charleston, South Carolina, region: evidence from the Tertiary stratigraphic record. *Geological Society of America Bulletin*, **114**, 24–42.

Weems, R.E., Lemon, E.M.J. & Nelson, M.S. (1994) Geology of the Pringletown, Ridgeville, Summerville, and Summerville northwest 7.5-minute quadrangles, Berkeley, Charleston, and Dorchester Counties, South Carolina. In: *U.S. Department of the Interior, U.S. Geological Survey*.

Weems, R.E., Lemon, E.M.J., McCartan, L., Bybell, L.M. & Sanders, A.E. (1982) Recognition and formalization of the Pliocene 'Goose Creek Phase' in Charleston, South Carolina, area. *U.S. Geological Survey Bulletin*, **1529H**, 137–148.

Wehmiller, J.F. & Belknap, D.F. (1978) Alternative kinetic models for the interpretation of amino acid enantiomeric ratios in Pleistocene mollusks: examples from California, Washington, and Florida. *Quaternary Research*, **9**, 330–348.

Wehmiller, J.F. & Belknap, D.F. (1982) Amino acid age estimates, quaternary Atlantic Coastal Plain: comparison with U-series dates, biostratigraphy, and paleomagnetic control. *Quaternary Research* **18**, 311–336.

Wehmiller, J.F., York, L.L. & Bart, M.L. (1995) Amino acid racemization geochronology of reworked Quaternary mollusks on U.S. Atlantic coast beaches: implications for chronostratigraphic, taphonomy, and coastal sediment transport. *Marine Geology*, **124**, 303–337.

Wehmiller, J.F., Harris, W.B., Boutin, B.S. & Farrell, K.M. (2012) Calibration of amino acid racemization (AAR) kinetics in United States mid-Atlantic Coastal Plain Quaternary mollusks using 87Sr/86Sr analyses: evaluation of kinetic models and estimation of regional Late Pleistocene temperature history. *Quaternary Geochrnology*, **7**, 21–36.

Wehmiller, J.F., Belknap, D.F., Boutin, B.S., Mirecki, J.E., Rahaim, S.D. & York, L.L. (1988) A review of the aminostratigraphy of Quaternary mollusks from United States Coastal Plain sites. *Geological Society of America Special Papers*, **277**, 69–110.

Wehmiller, J.F., Thieler, R.E., Hoffman, C.W., Riggs, S., Pellerito, V., York, L., MALLINSON, D.J. & Culver, S. (2004a) Aminostratigraphy of Quaternary coastal units, North Carolina Coastal Plain. *Geological Society of America Abstracts with Programs* **36**, 71.

Wehmiller, J.F., Simmons, K.R., Cheng, H., Edwards, R.L., Martin-McNaughton, J., York, L.L., Krantz, D.E. & Shen, C.-C. (2004b) Uranium-series coral ages from the US Atlantic Coastal Plain--the "80 Ka problem" revisited. *Quaternary International*, **120**, 3–14.

Wehmiller, J.F., Thieler, E.R., Miller, D., Pellerito, V., Keeney, V.B., Riggs, S.R., Culver, S., Mallinson, D., Farrell, K.M., York, L.L., Pierson, J. & Parham, P.R. (2010) Aminostratigraphy of surface and subsurface Quaternary sediments, North Carolina coastal plain, USA. *Quaternary Geochronology*, **5**, 459–494.

Wentworth, C.K. (1930) Sand and gravel resources of the coastal plain of Virginia *Virginia Division Mineral Resources Bulletin*, **32**, 1–146.

Willard, D.A. (1994) Palynological record from the North Atlantic region at 3 Ma: vegetational distribution during the period of global warmth. *Review of Paleobotany and Palynology*, **83**, 275–97.

Willard, D.A., Cronin, T.M., Ishman, S.E. & Litwin, R.J. (1993) Terrestrial and marine records of climatic and environmental changes during the Pliocene in subtropical Florida. *Geology*, **21**, 679–682.

Williams, M., Haywood, A.M., Harper, E.M., Johnson, A.L.A., Knowles, T., Leng, M.J., Lunt, D.J., Okamura, B., Taylor, P.D. & Zalasiewicz, J. (2009) Pliocene climate and seasonality in North Atlantic shelf seas. *Philosophical Transactions of the Royal Society A*, **367**, 85–108.

York, L.L., Doar, W.R.I. & Wehmiller, J.F. (2001) Late Quaternary aminostratigraphy and geochronology of the St. Helena island area, South Carolina coastal plain. *Geological Society of America Abstracts with Programs*, **33**, 26.

Zullo, V.A. & Harris, W.B. (1992) Sequence stratigraphy of marine Pliocene and lower Pleistocene deposits in southwestern Florida: Preliminary assessment. *Plio-Pleistocene stratigraphy and paleontology of southern Florida* (ed. by T.M. Scott and W.D. Allmon), pp. 27–40. Florida Geological Survey Special Publication.

Zullo, V.A. & Portell, R.W. (1993) Unusual examples of serial growth and succession in Pliocene and Pleistocene coral-inhabiting barnacles. *Geological Society of America Abstracts with Programs*, **25**, 79.

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.

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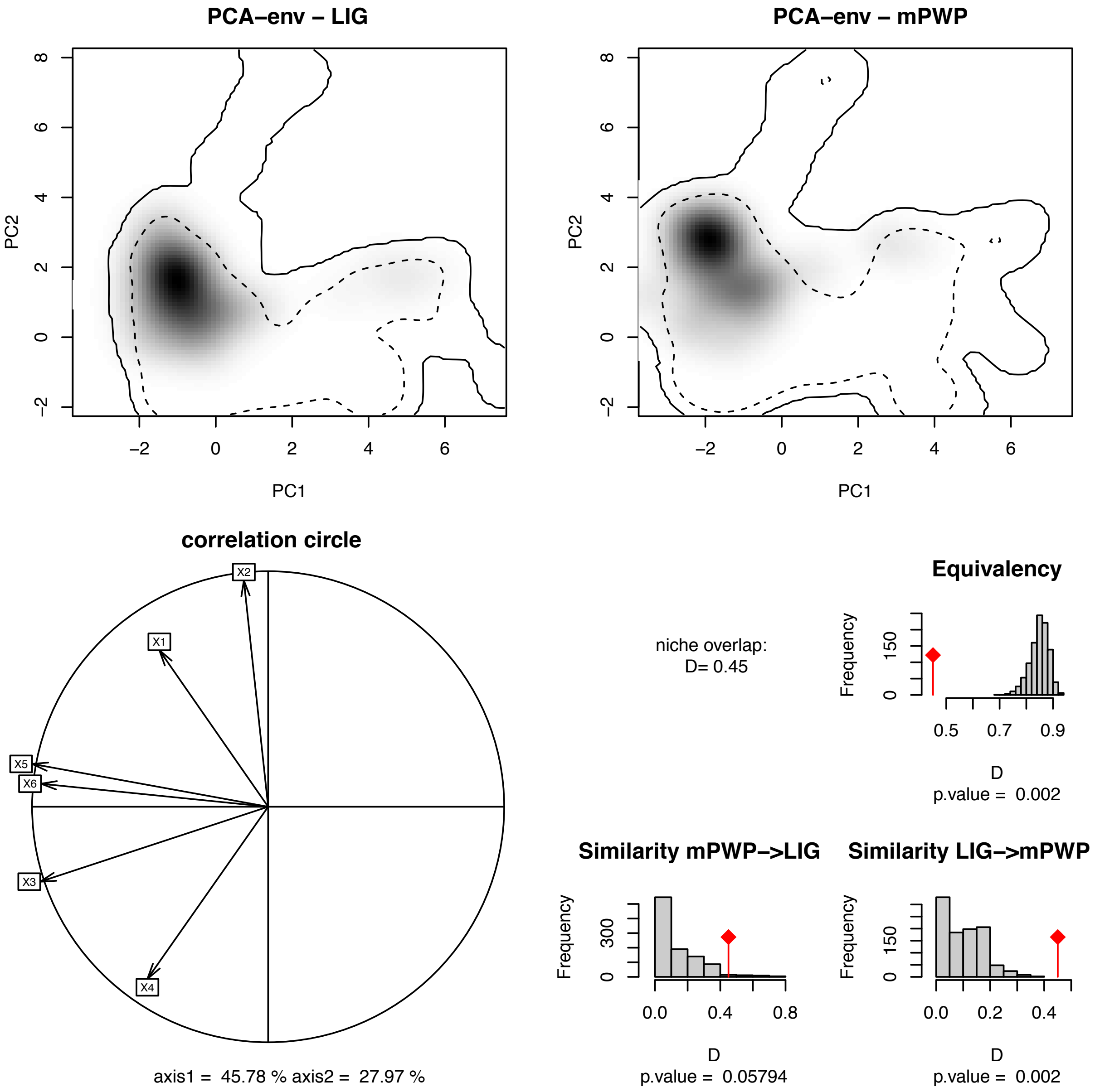

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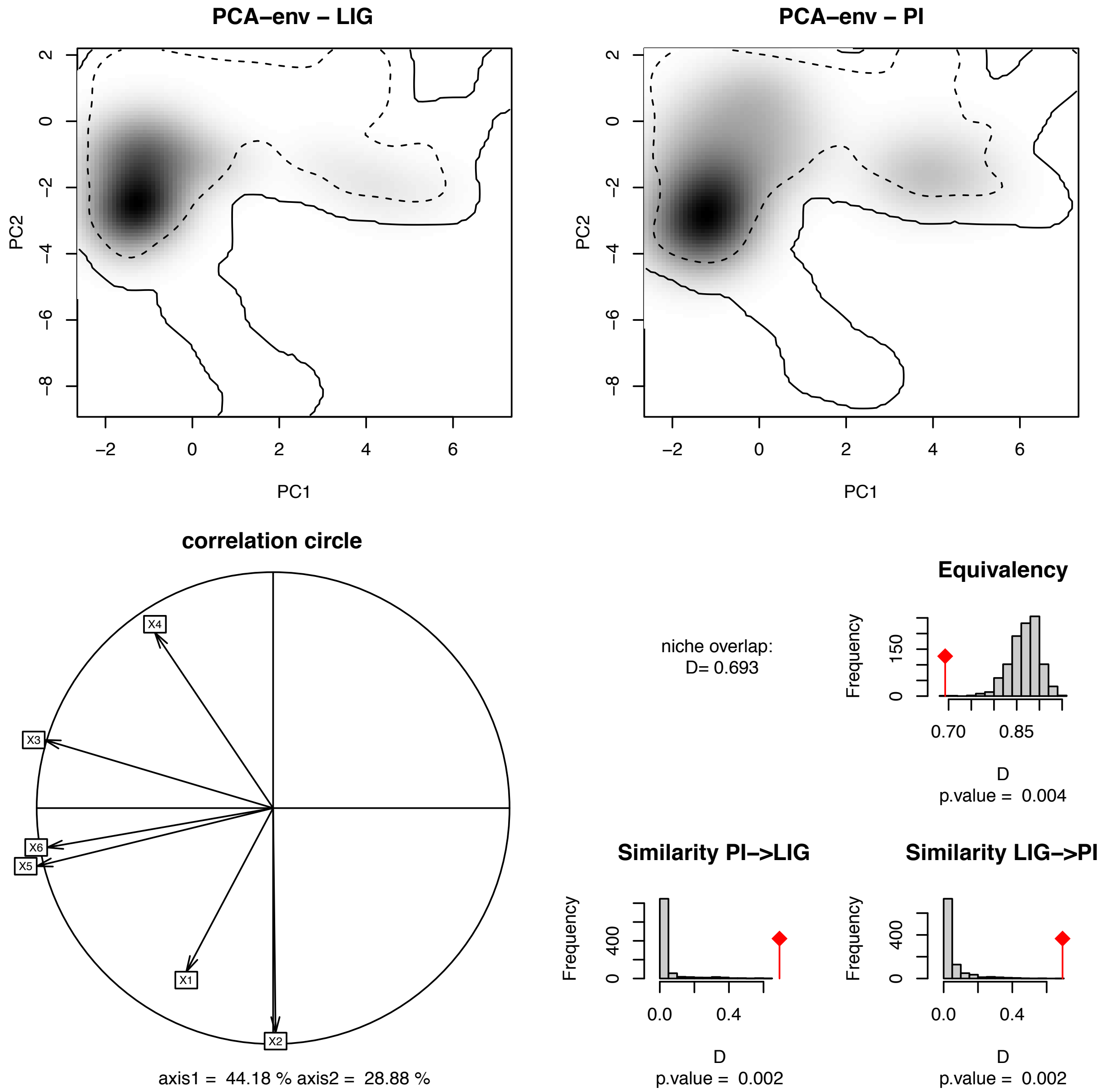

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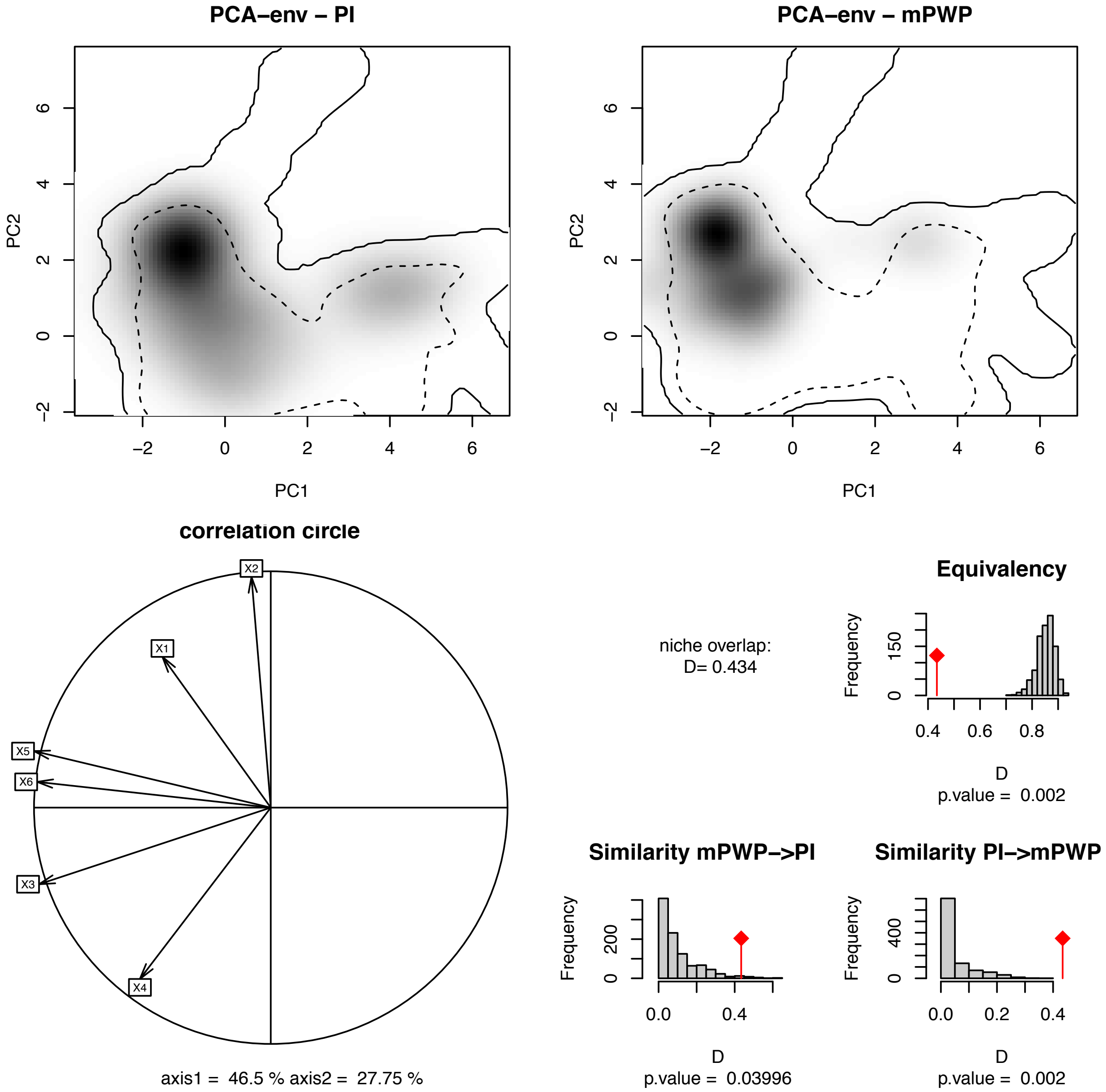
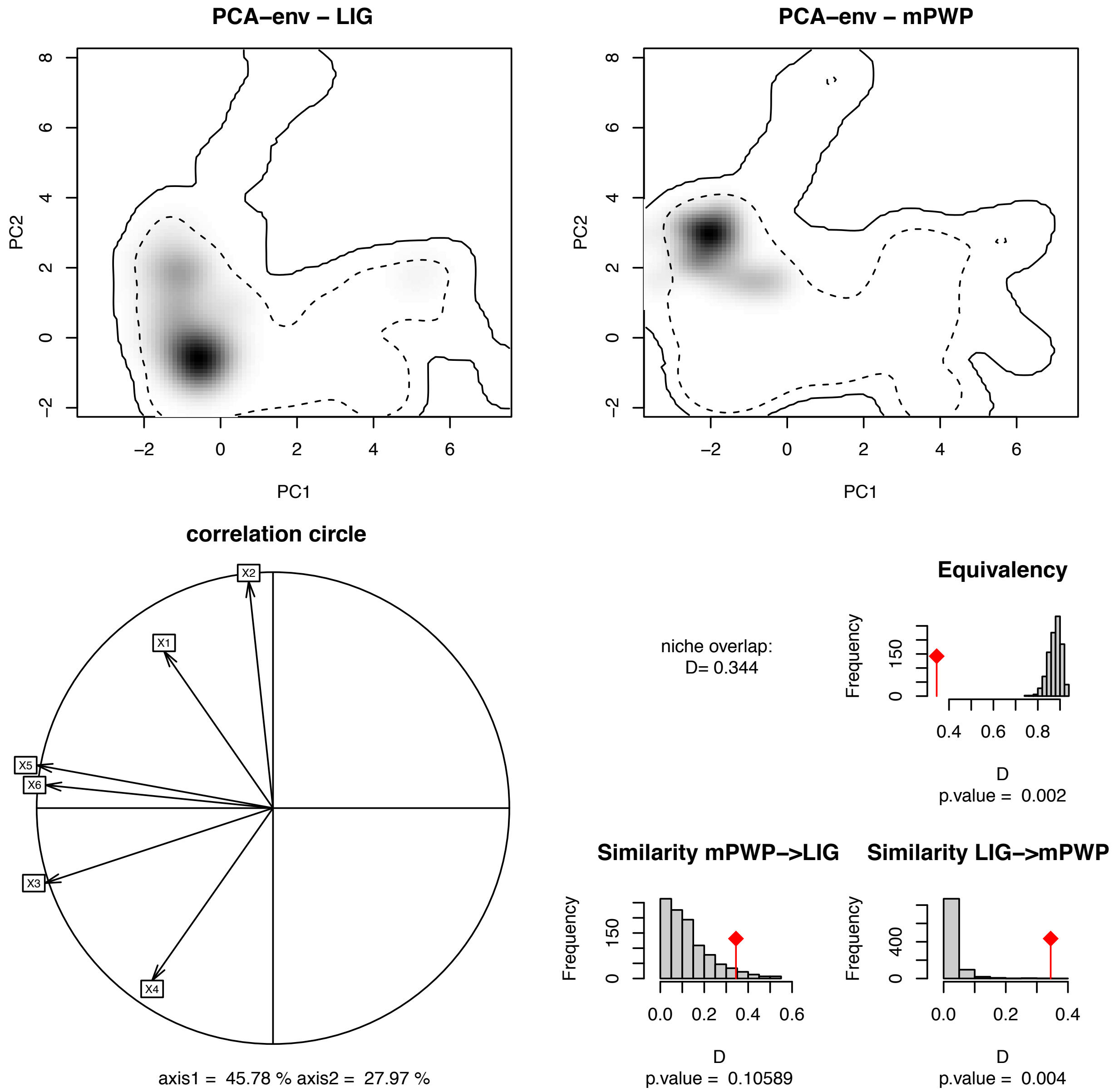


Bulla occidentalis: **LIG—mPWP**



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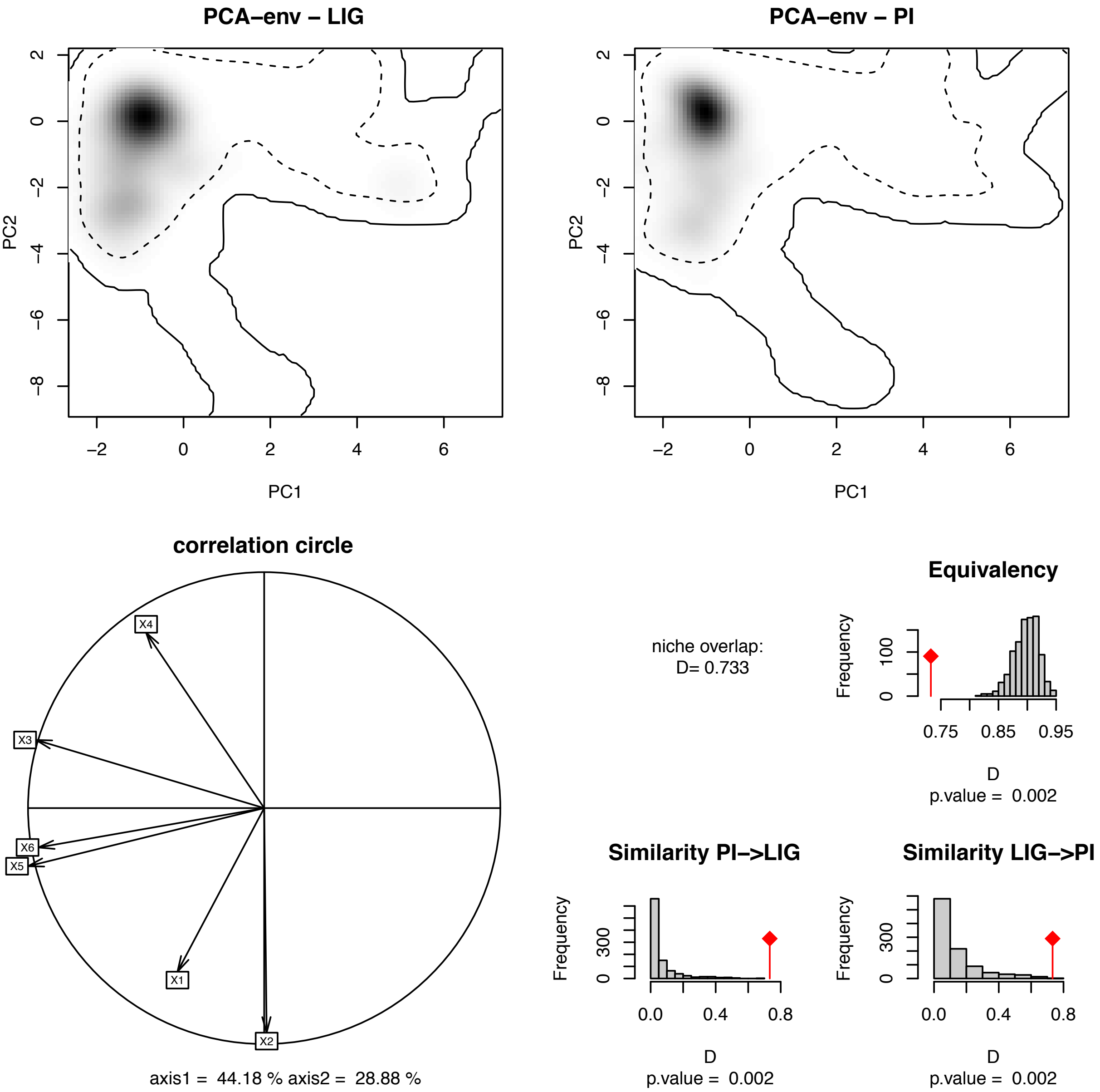

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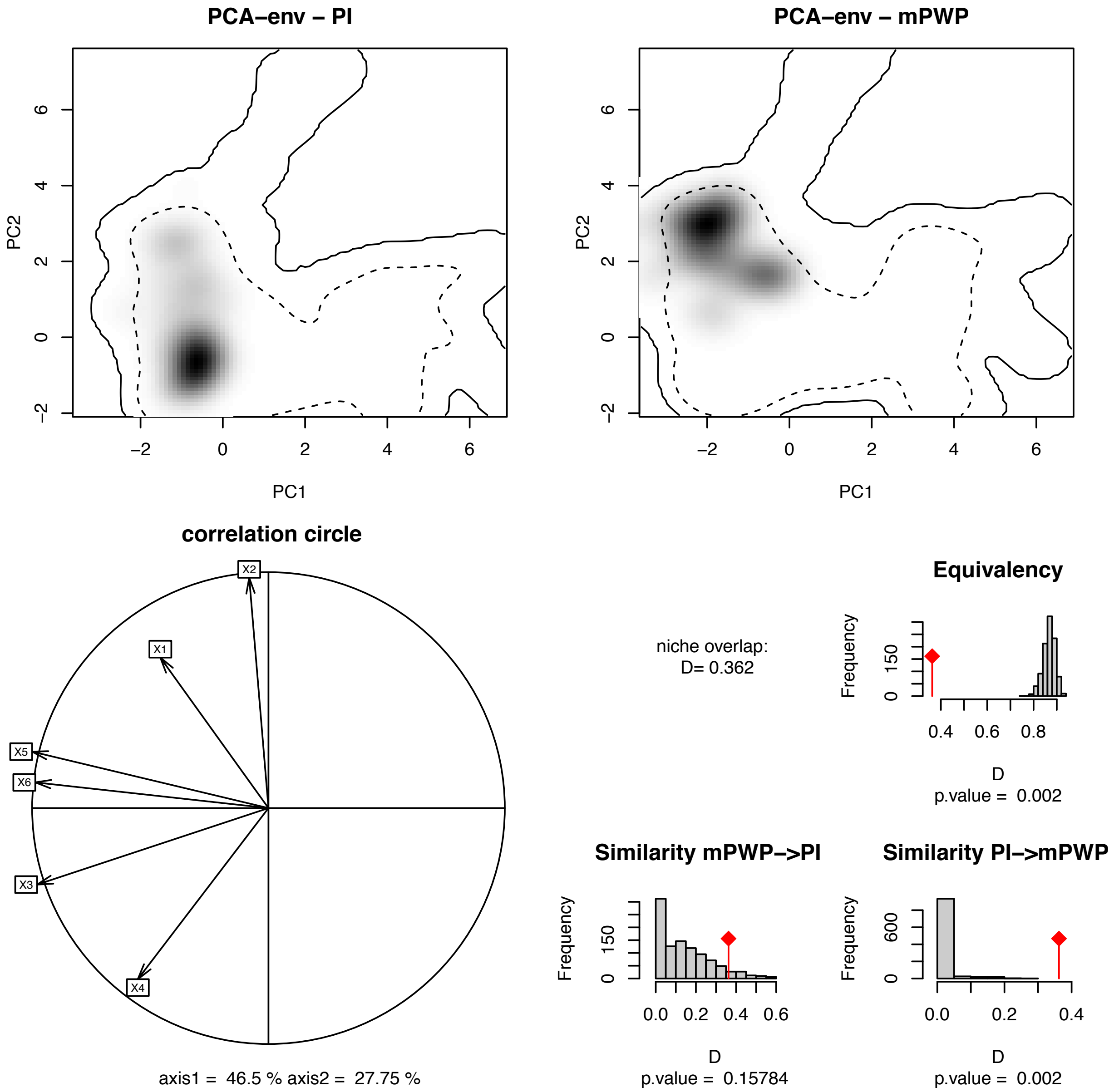
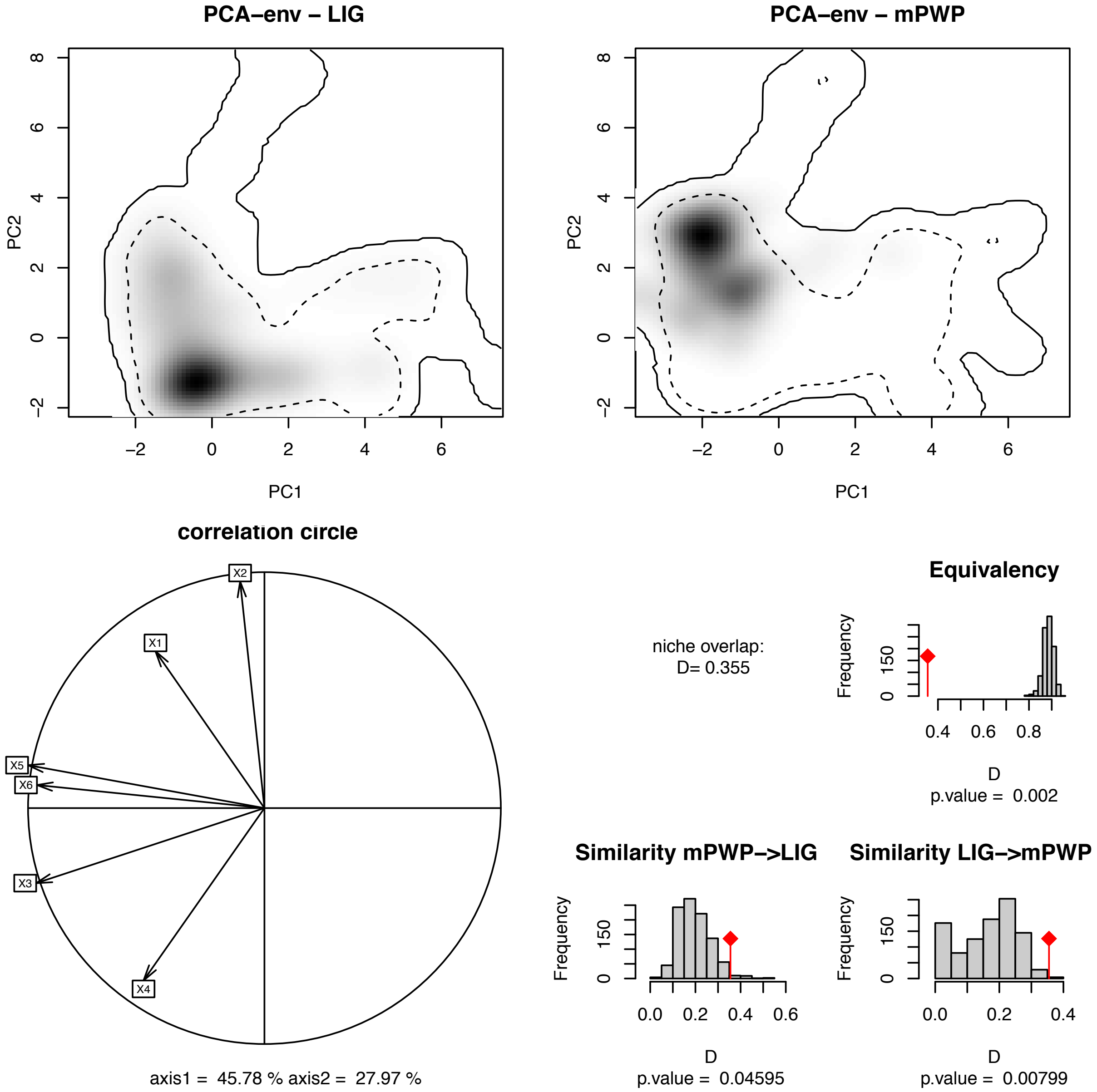


Crassostrea virginica: **LIG—mPWP**



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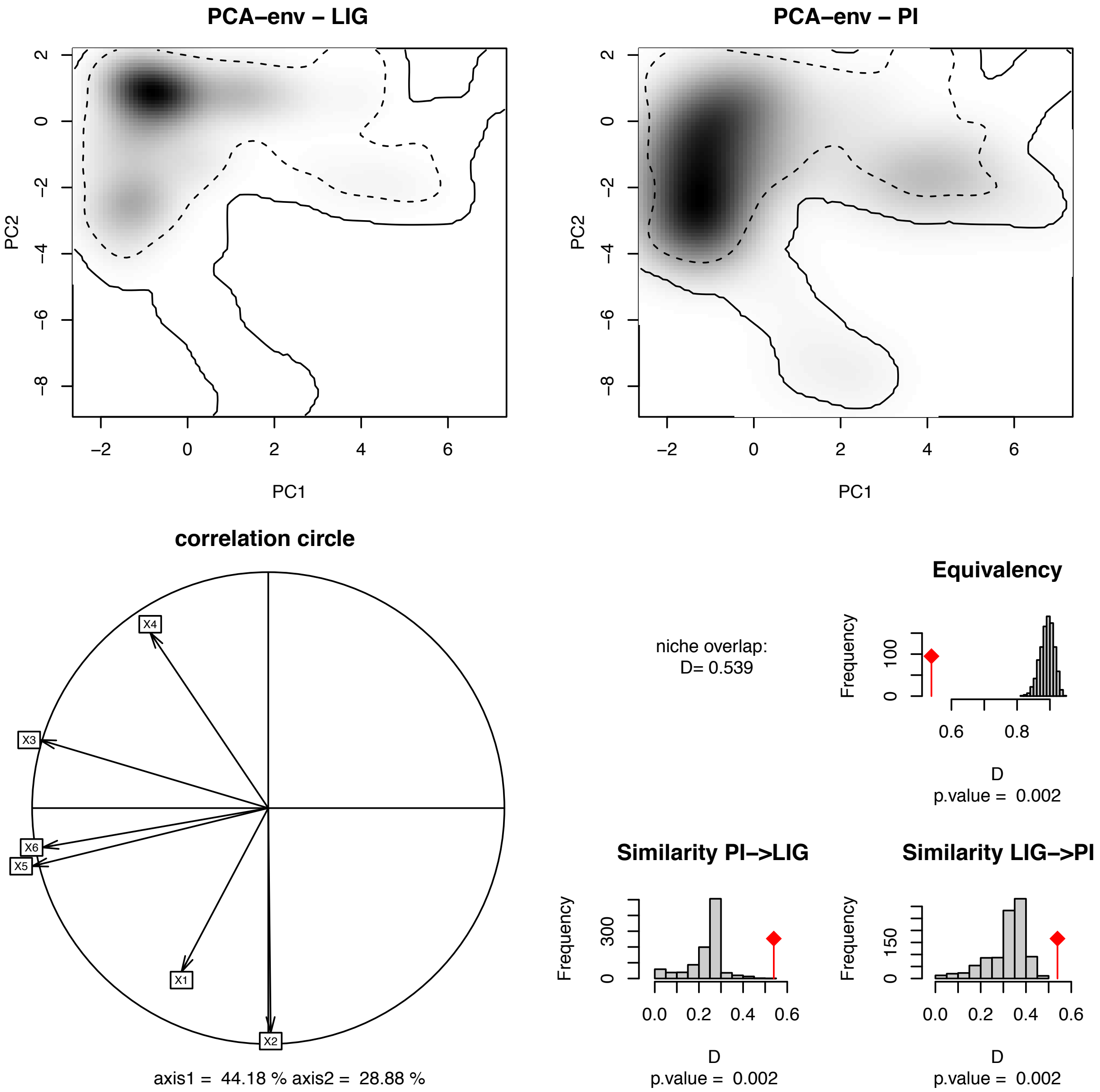

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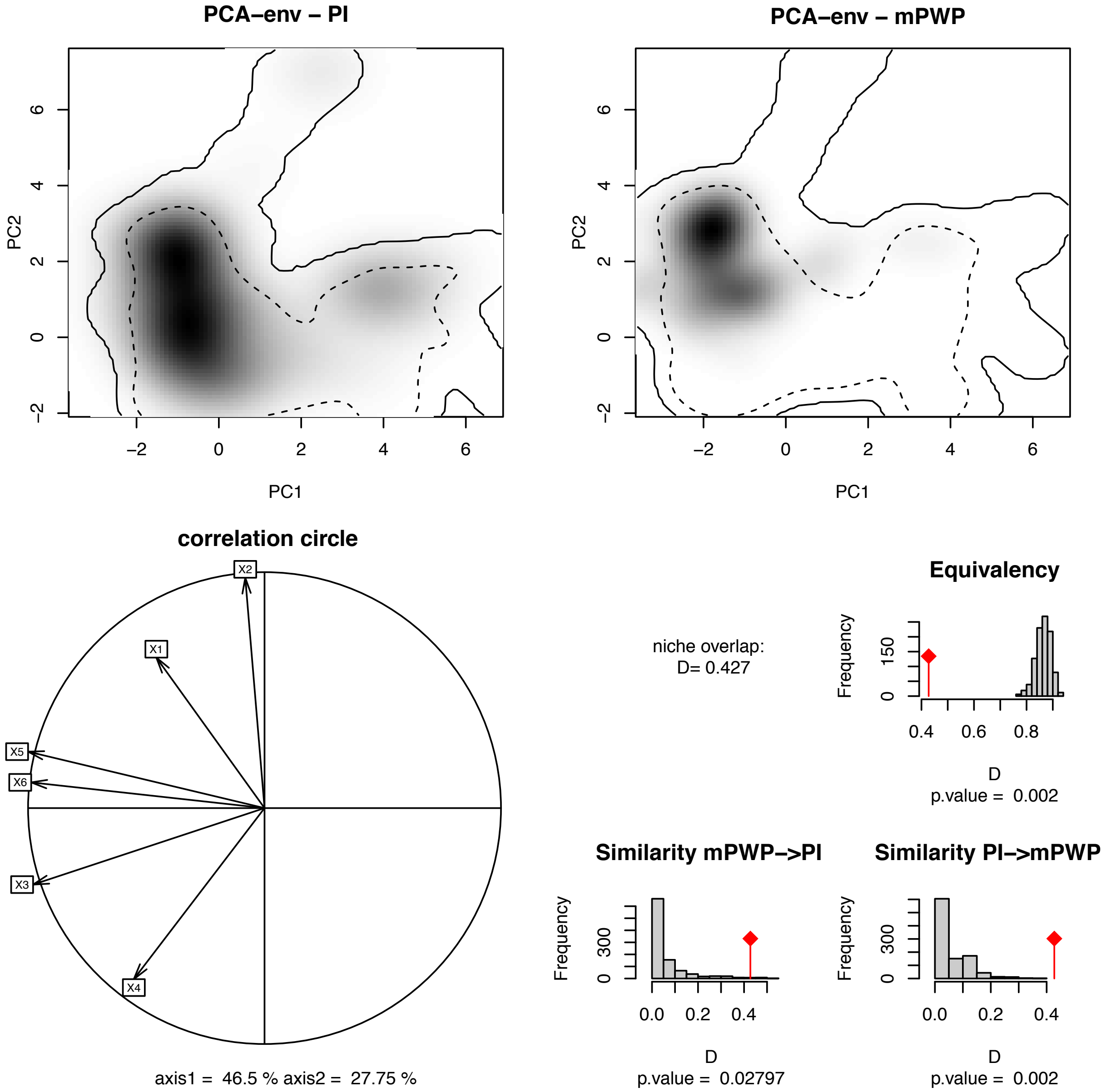

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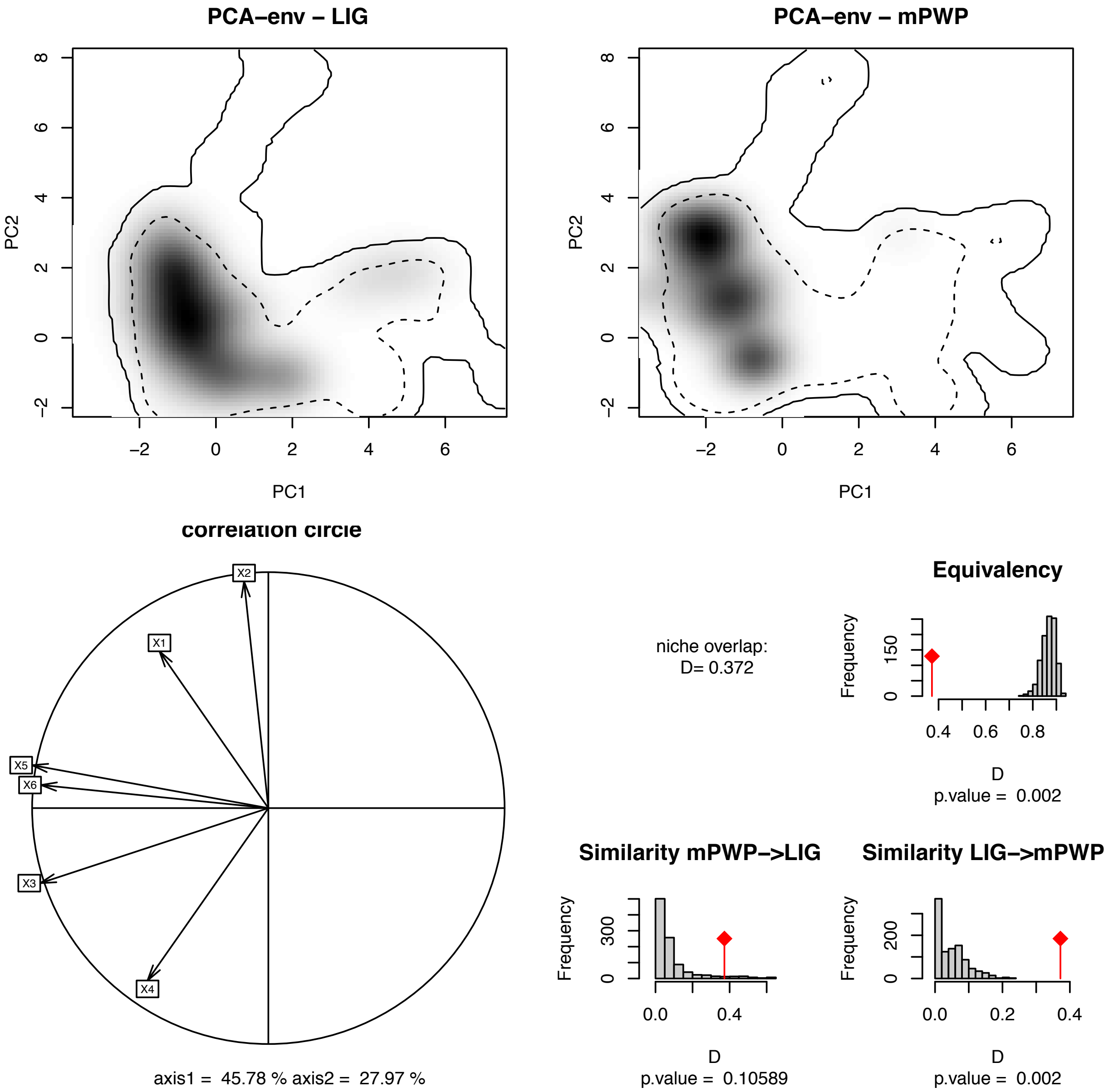

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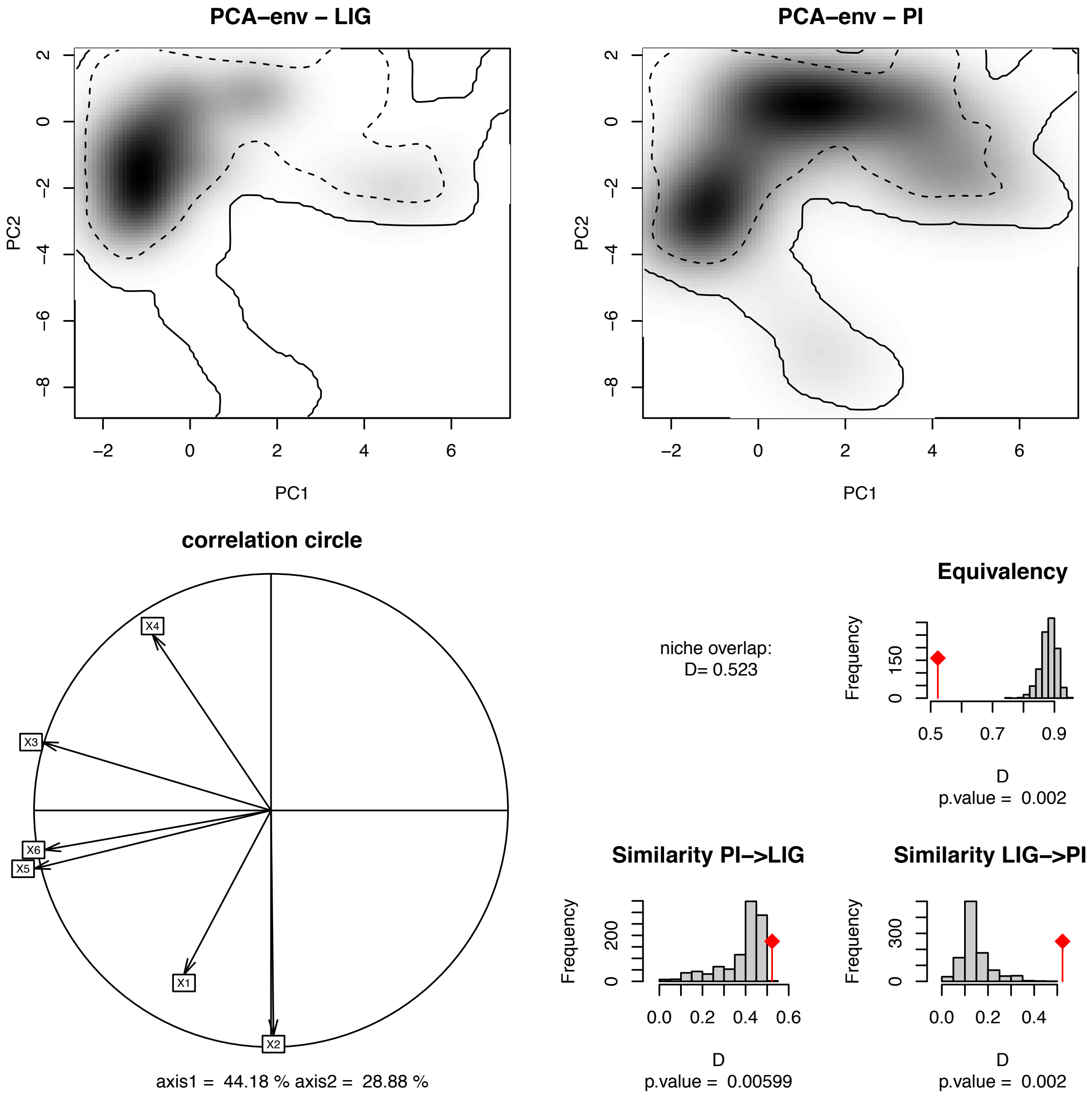

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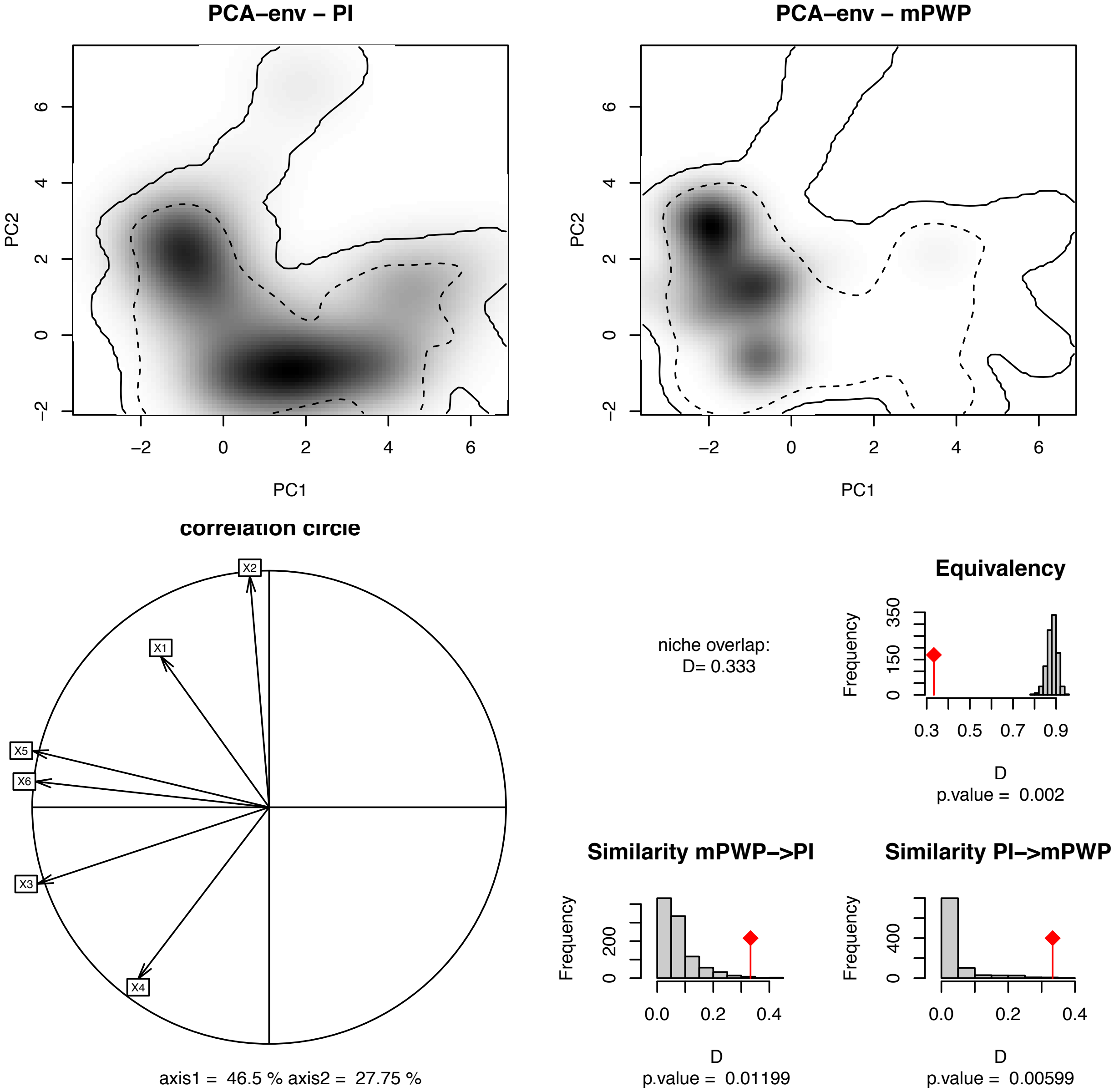
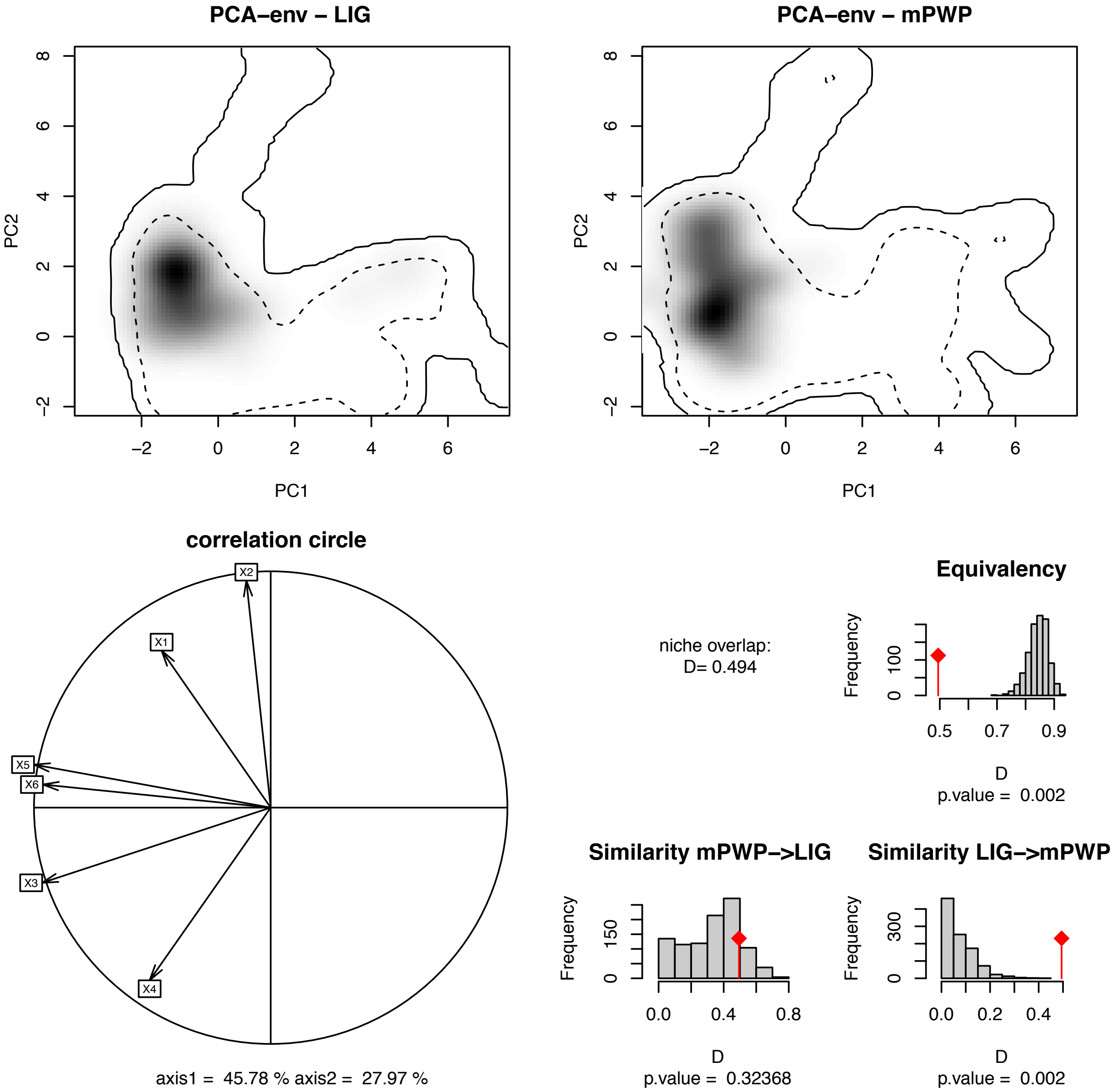
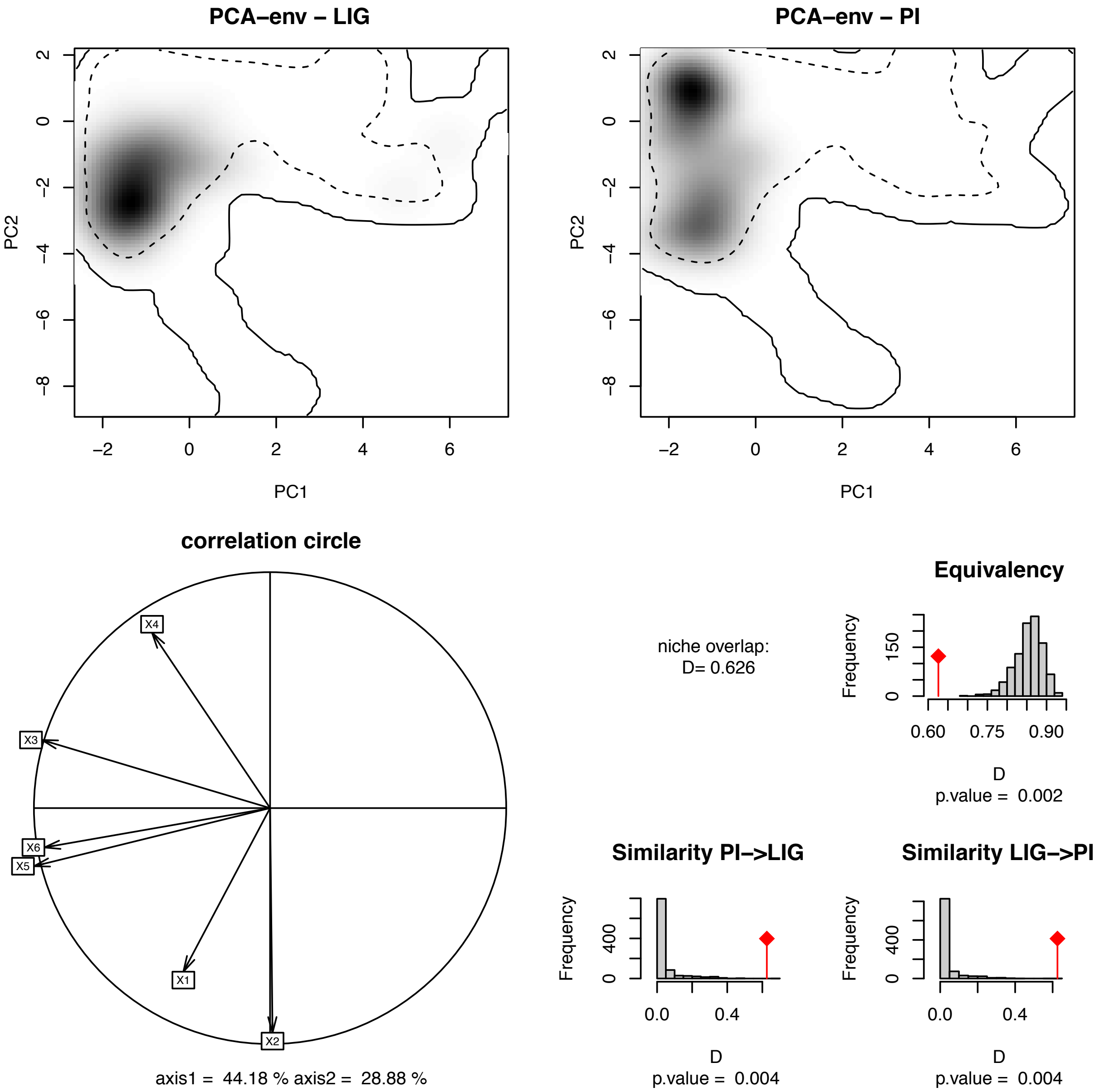


Dinocardium robustum: **LIG—mPWP**



***Dinocardium robustum*: LIG—PI**



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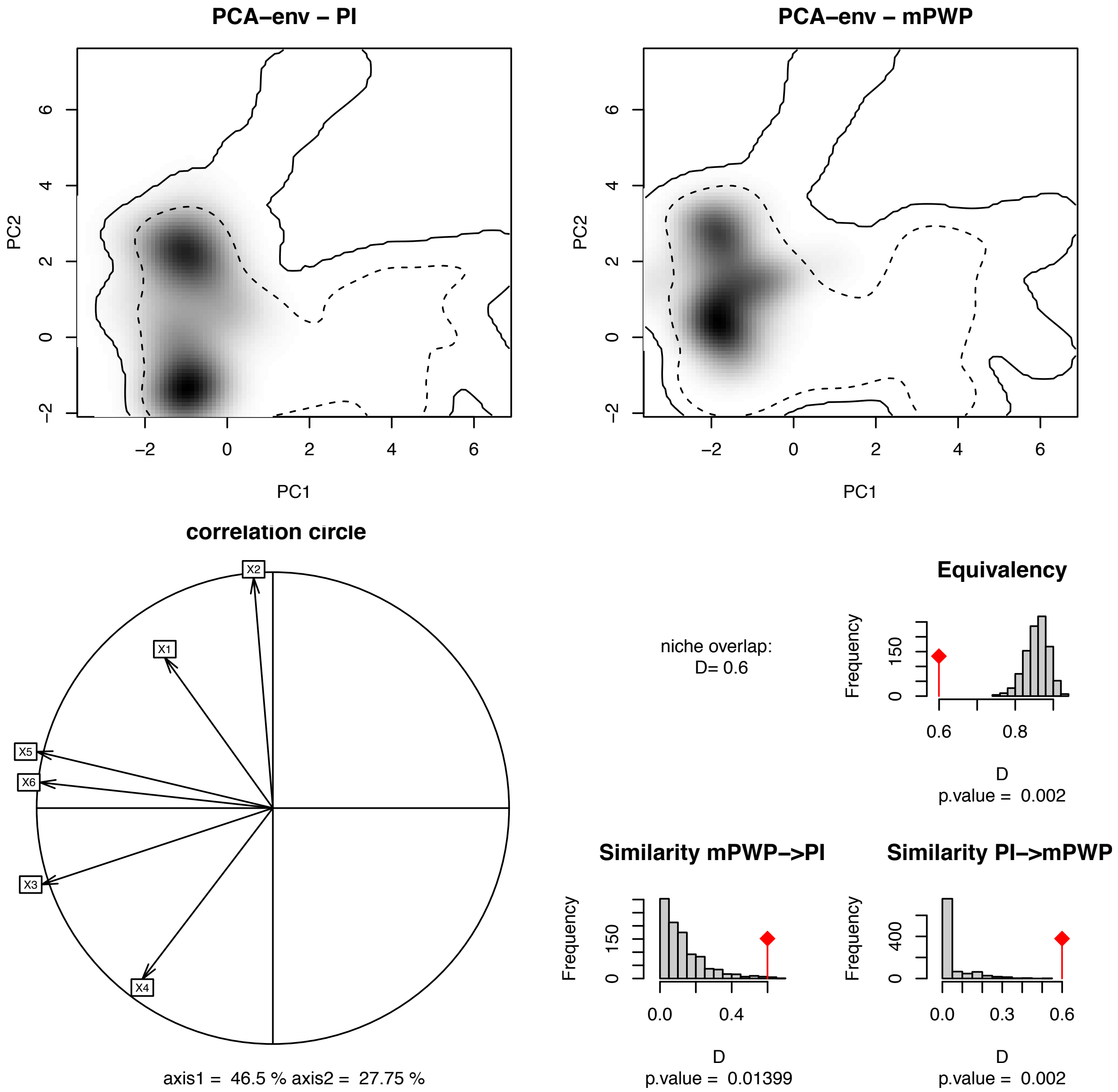
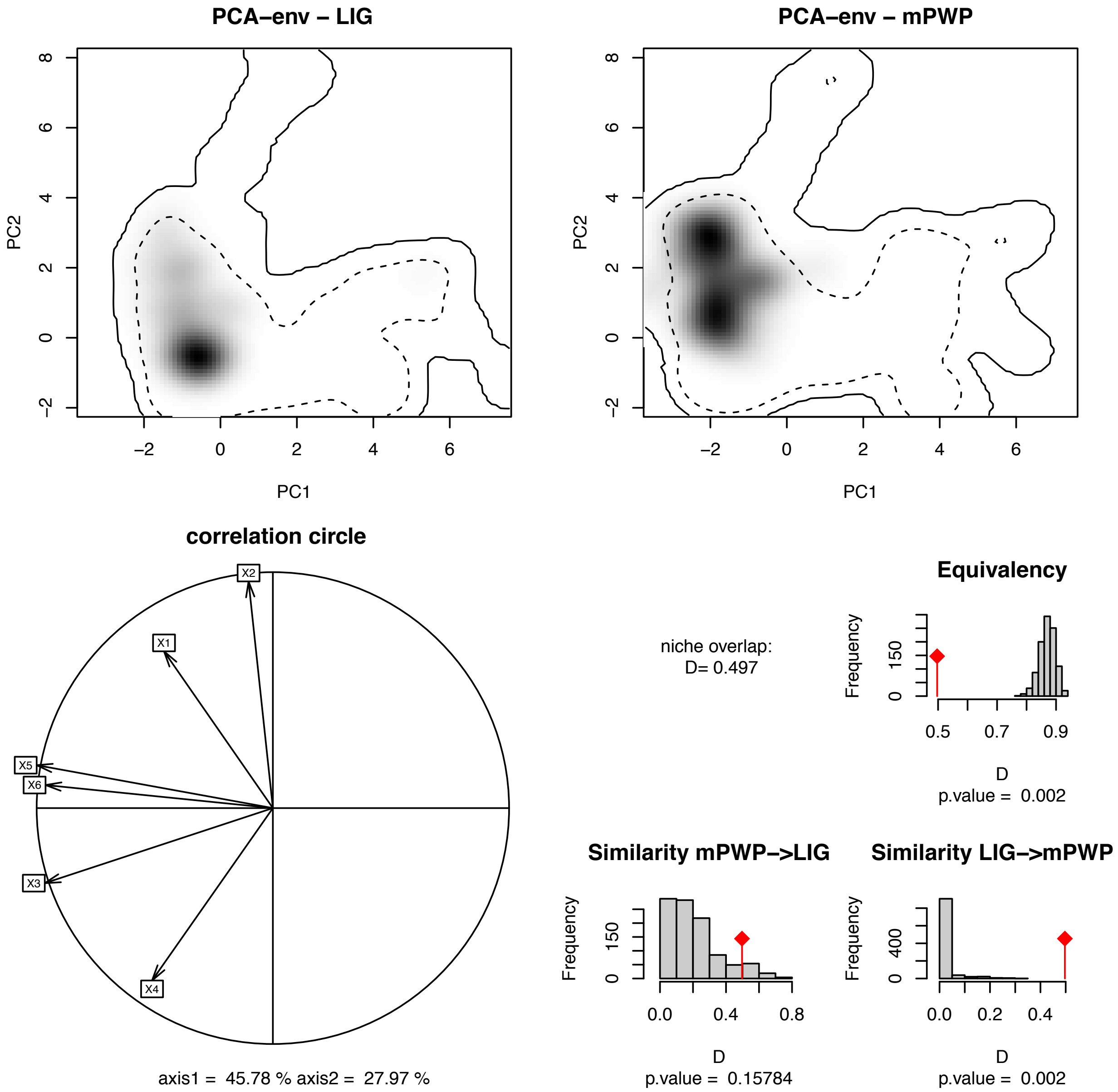


Lucina pensylvanica: **LIG—mPWP**



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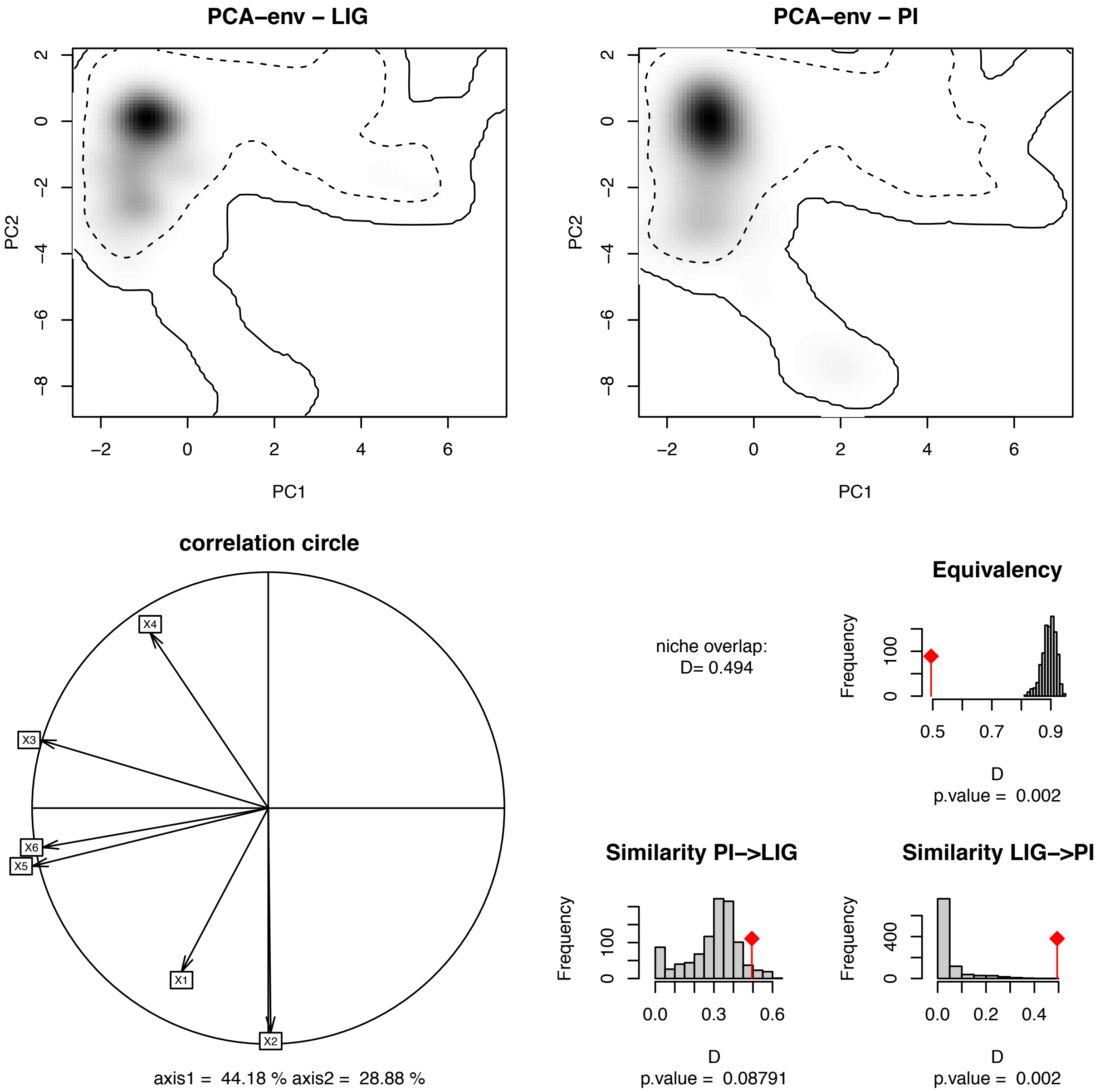

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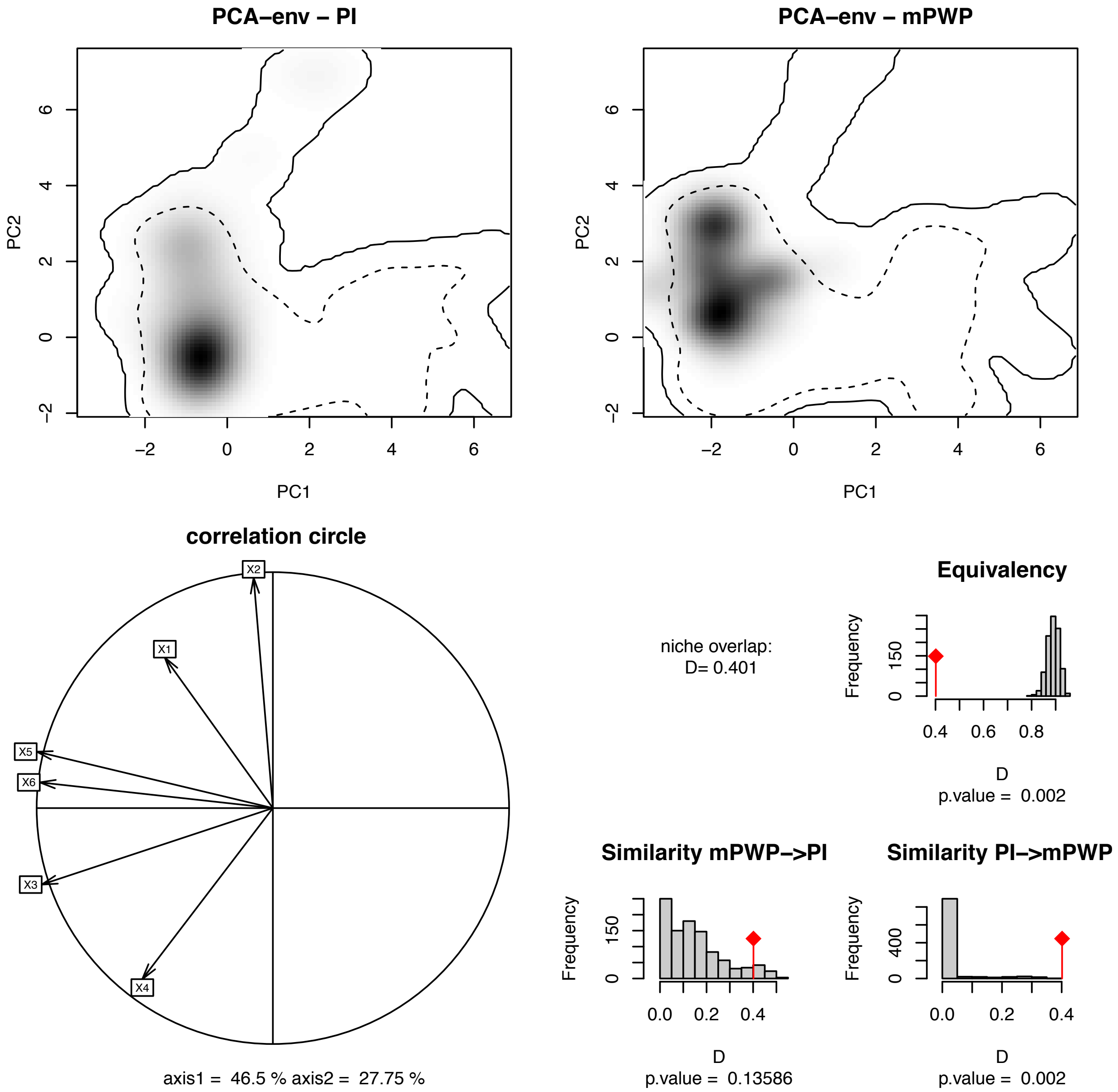
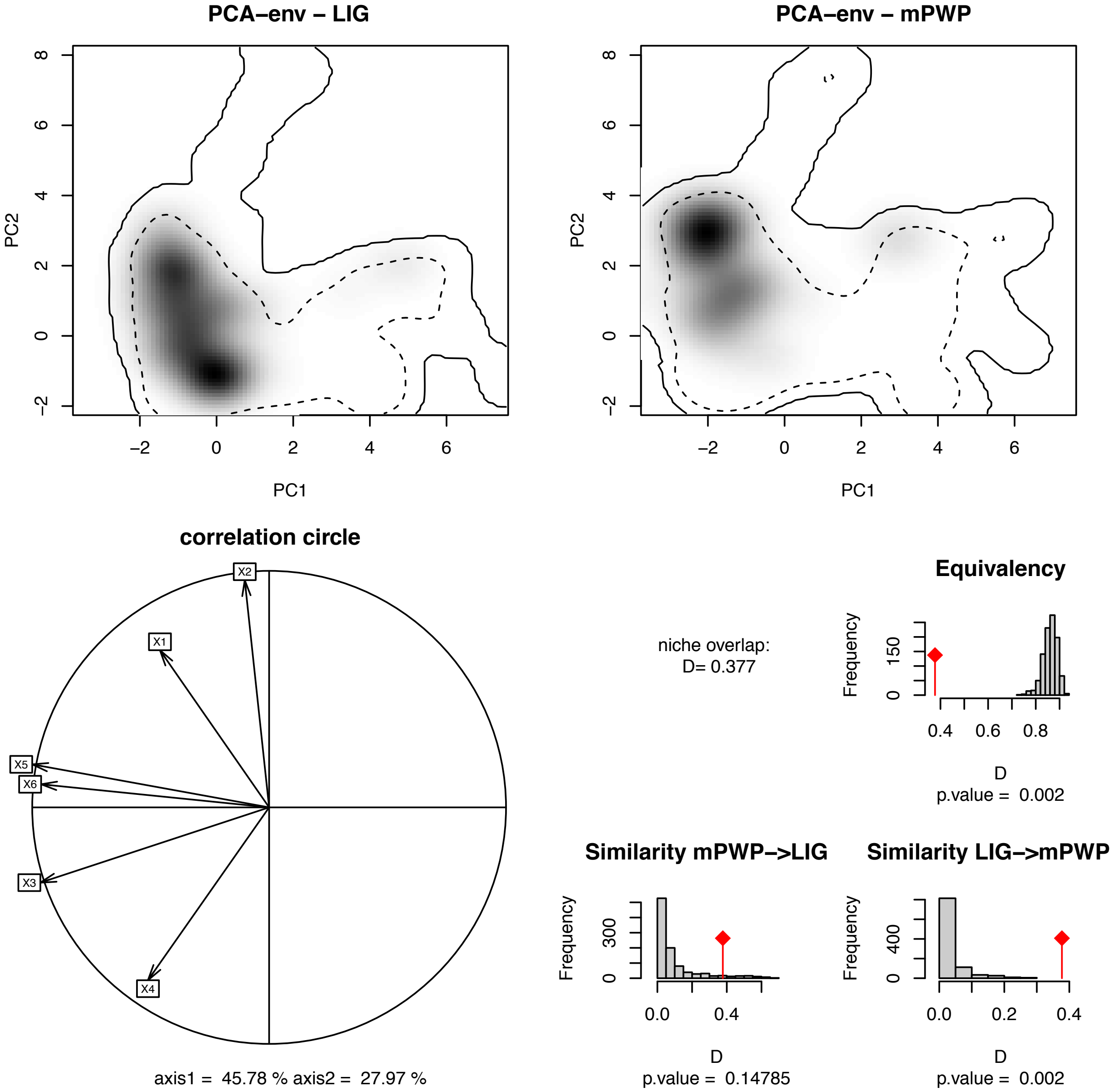


Mercenaria campechiensis: **LIG—mPWP**



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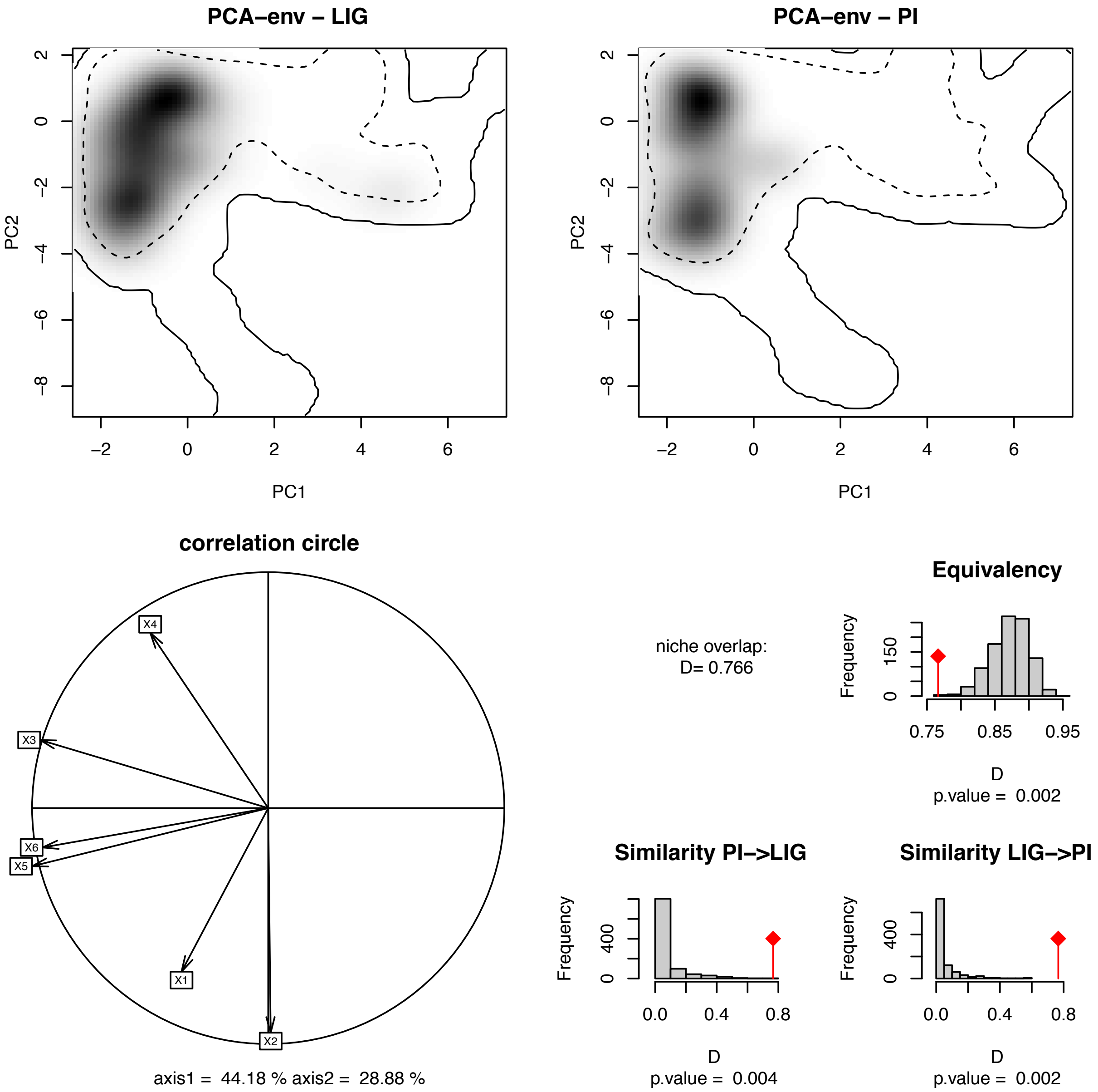

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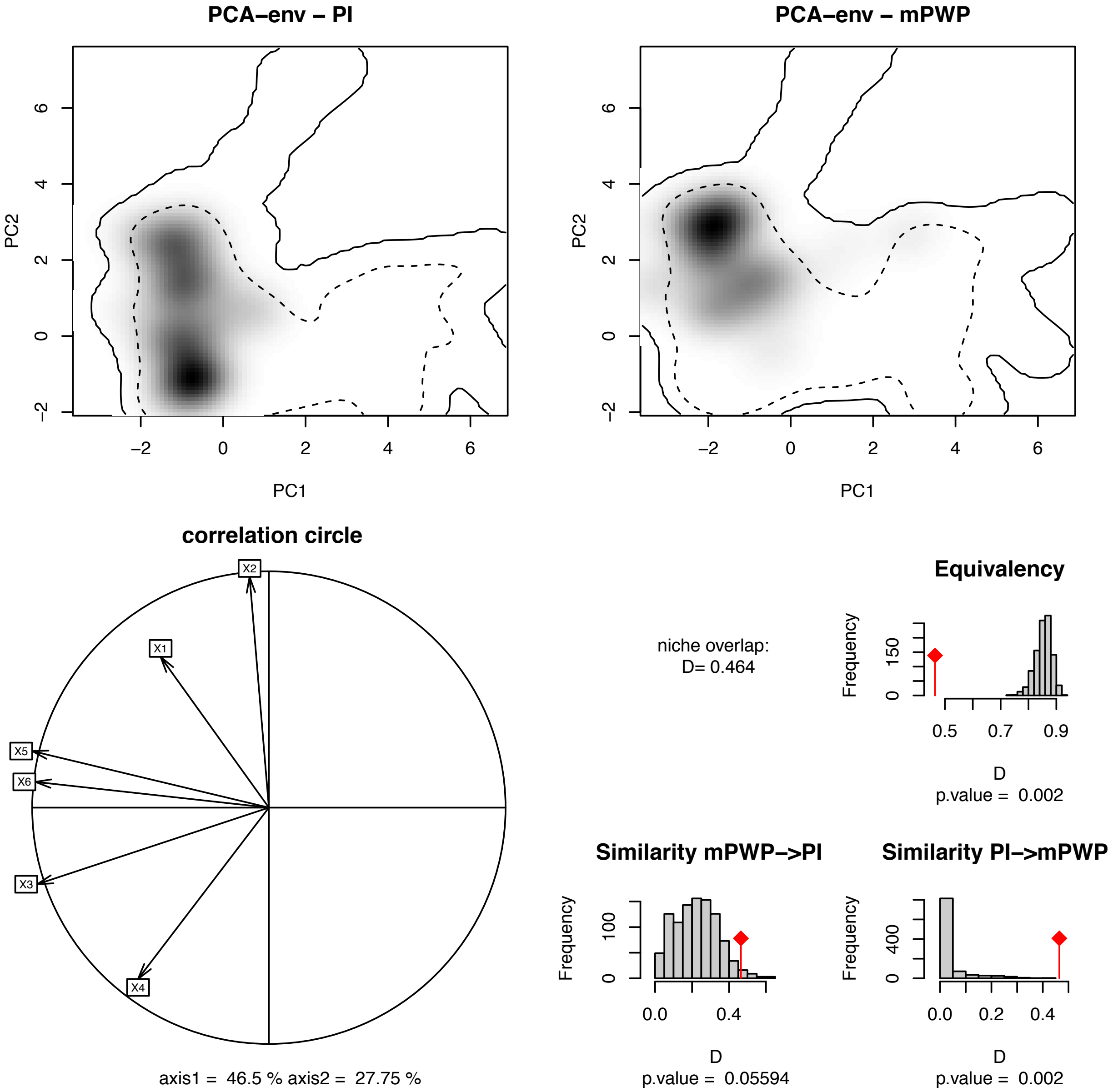

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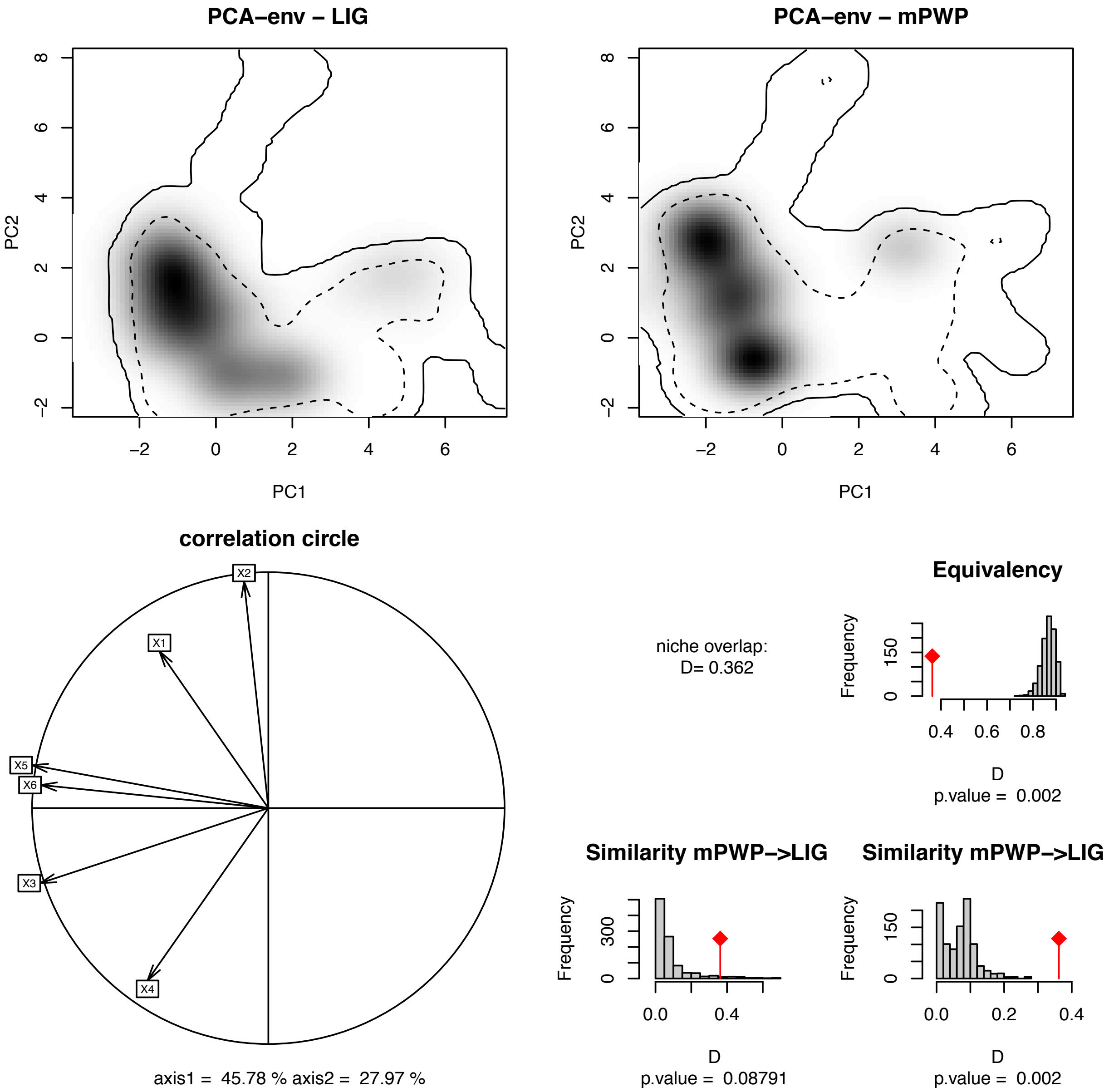

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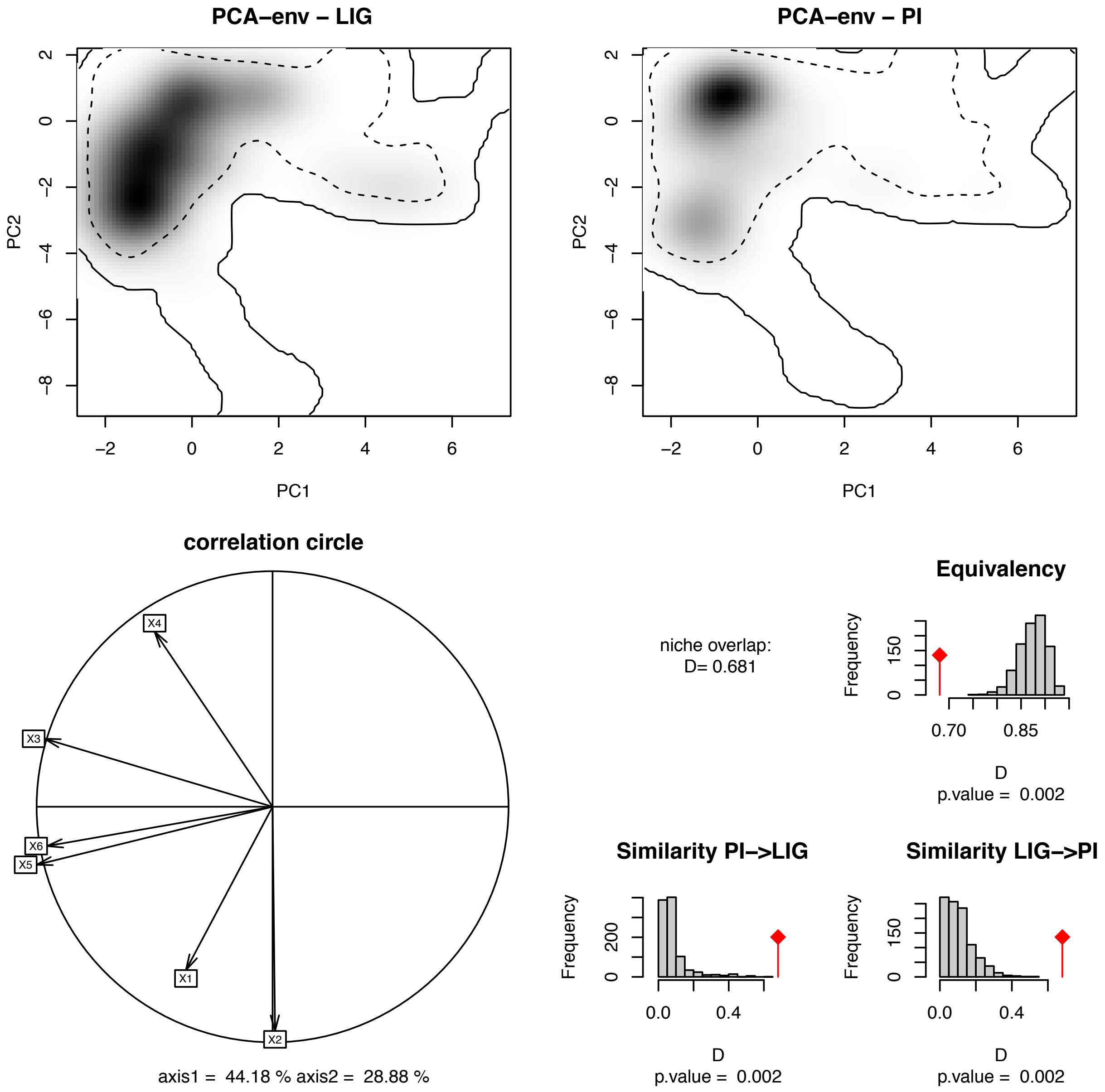

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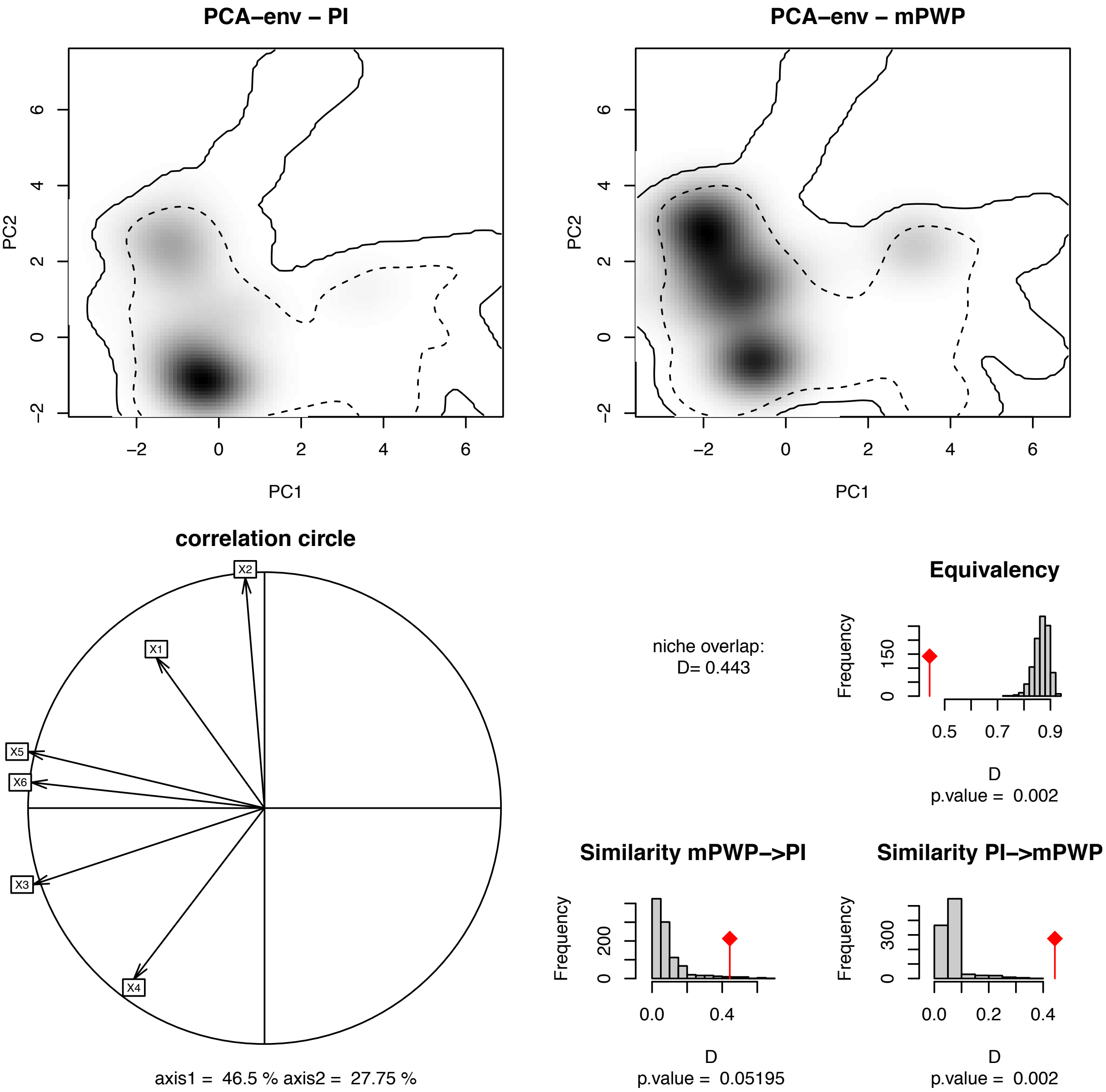

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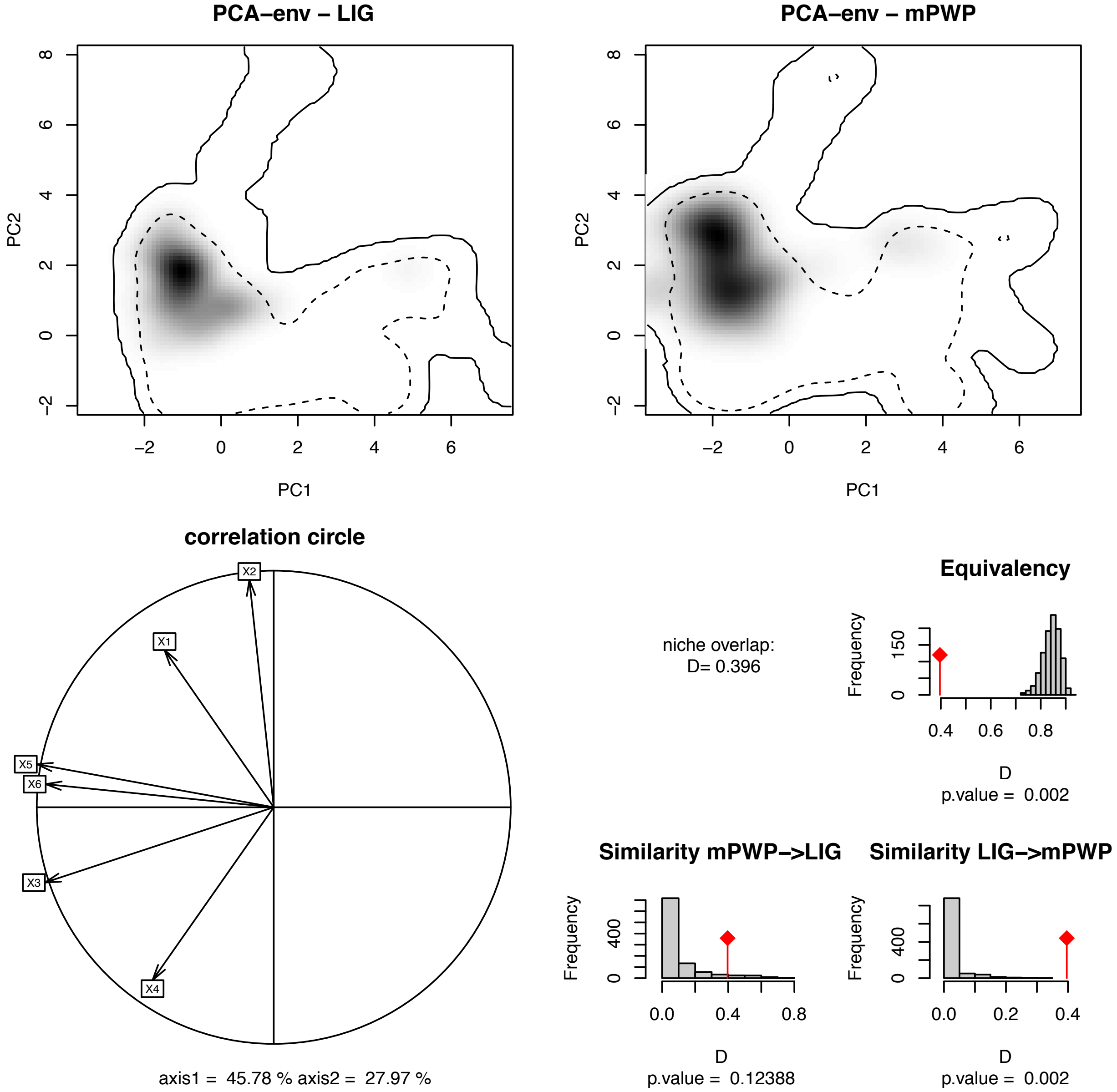

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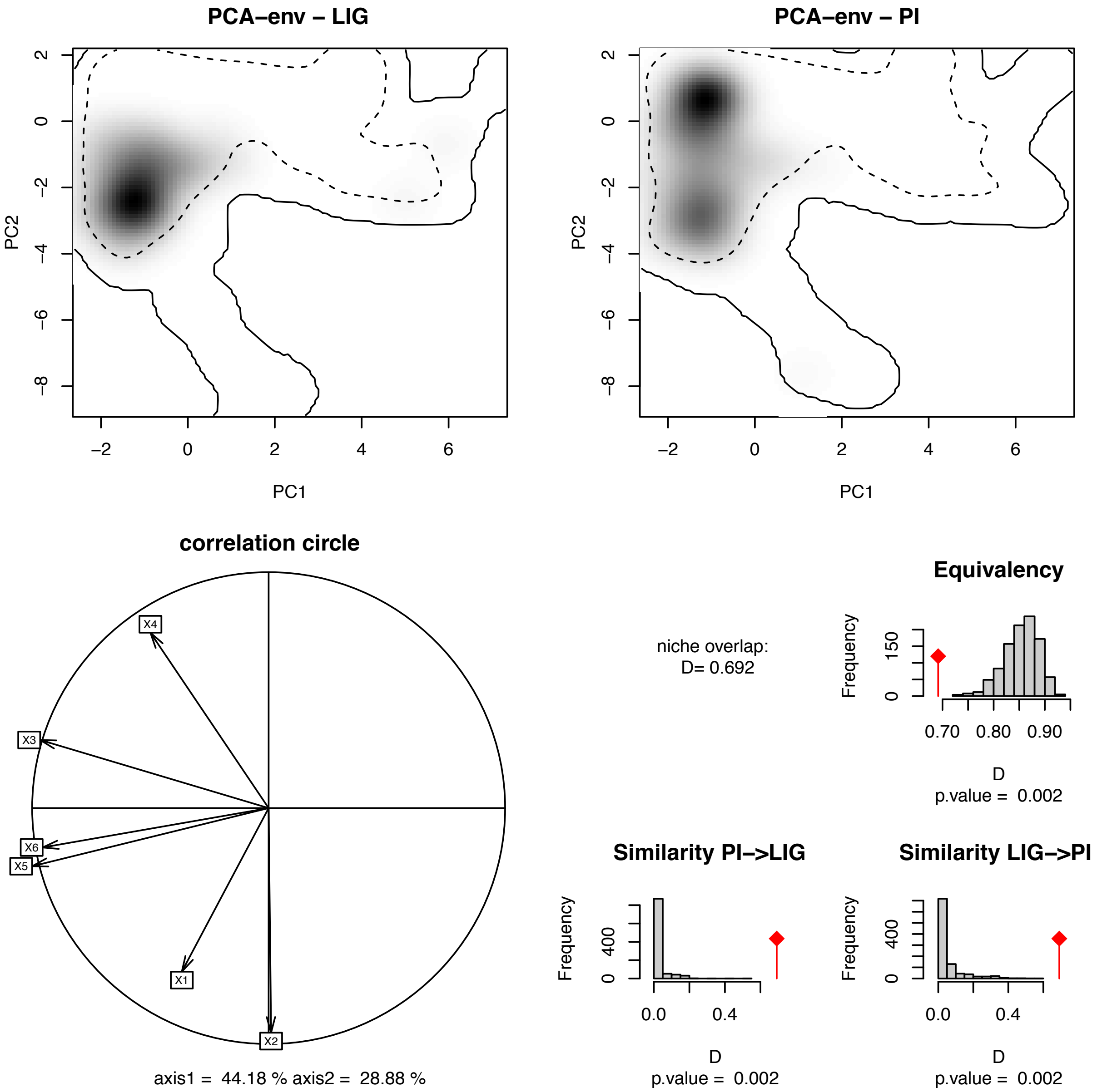

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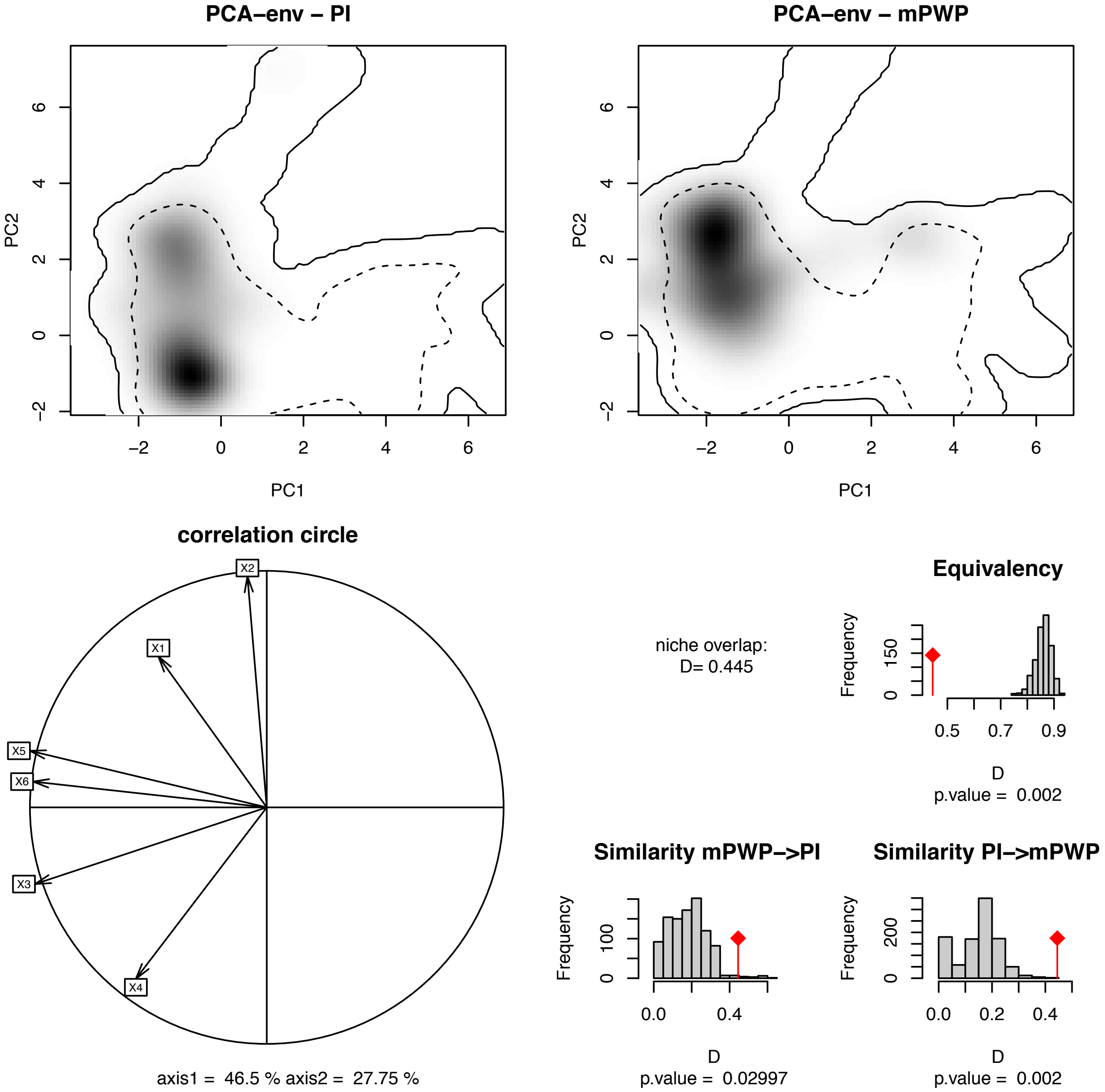
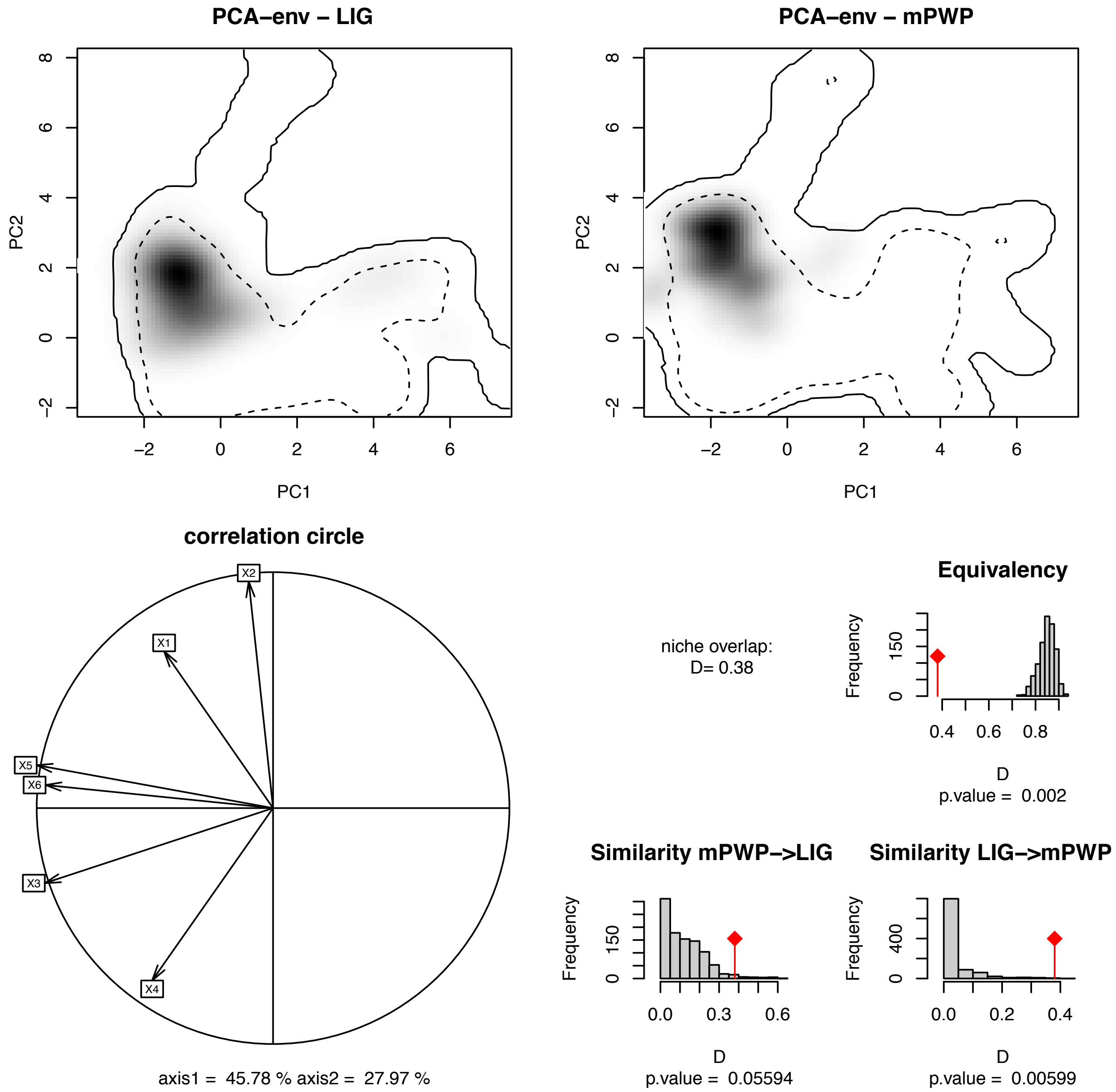
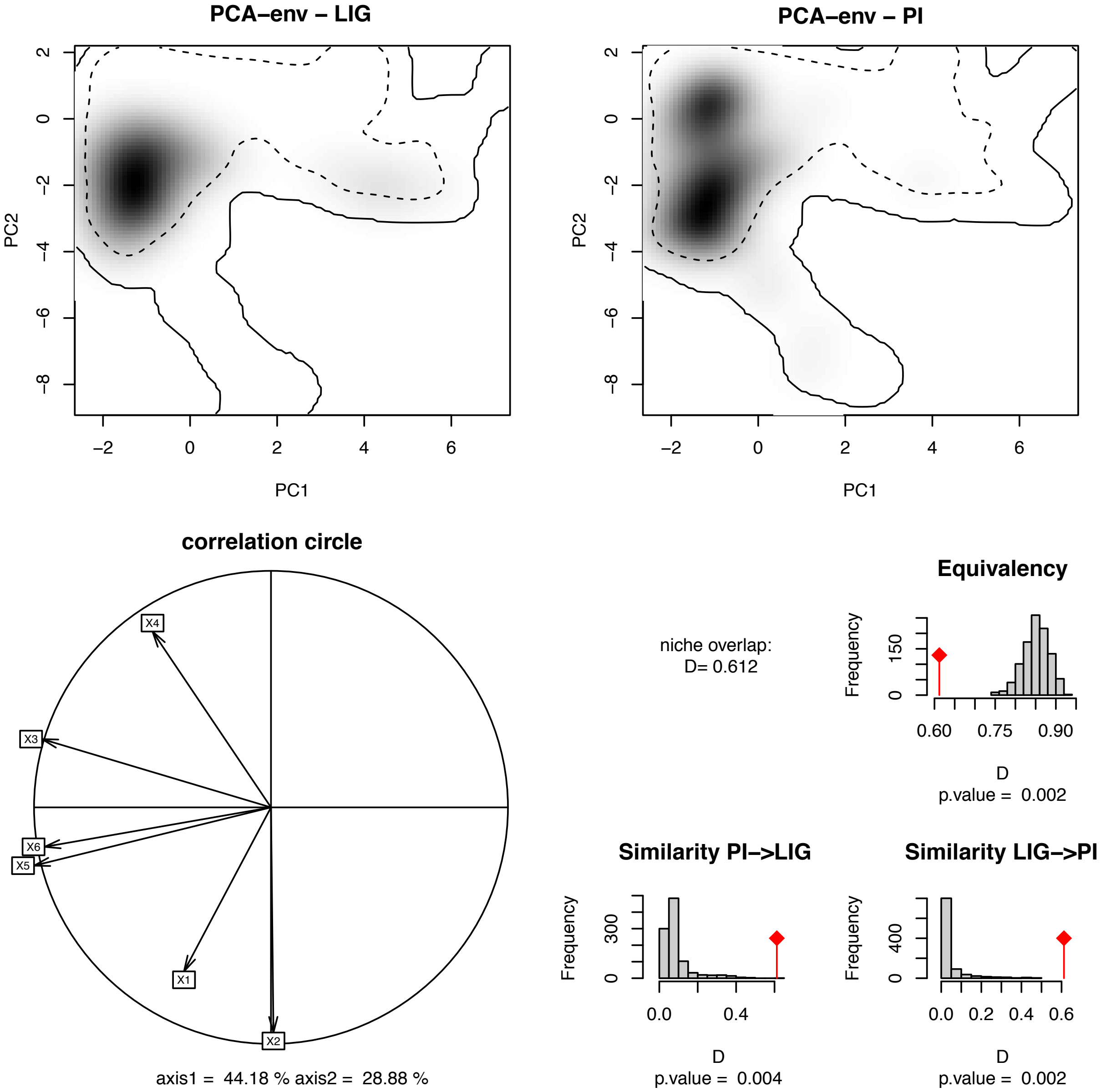


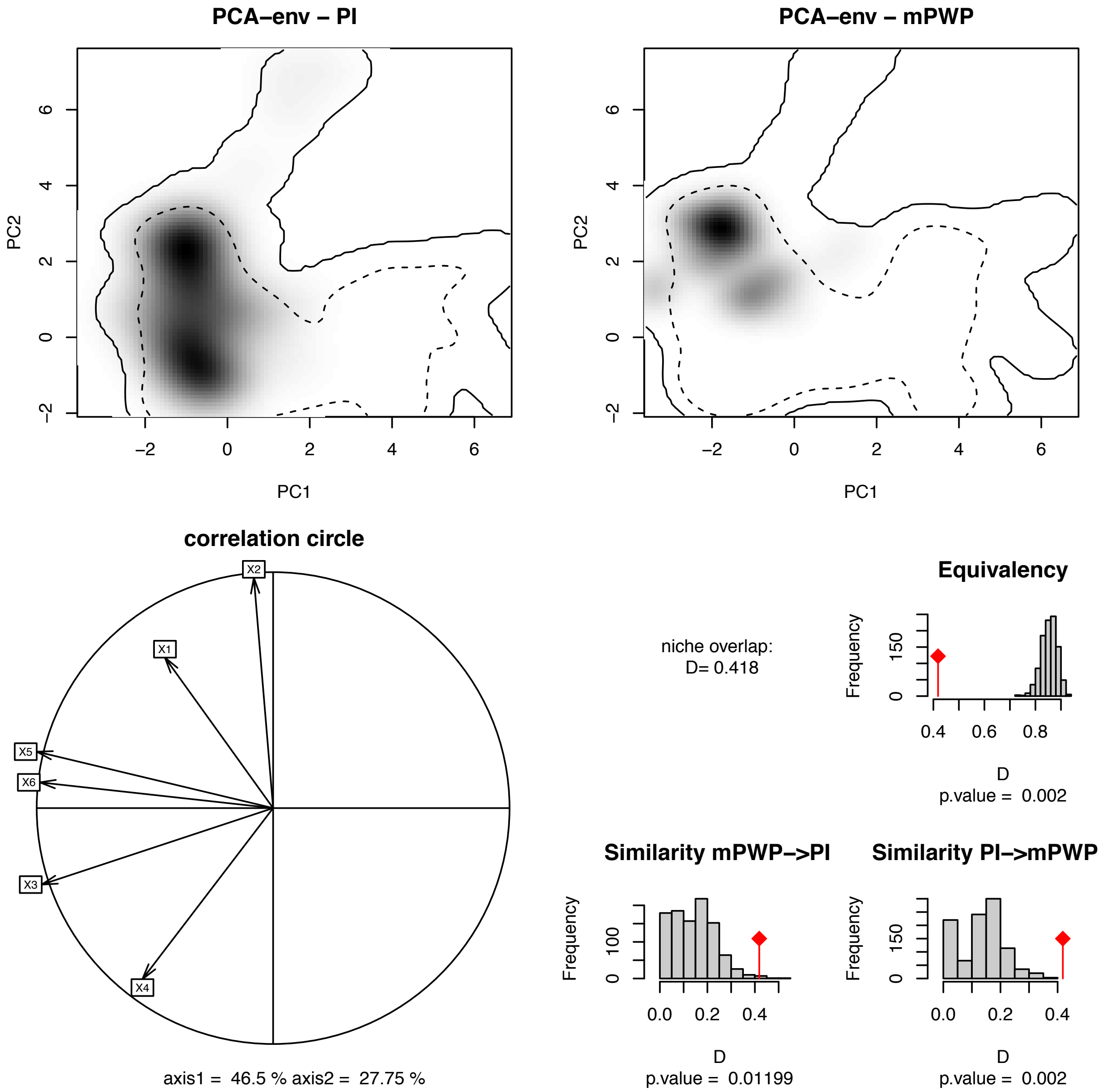
Terebra dislocata: **LIG—mPWP**



Terebra dislocata: **LIG—PI**



Terebra dislocata: **PI—mPWP**



PCA–env – PI

PCA–env – mPWP

correlation circle

Equivalency

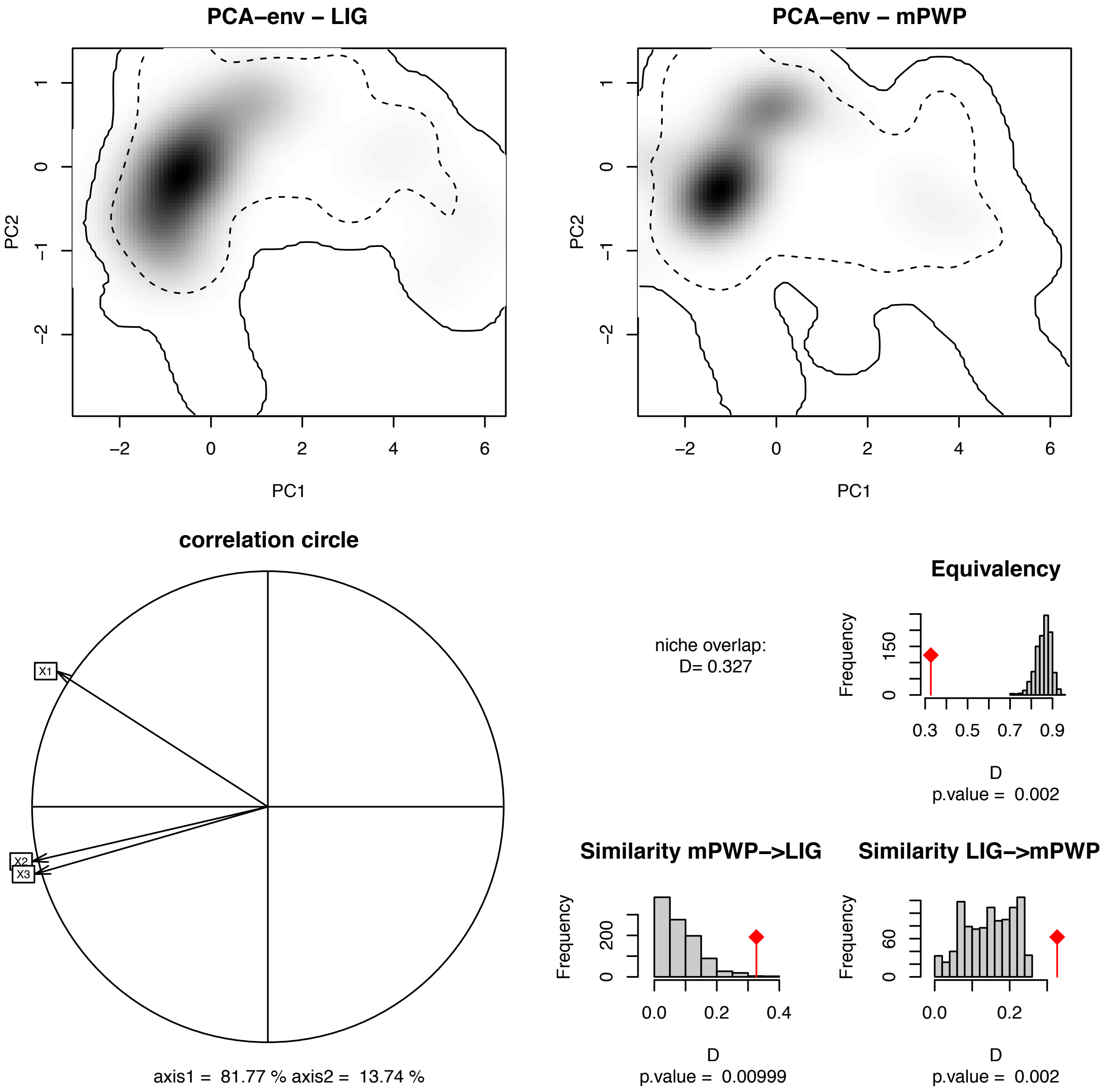
Similarity mPWP–>PI

Similarity PI–>mPWP

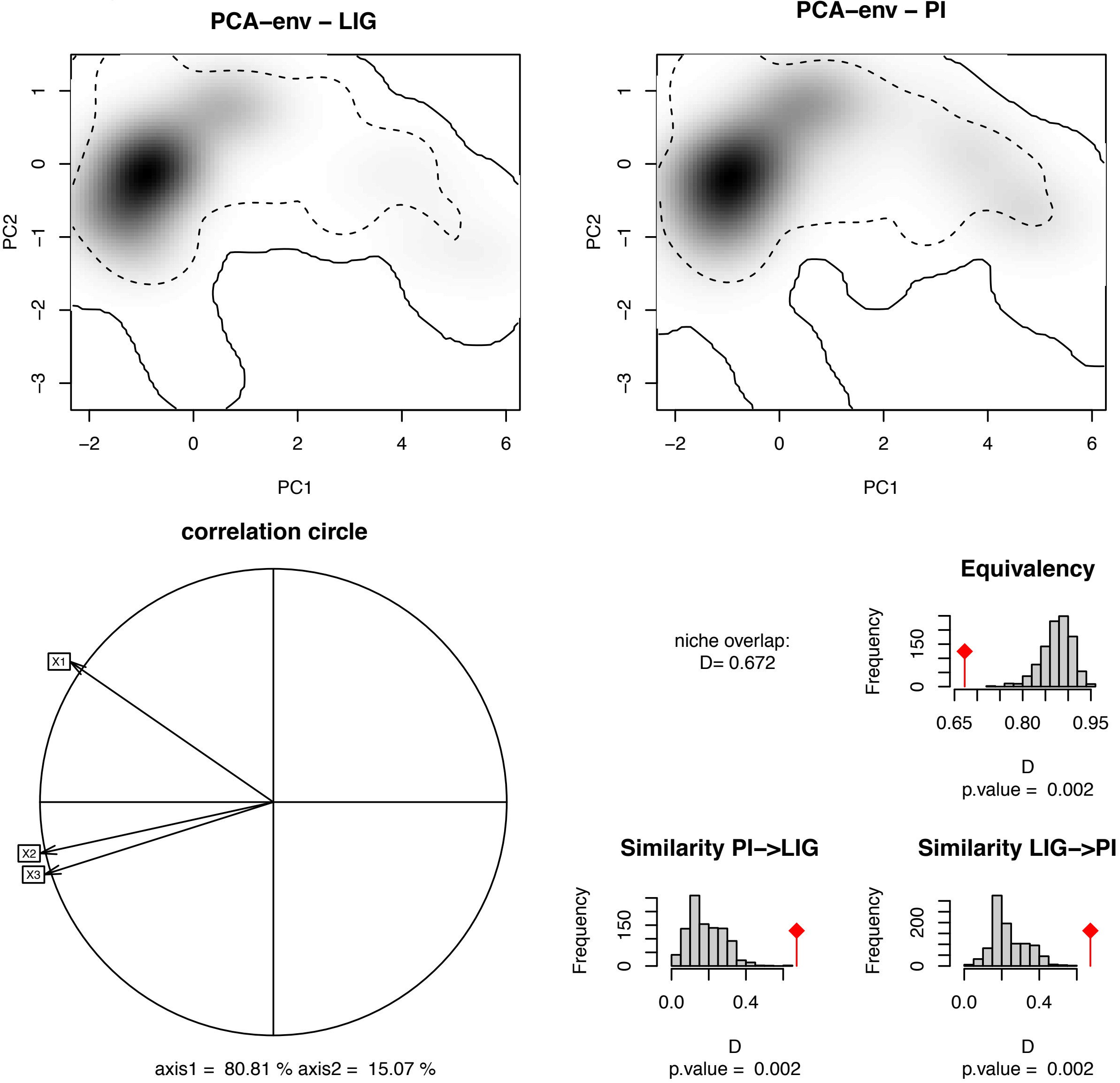
Appendix S2.3b. Environmental comparisons using a PCA applied to the three most important variables

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.

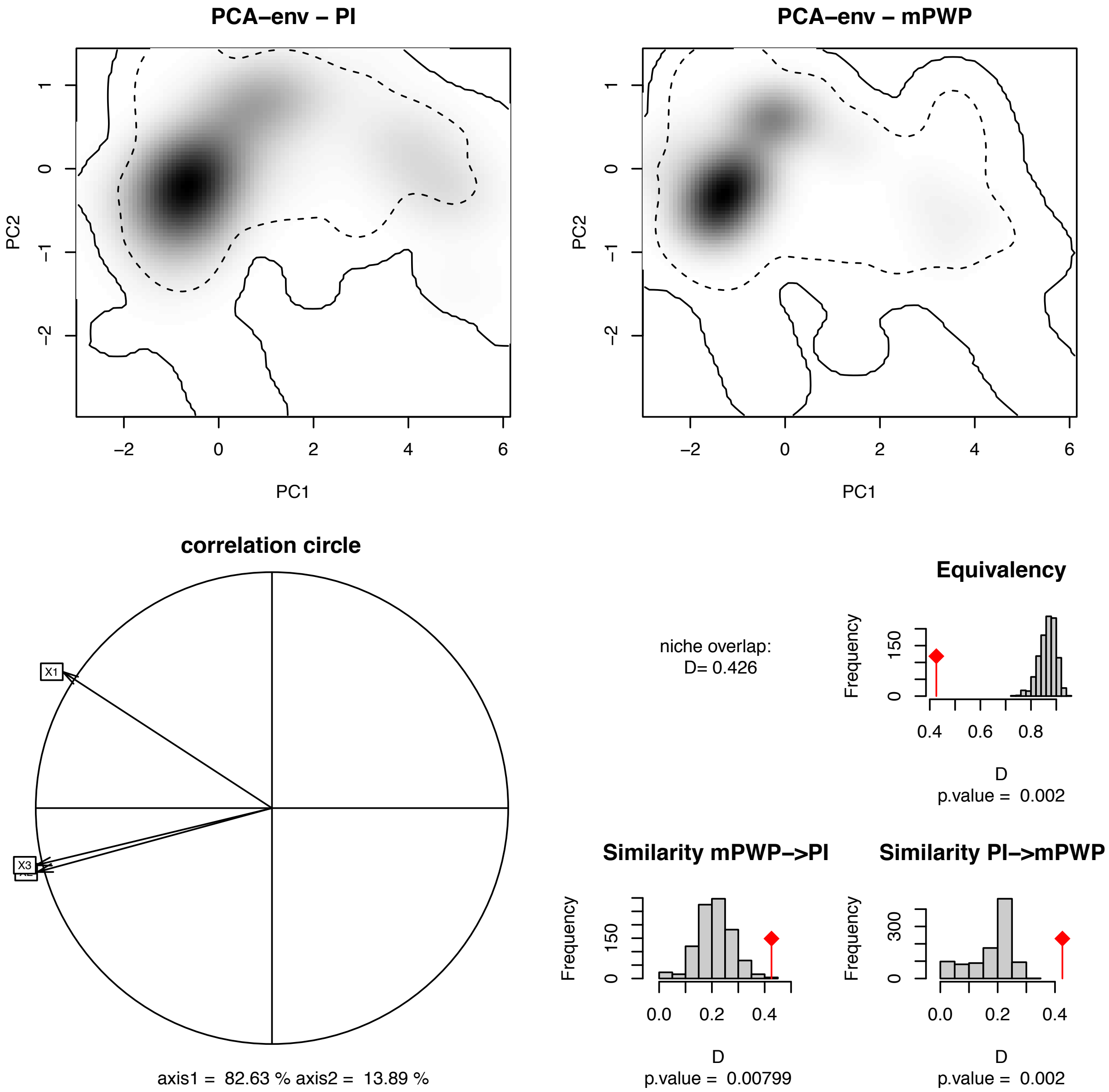
Anomia simplex: **LIG—mPWP**



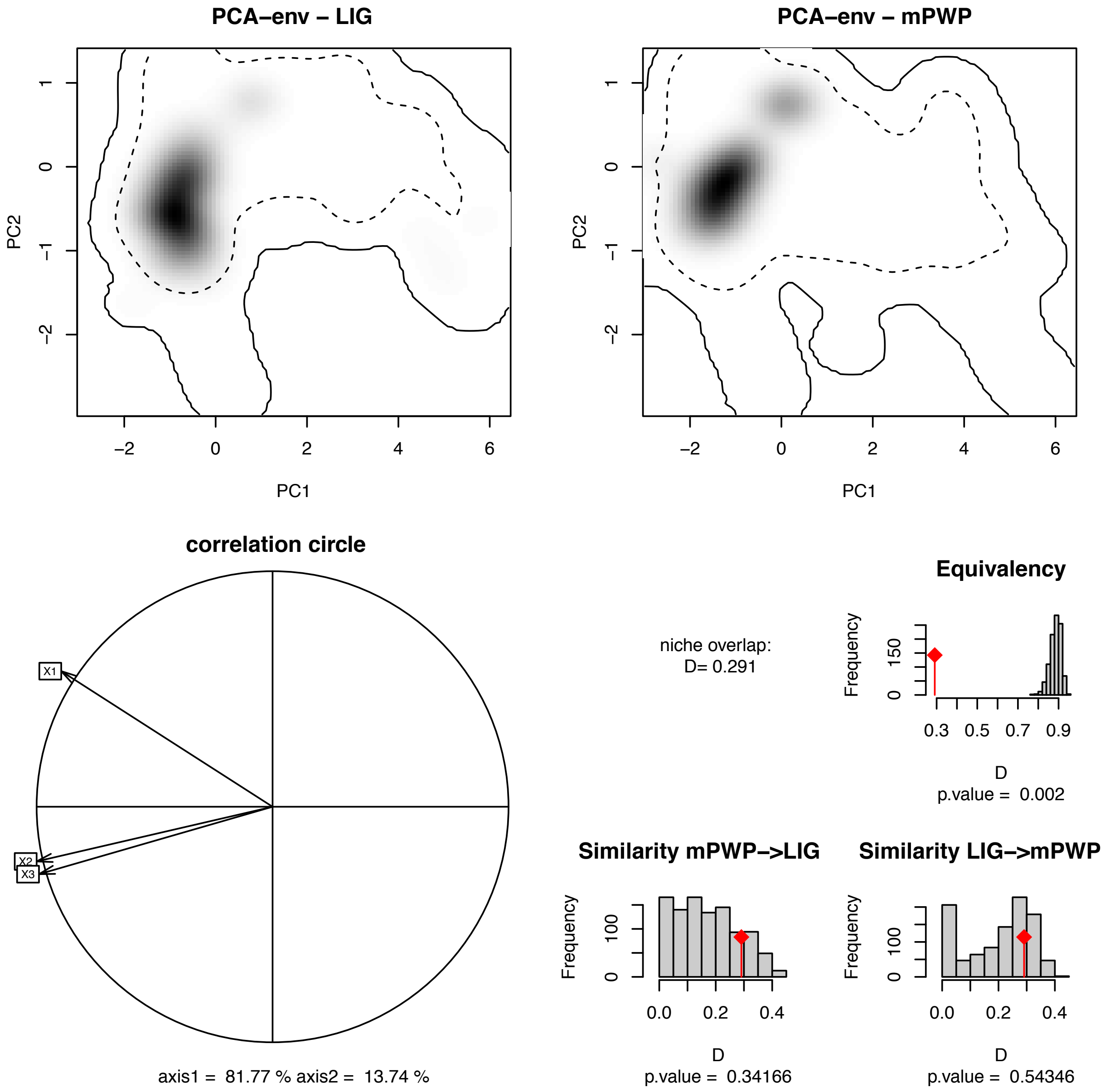
Anomia simplex: **LIG—PI**



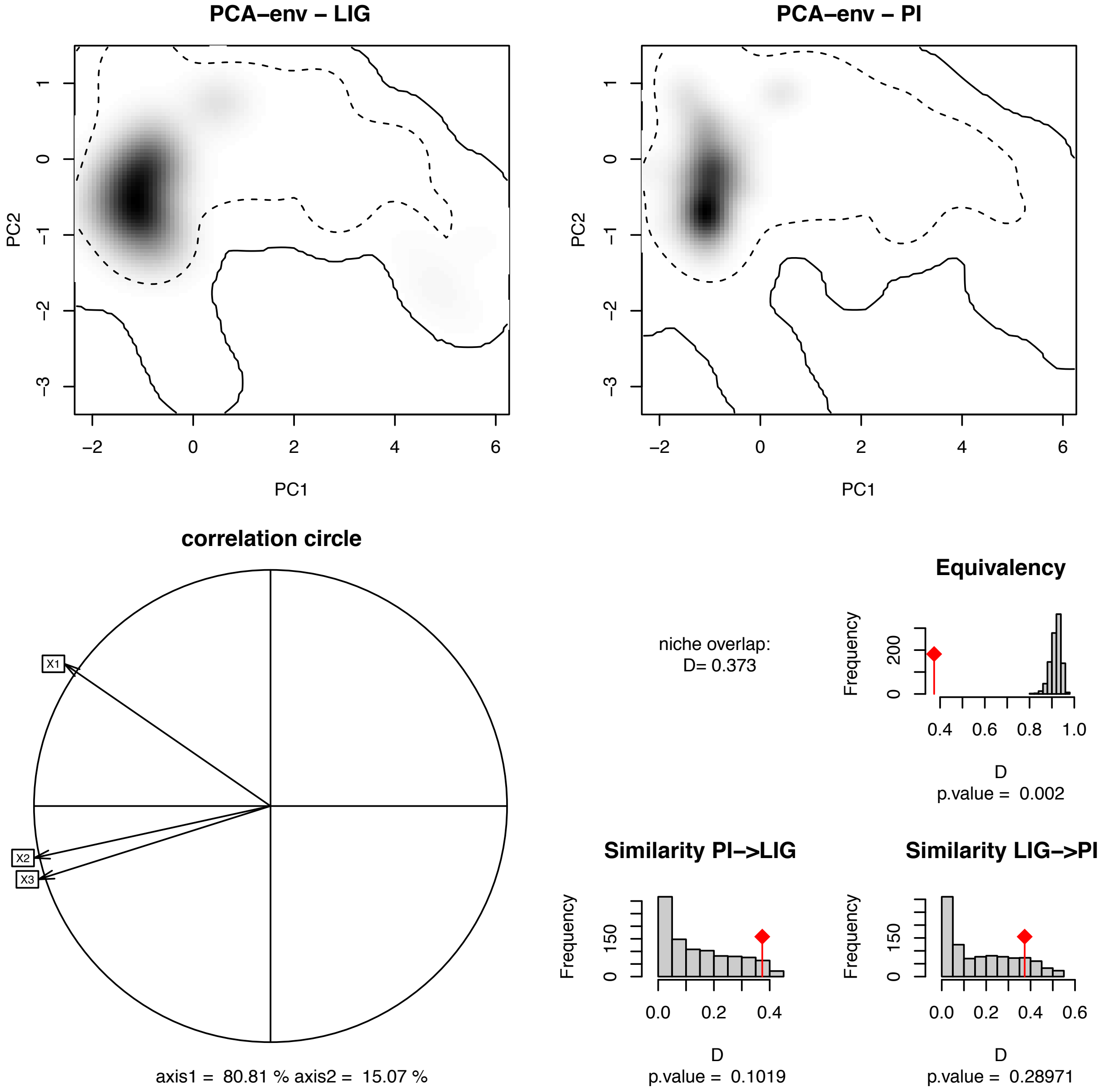
Anomia simplex: **PI—mPWP**



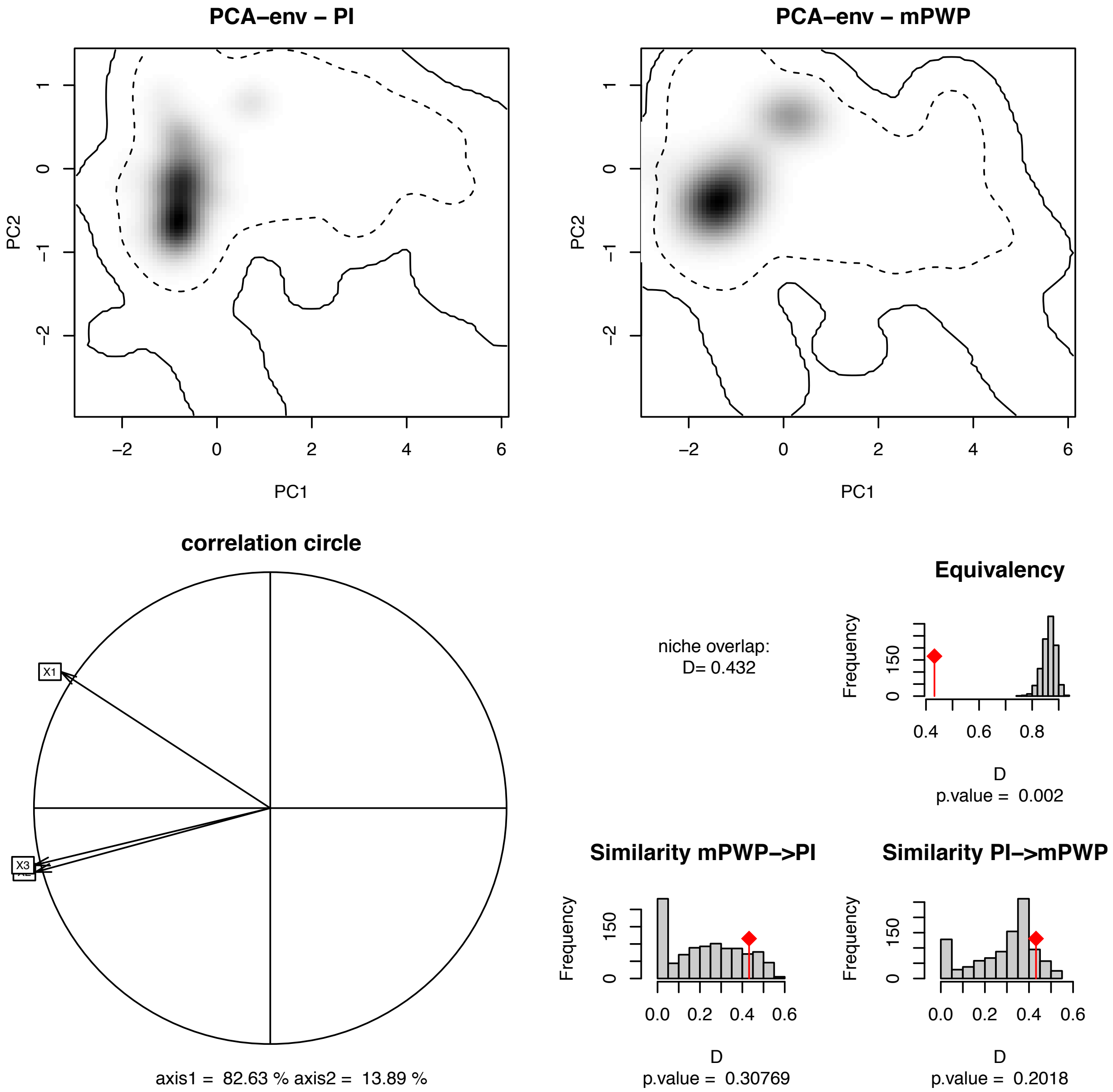
Bulla occidentalis: **LIG—mPWP**



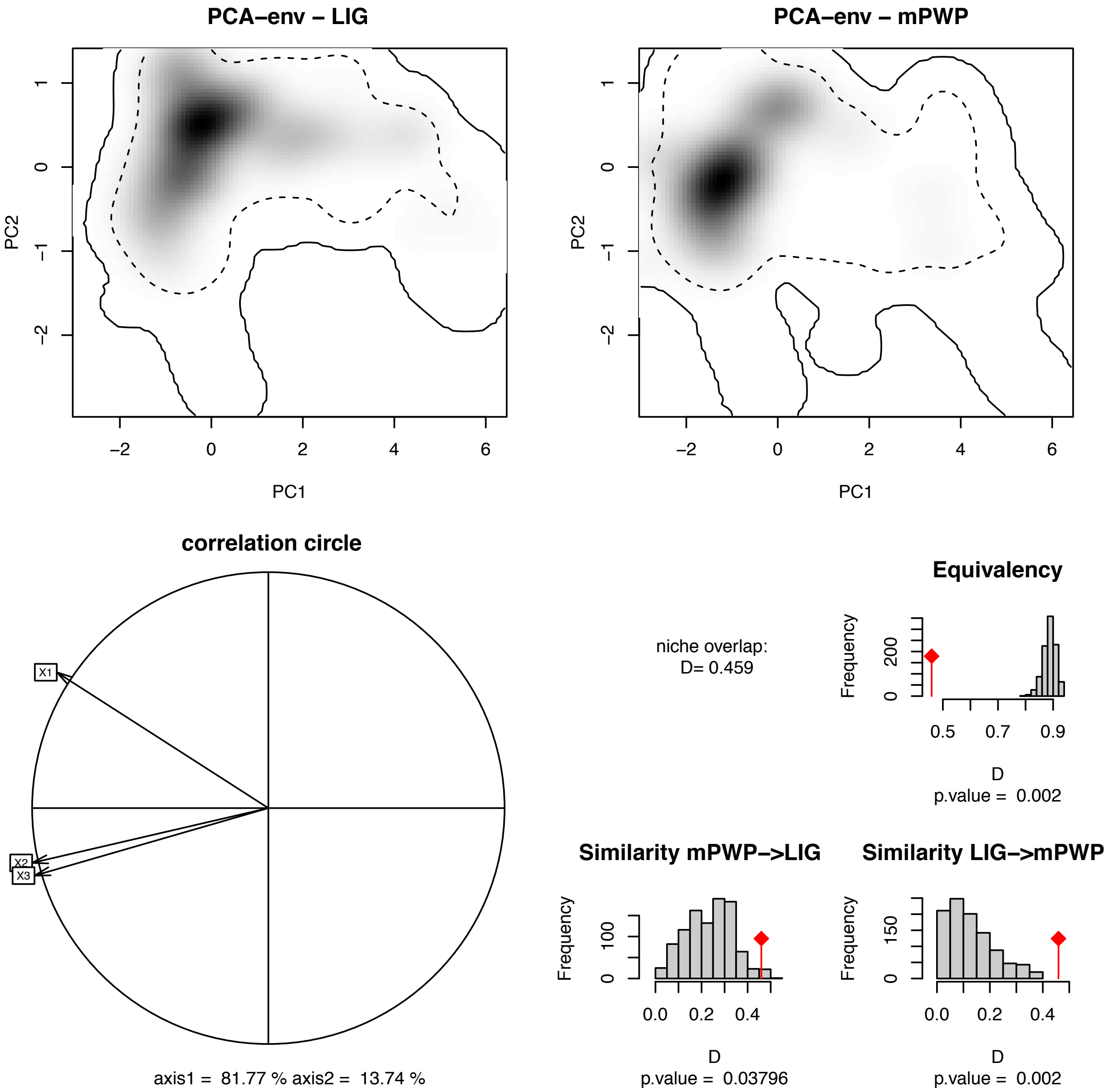
Bulla occidentalis: **LIG—PI**



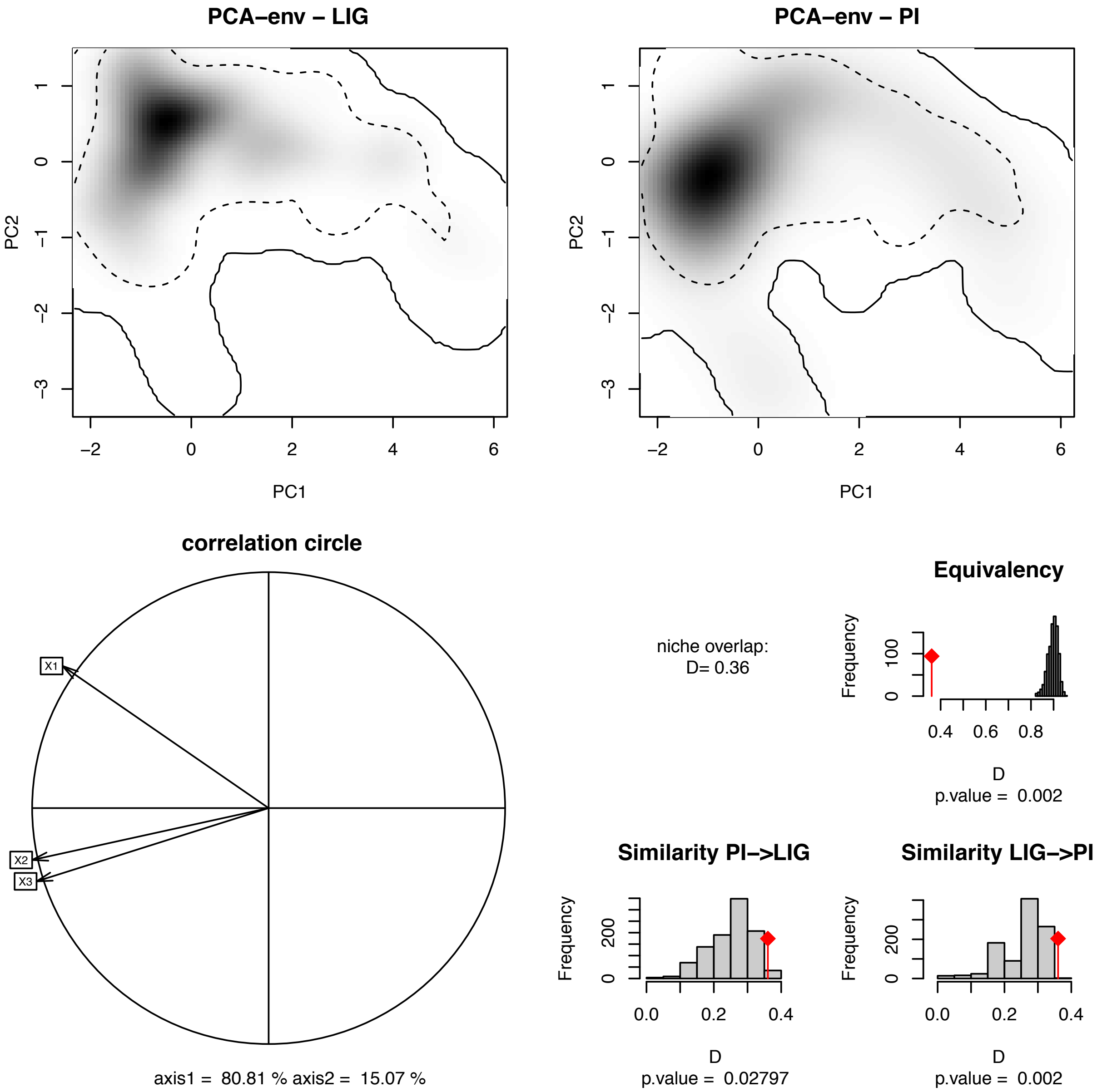
Bulla occidentalis: **PI—mPWP**



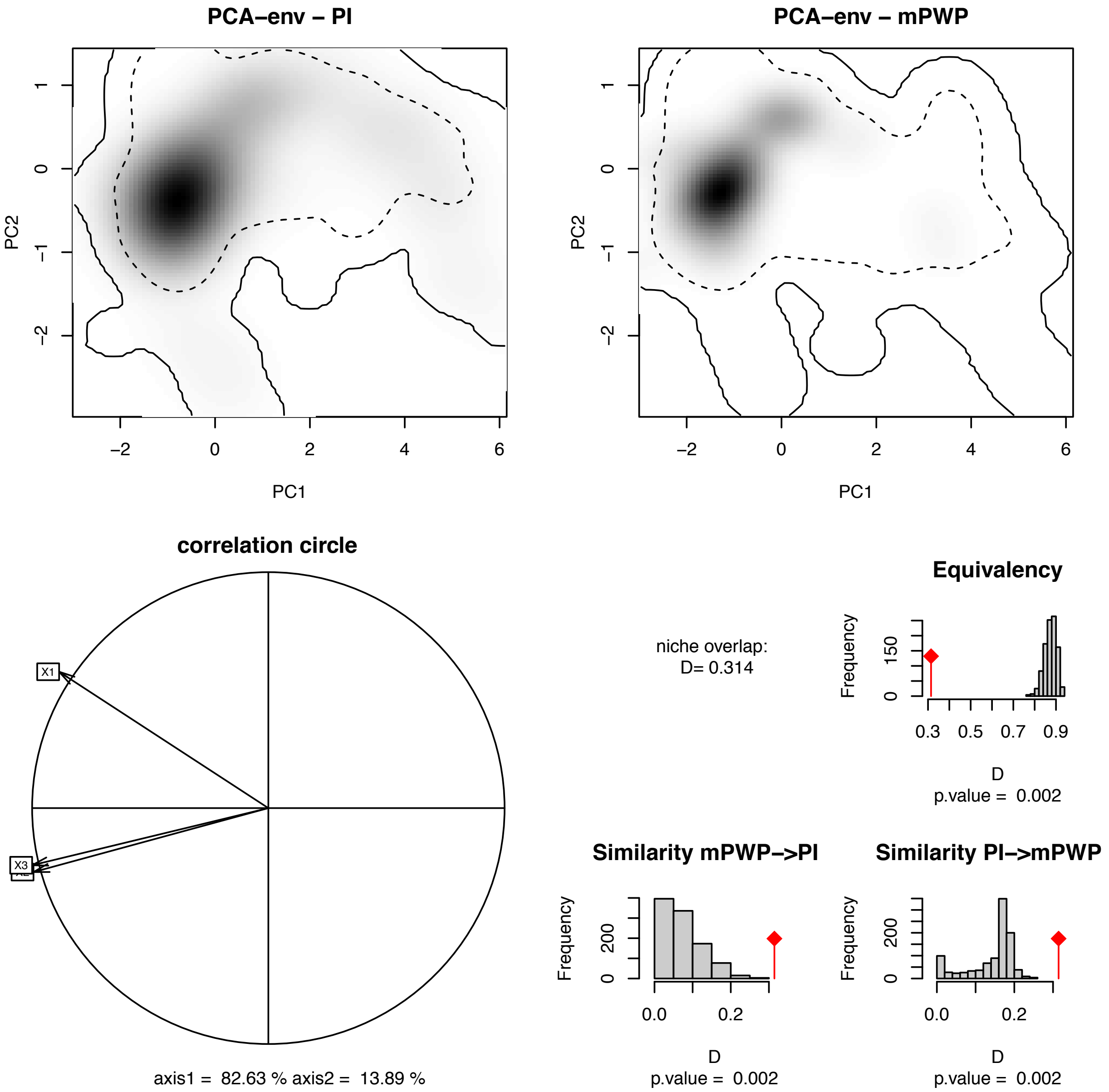
Crassostrea virginica: **LIG—mPWP**



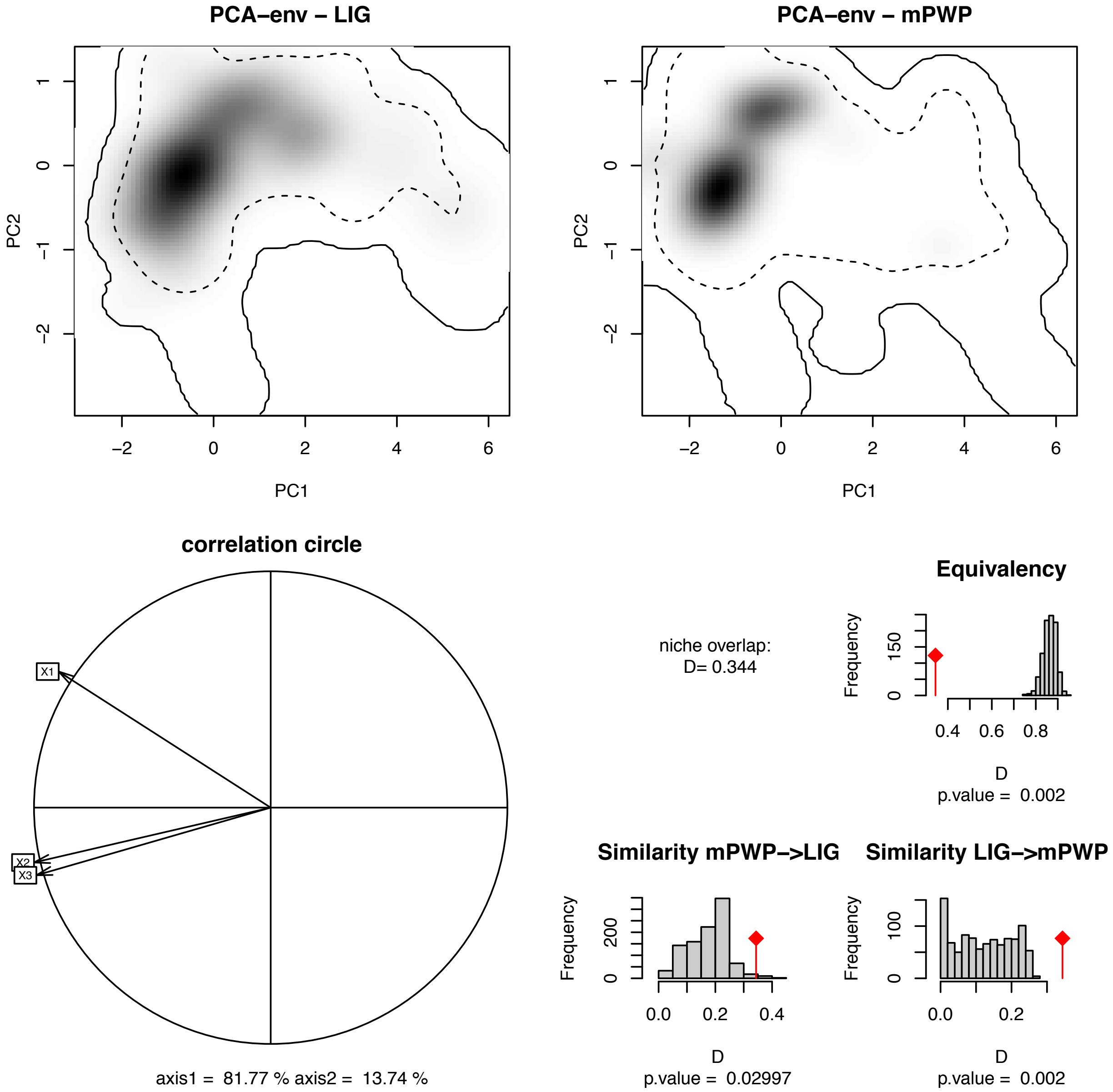
Crassostrea virginica: **LIG—PI**



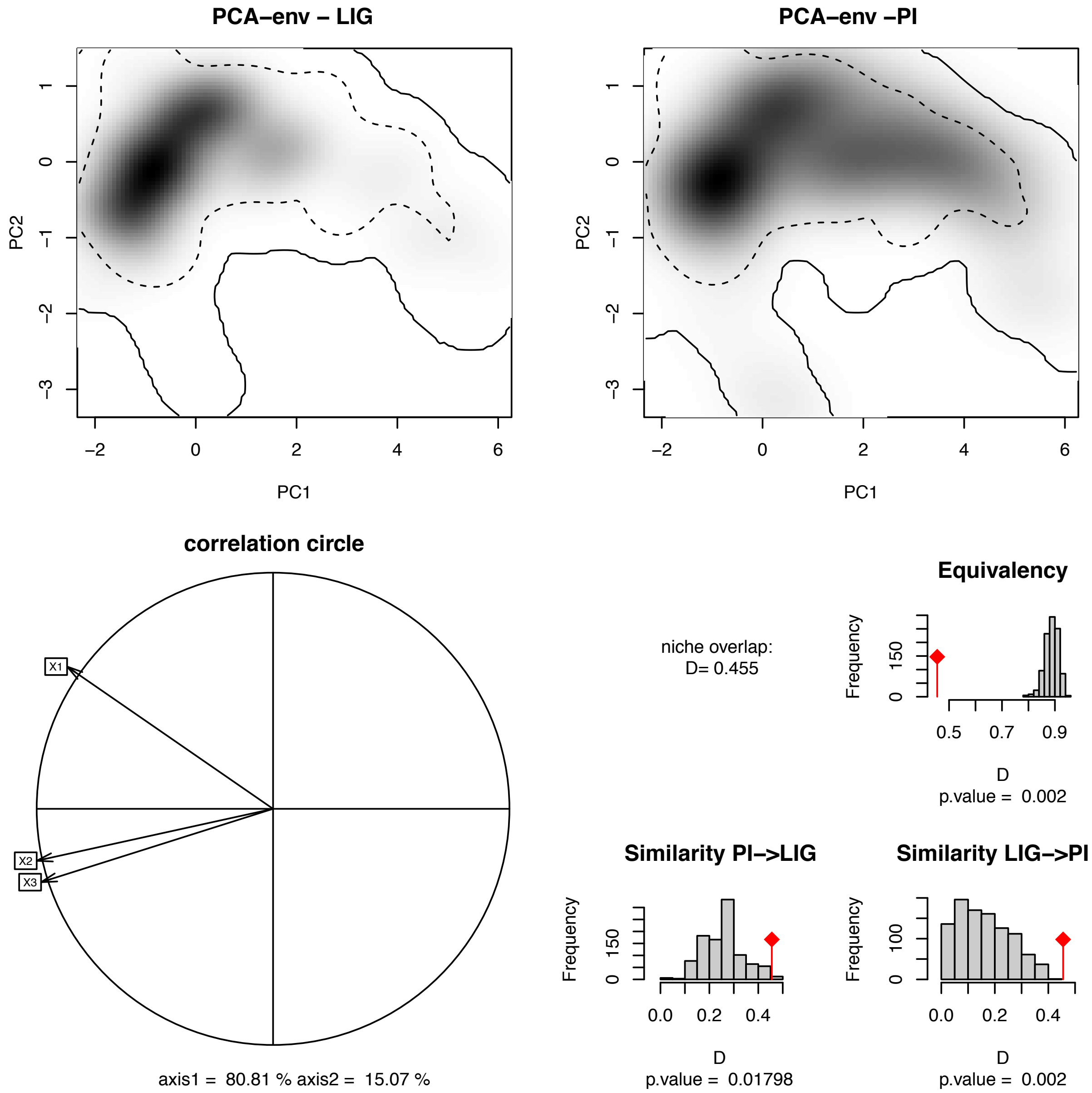
Crassostrea virginica: **PI—mPWP**



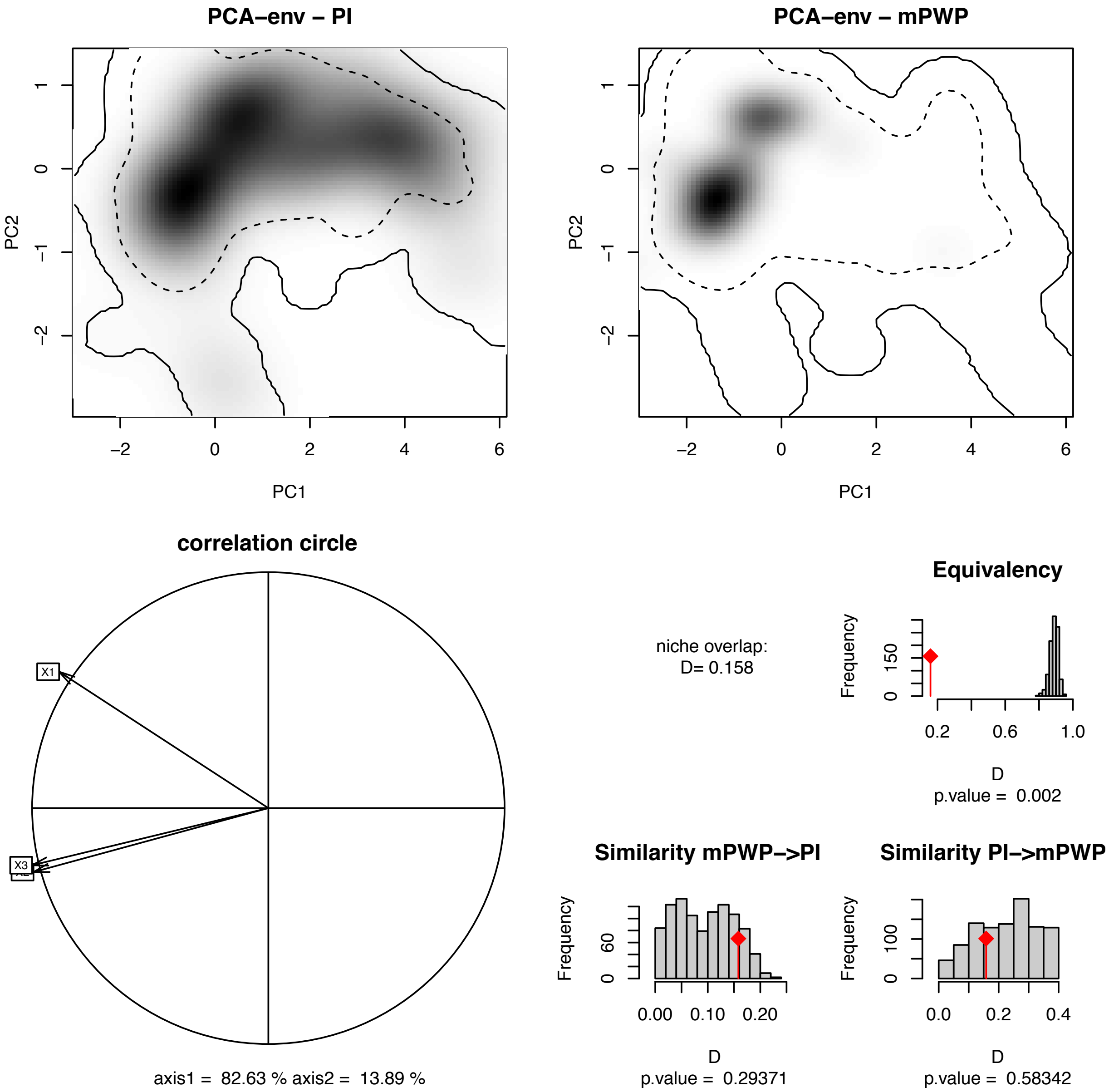
Crepidula fornicata: **LIG—mPWP**



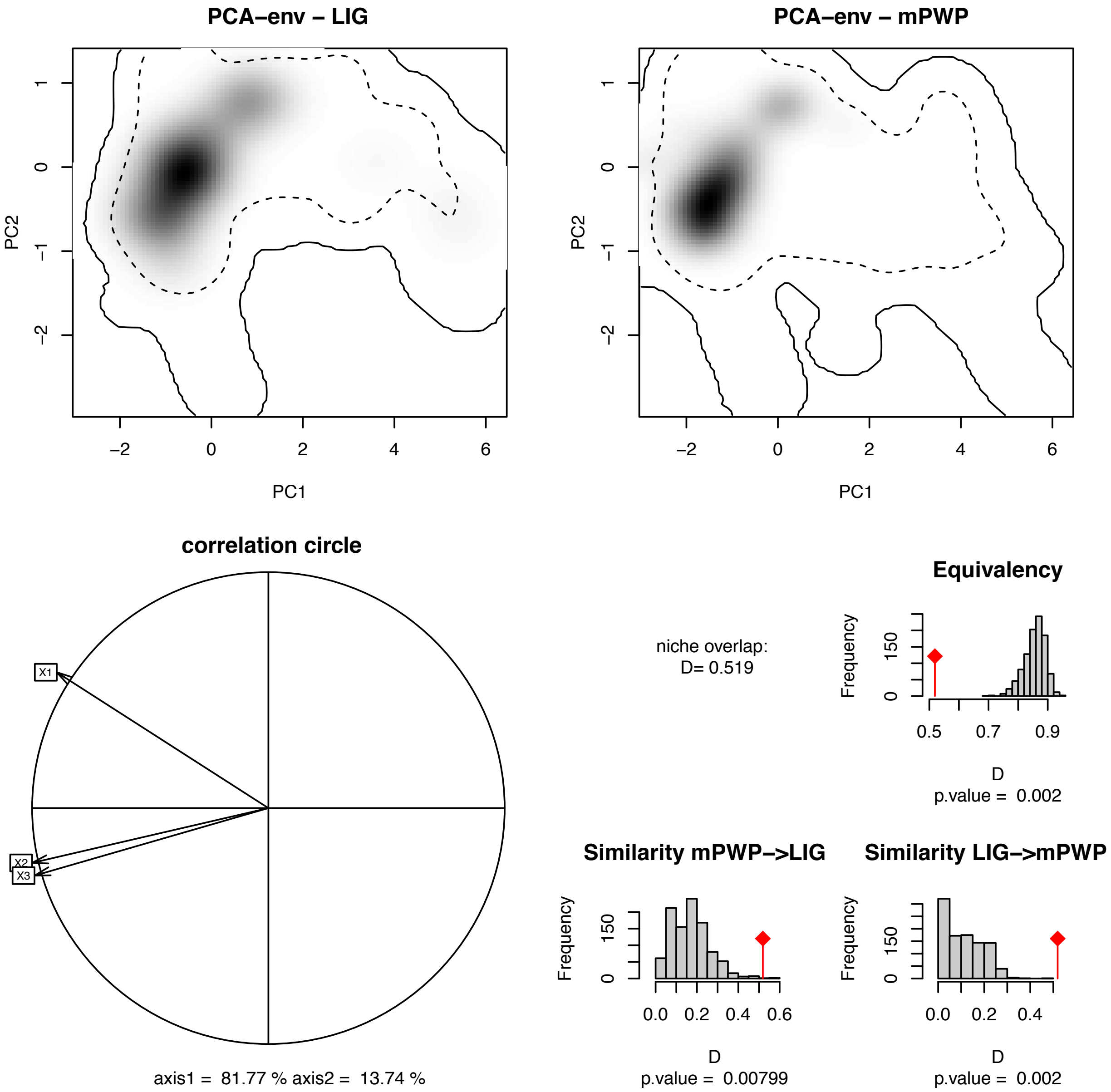
Crepidula fornicata: **LIG—PI**



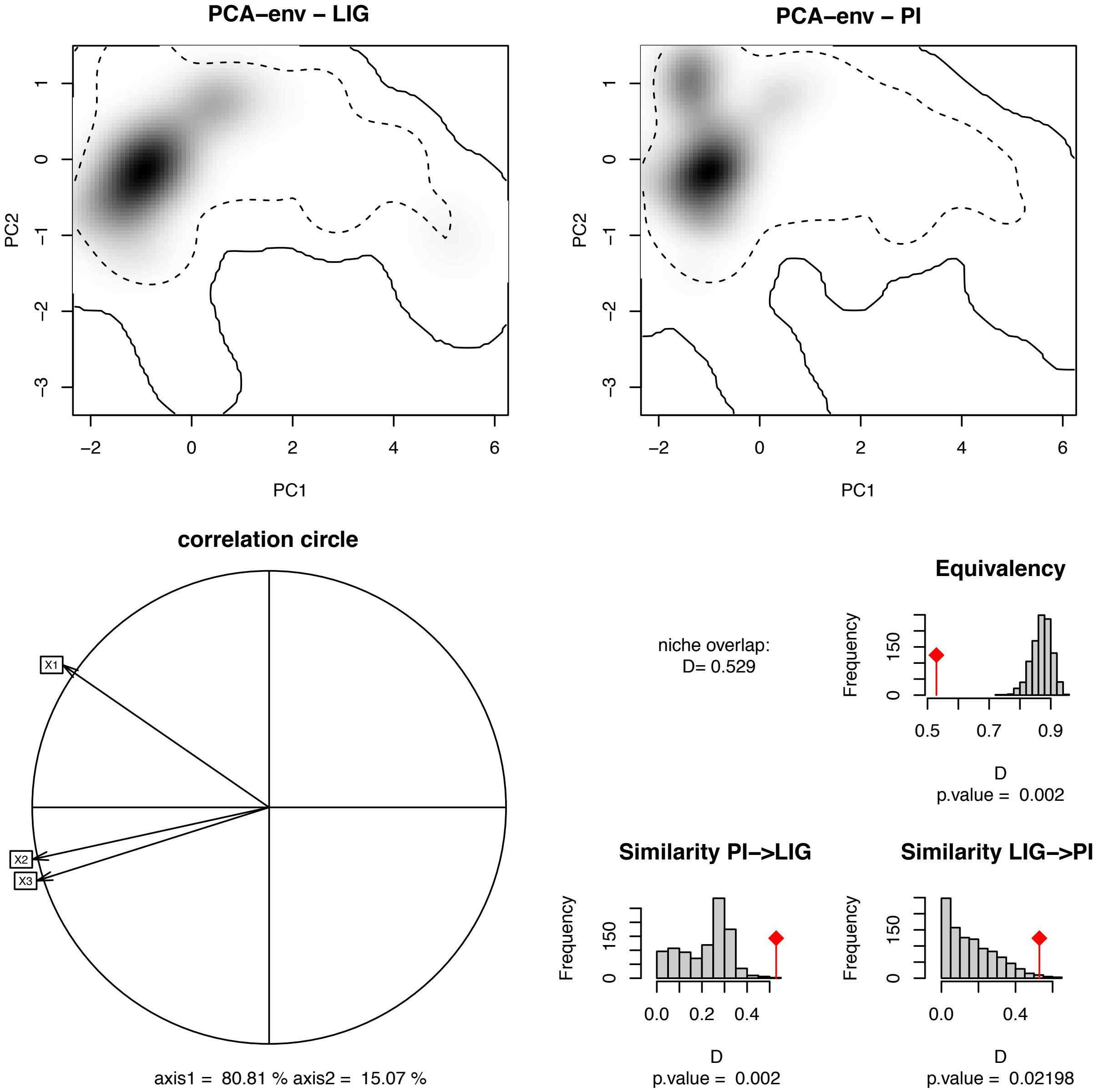
Crepidula fornicata: **PI—mPWP**



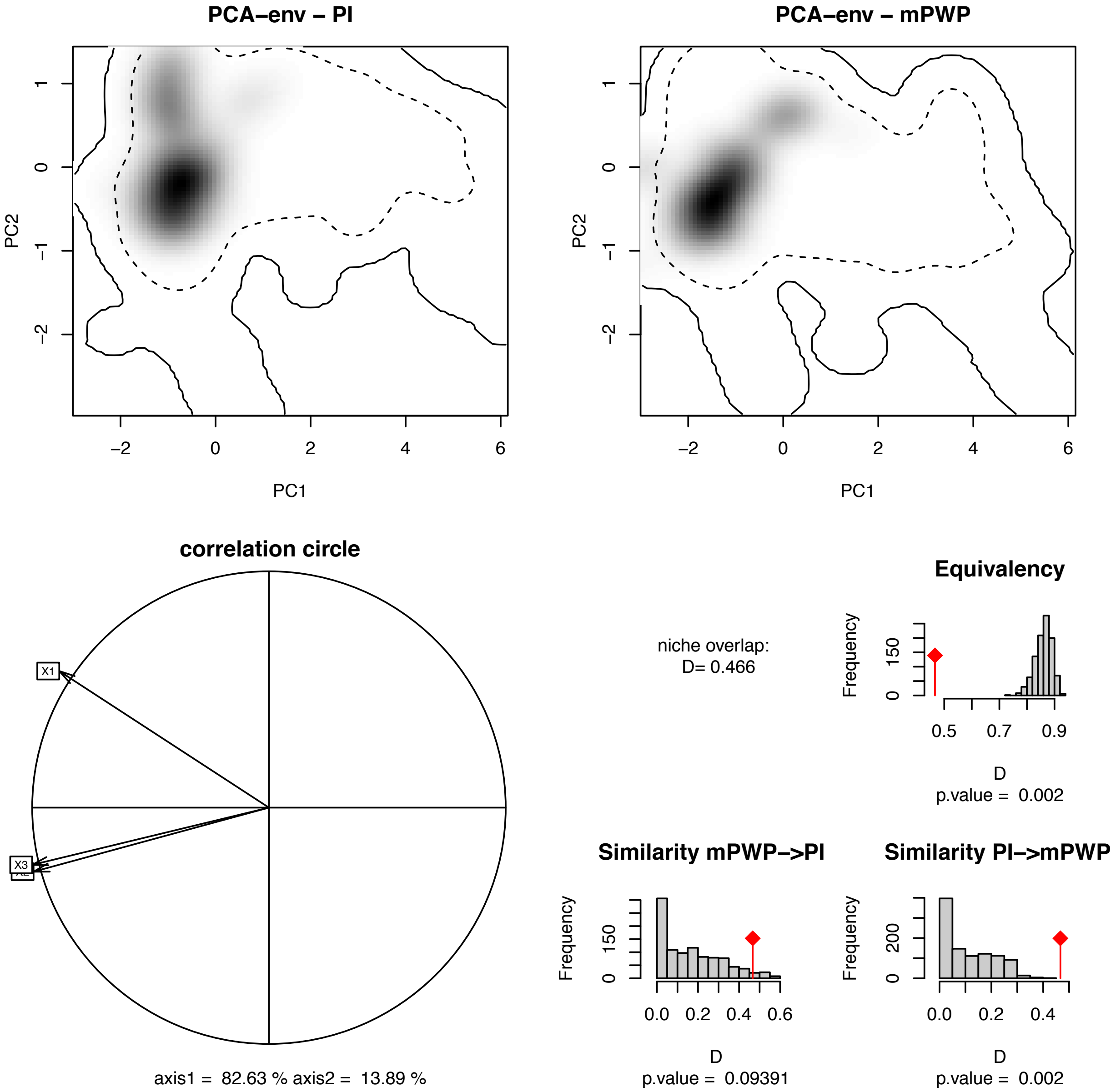
Dinocardium robustum: **LIG—mPWP**



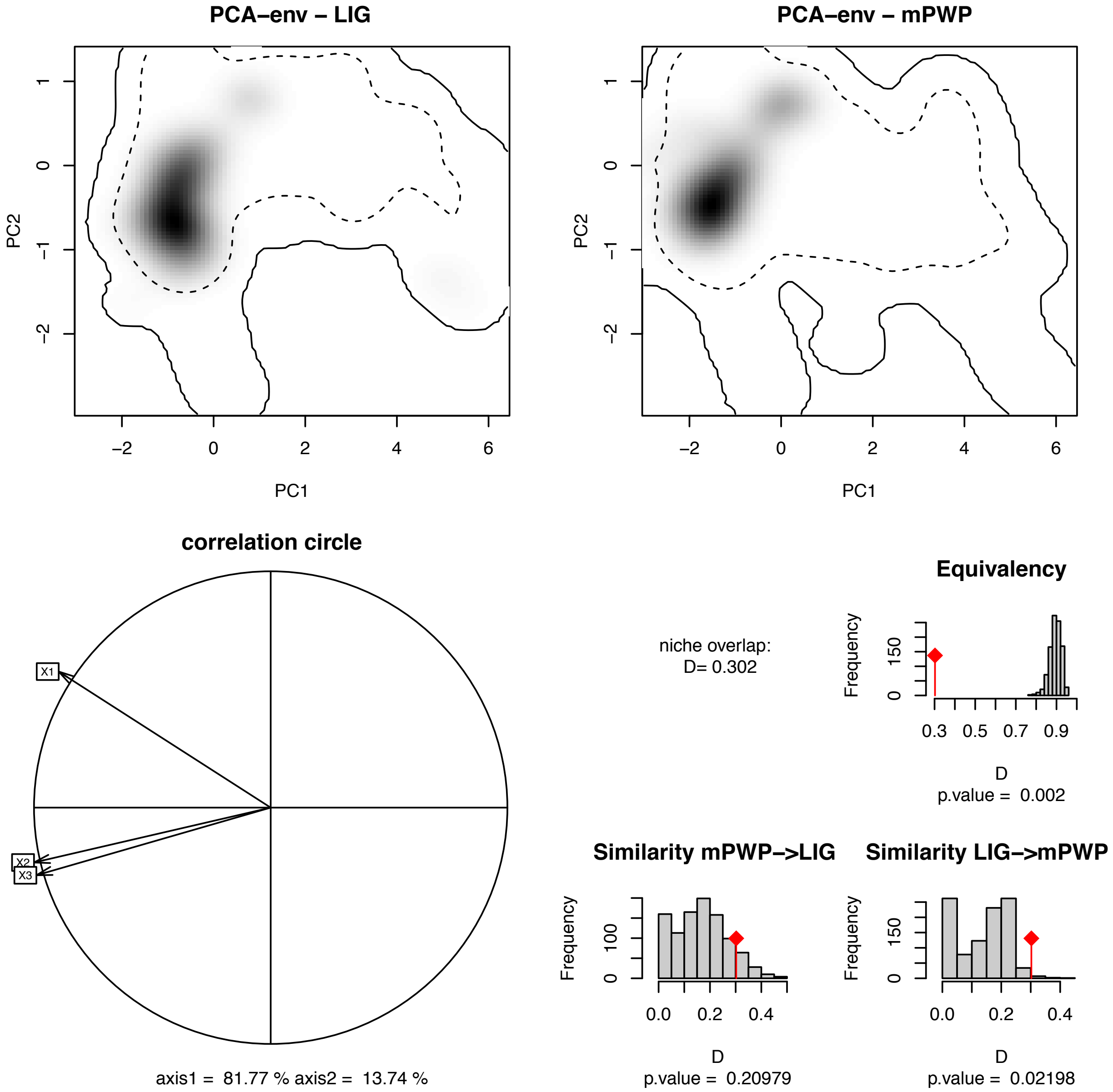
Dinocardium robustum: **LIG—PI**



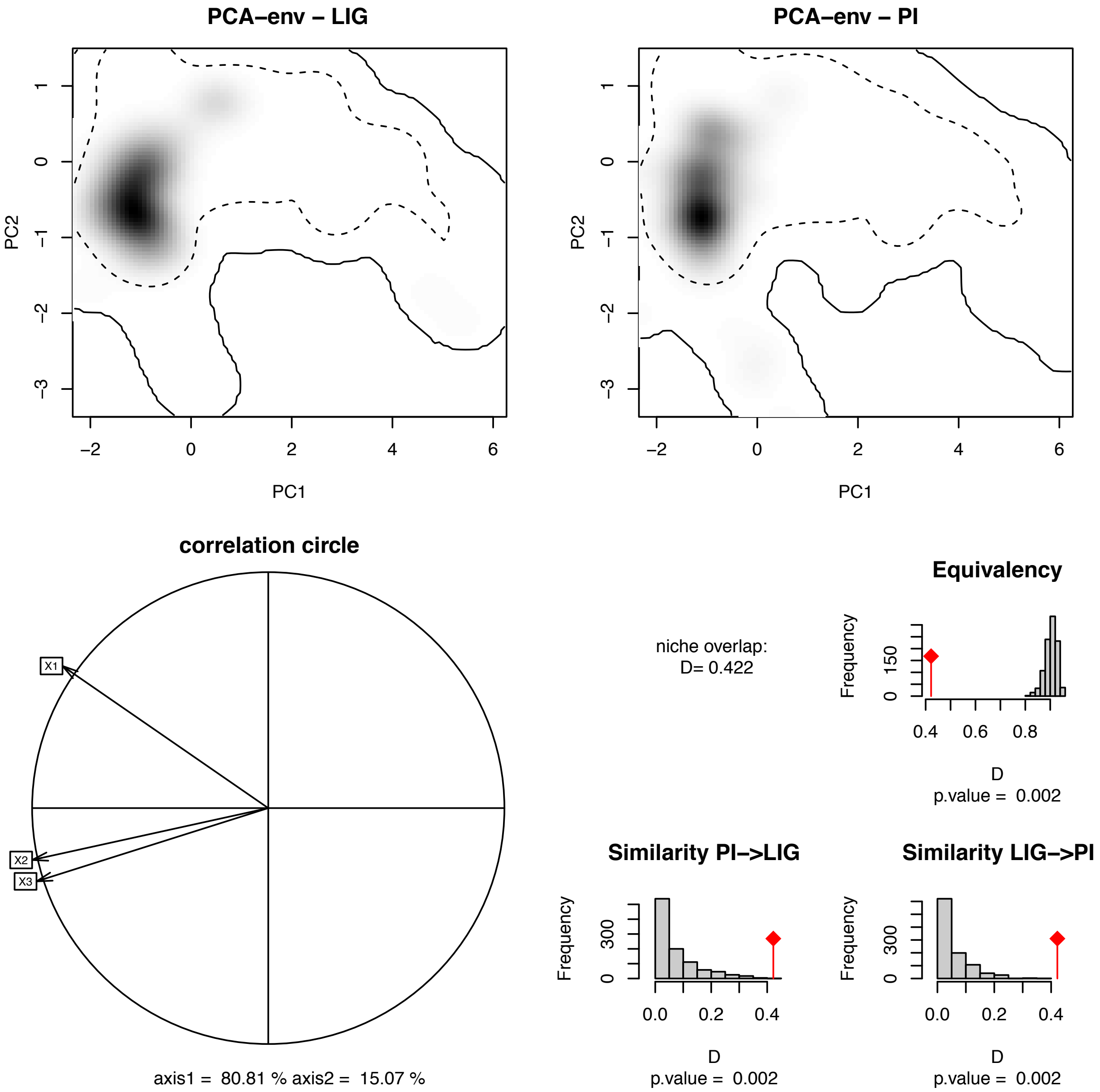
Dinocardium robustum: **PI—mPWP**



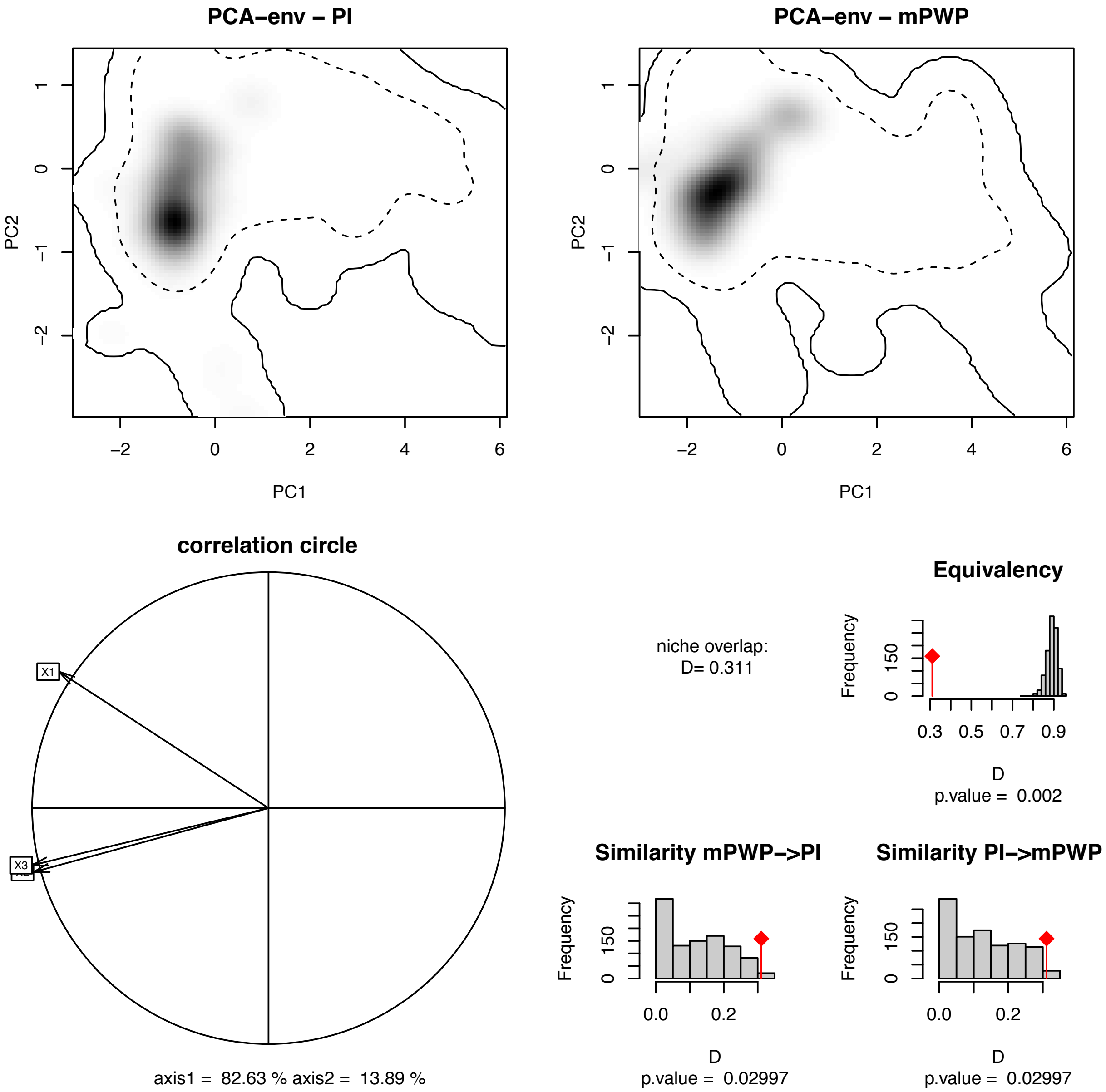
Lucina pensylvanica: **LIG—mPWP**



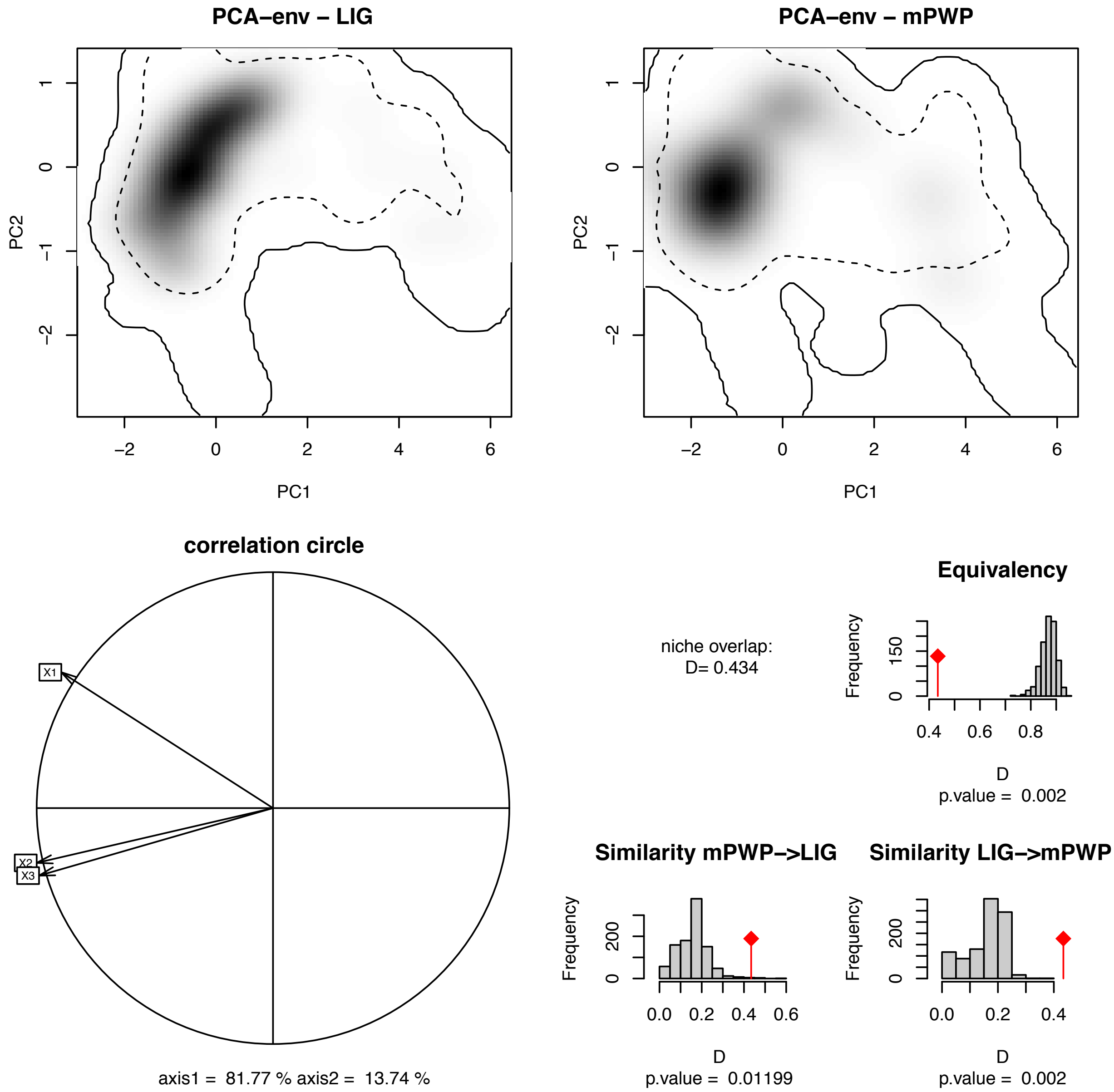
Lucina pensylvanica: **LIG—PI**



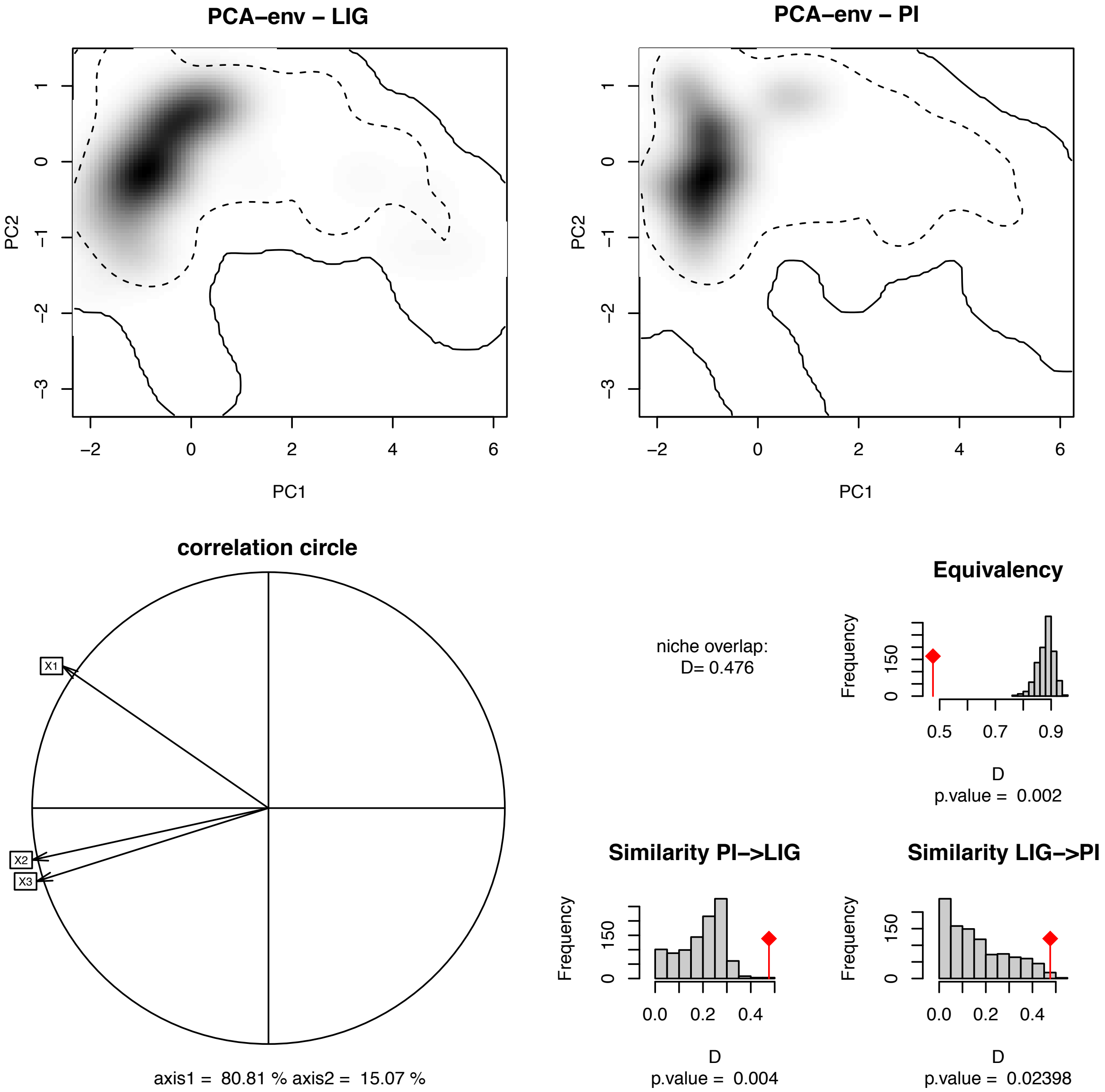
Lucina pensylvanica: **PI—mPWP**



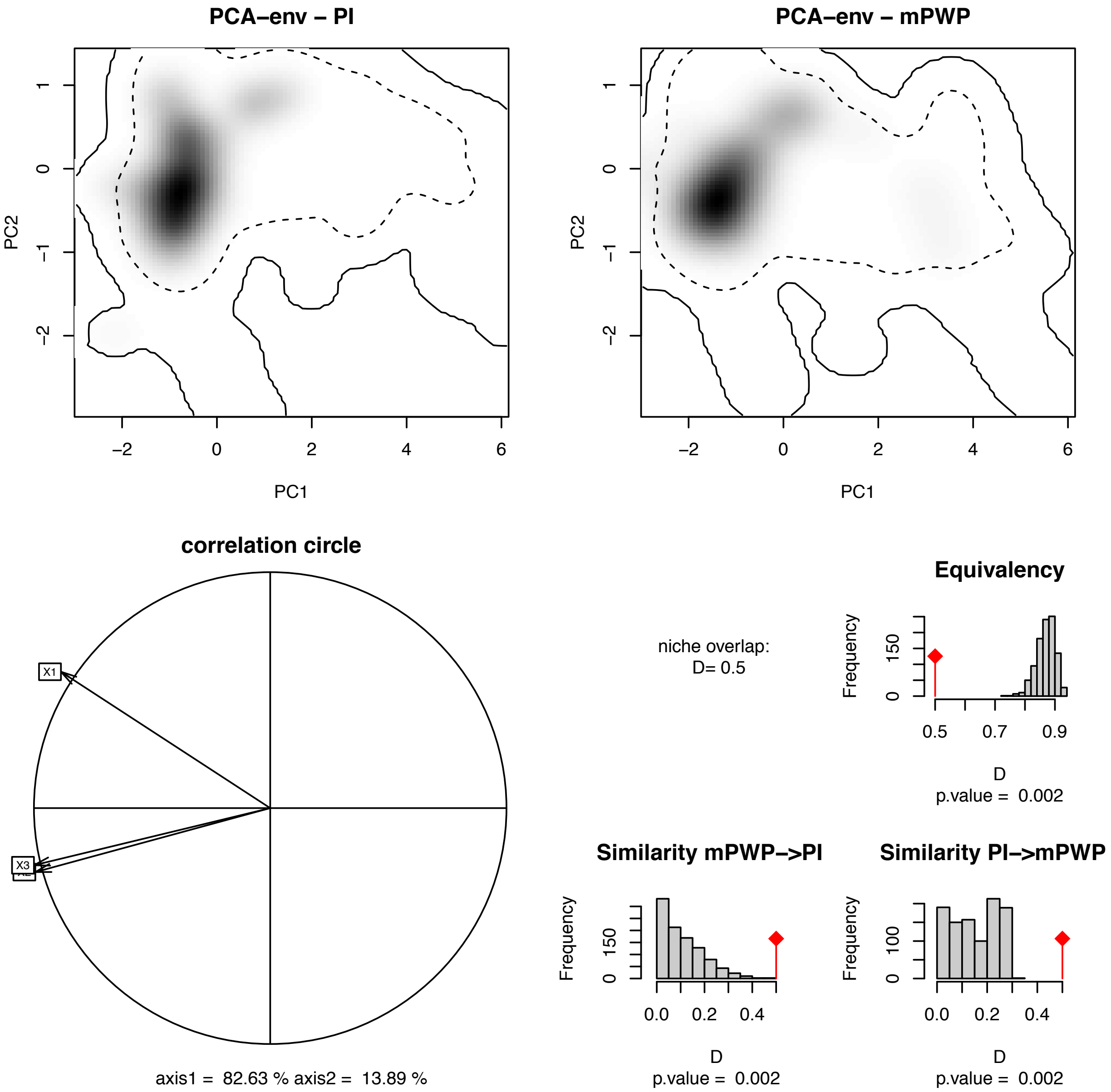
Mercenaria campechiensis: **LIG—mPWP**



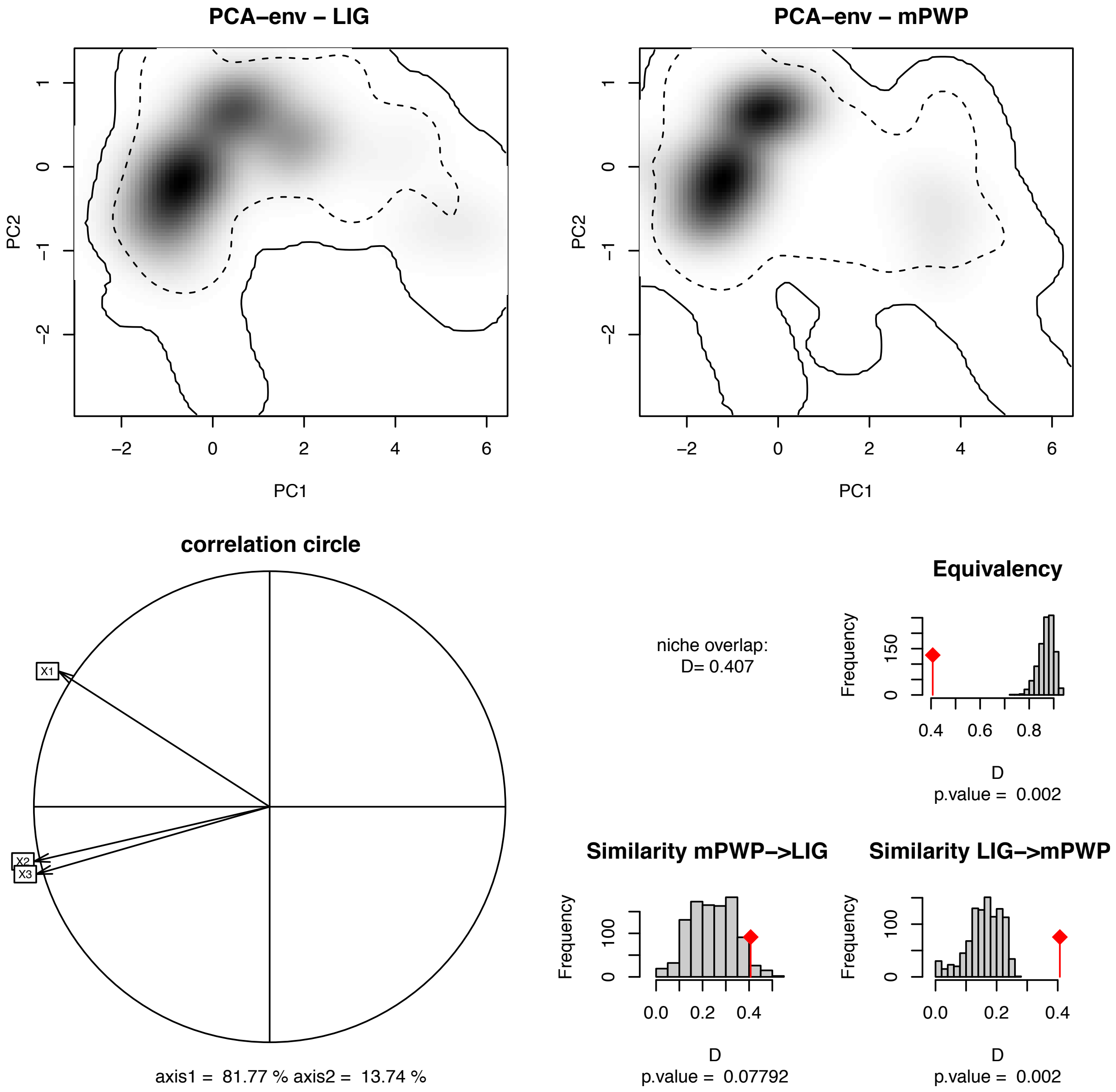
Mercenaria campechiensis: **LIG—PI**



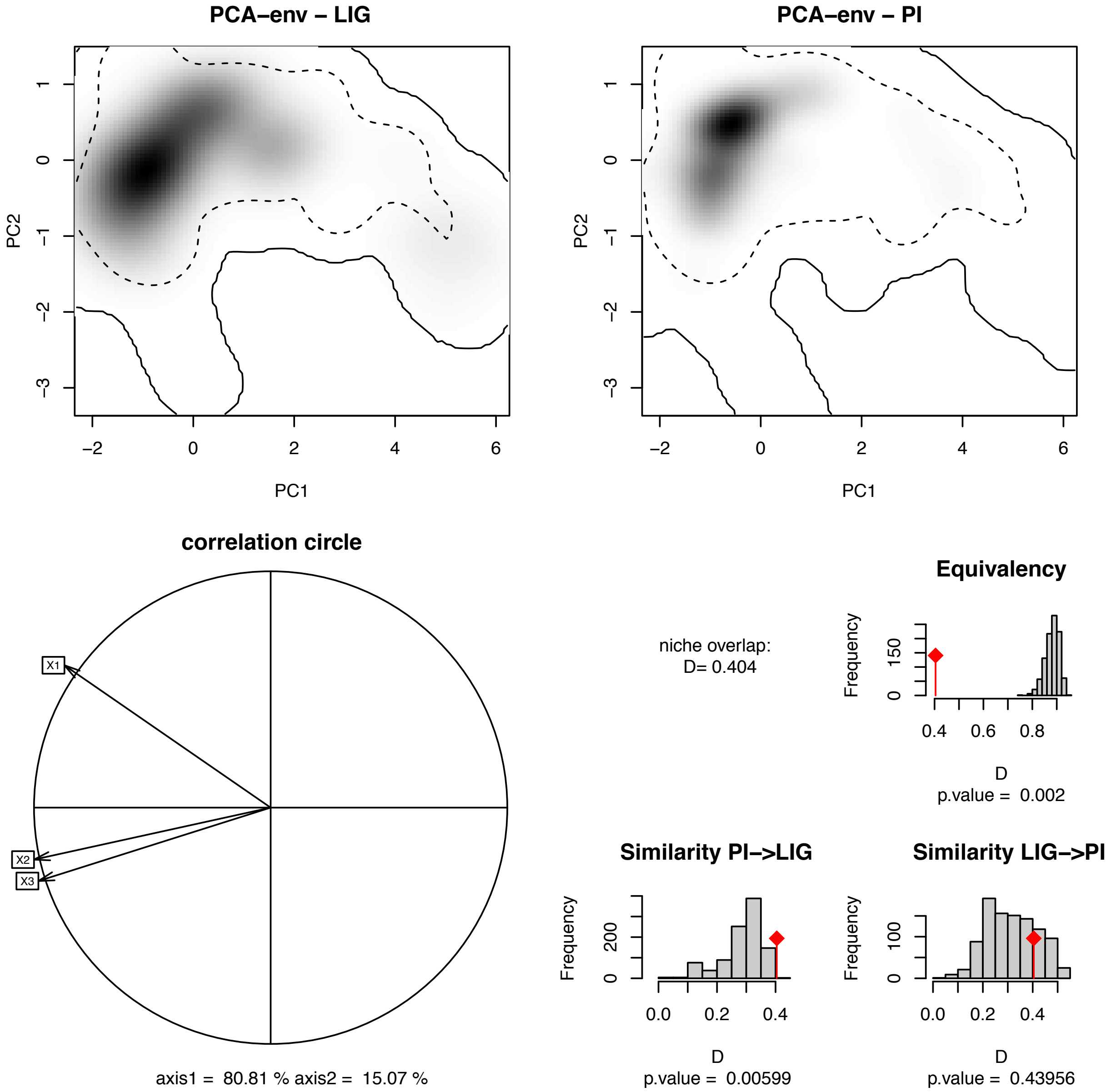
Mercenaria campechiensis: **PI—mPWP**



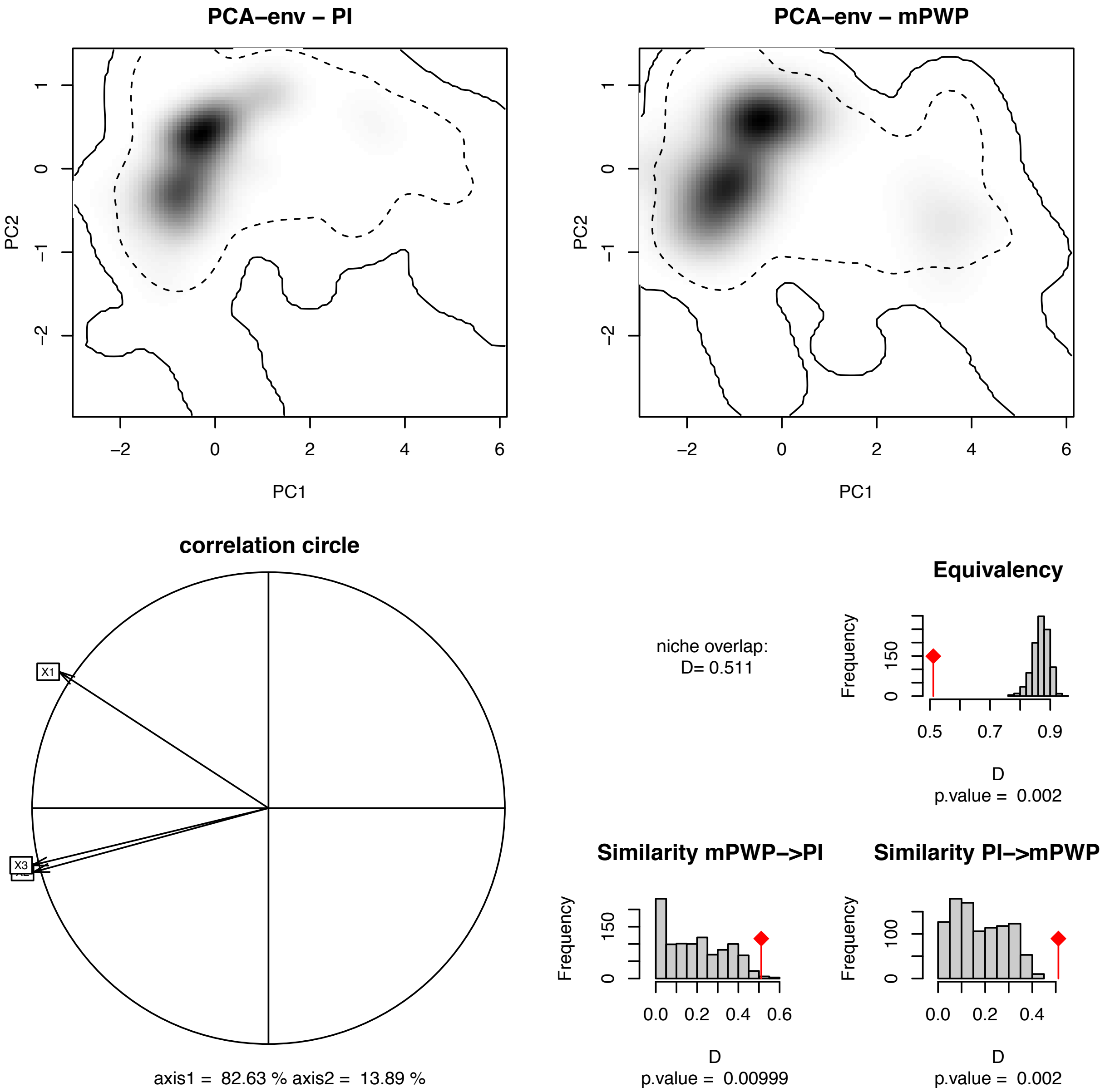
Neverita duplicata: **LIG—mPWP**



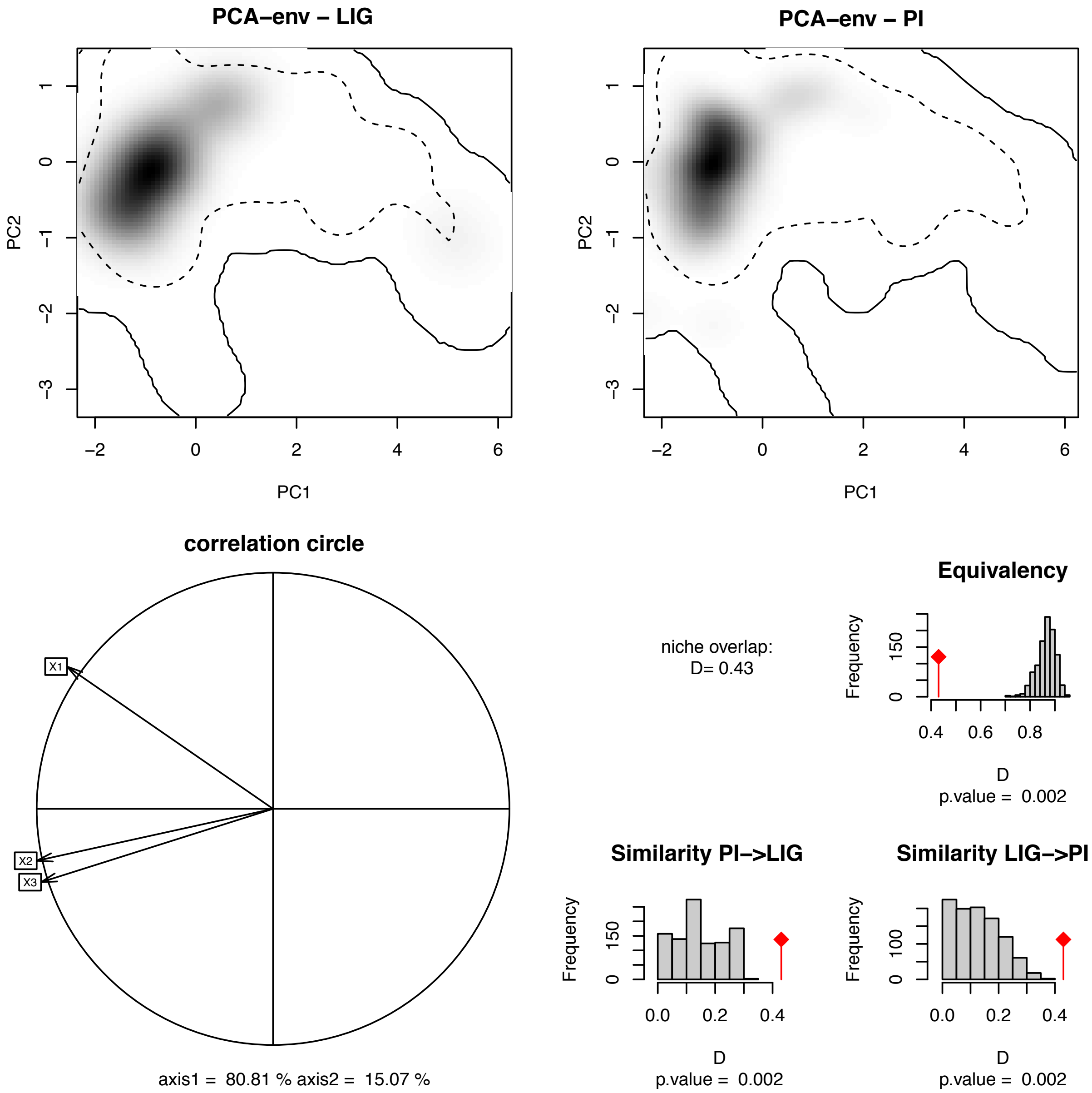
Neverita duplicata: **LIG—PI**



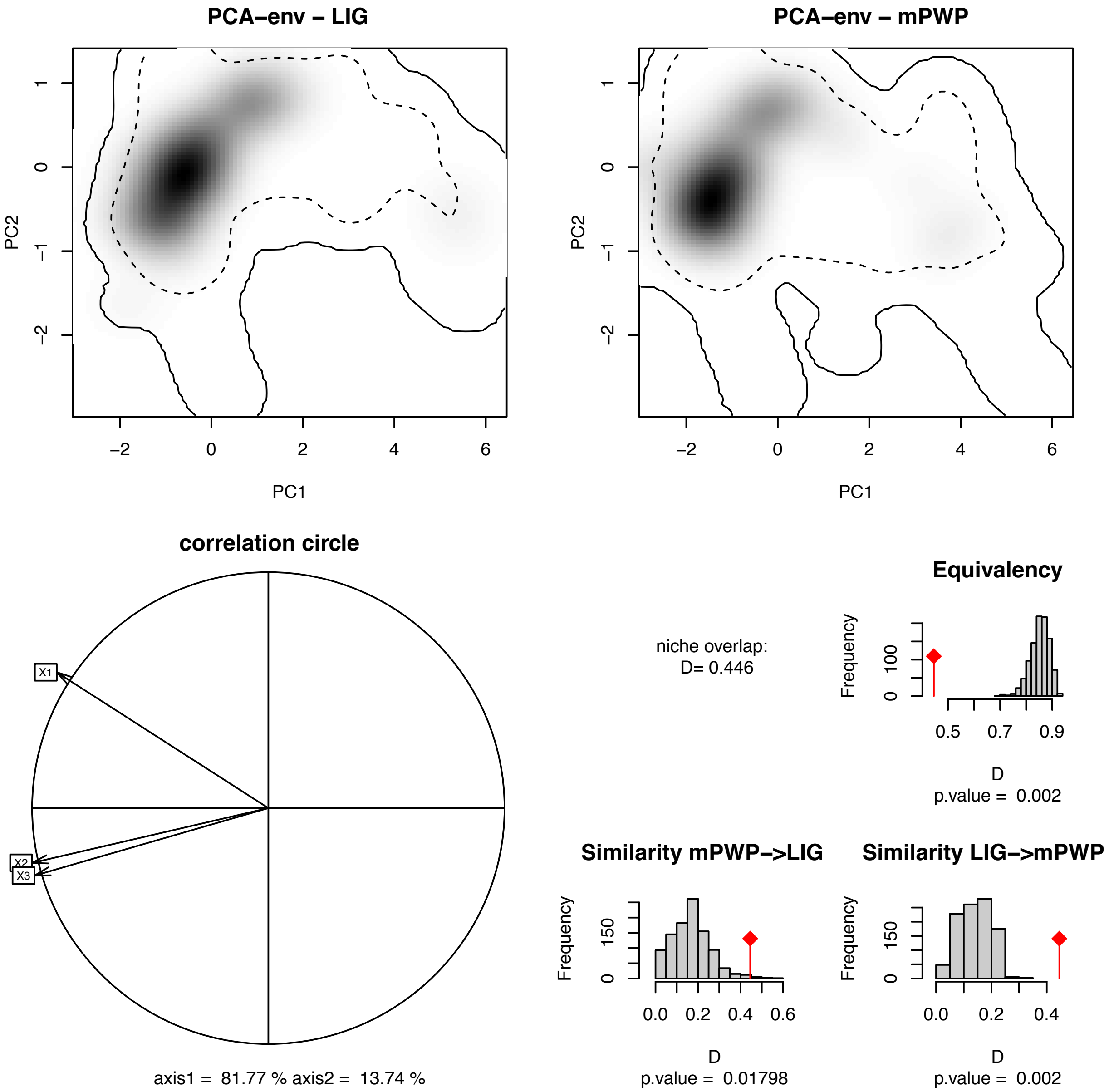
Neverita duplicata: **PI—mPWP**



Oliva sayana: **LIG—PI**



Oliva sayana: **LIG—mPWP**


PCA–env – LIG

PCA–env – mPWP

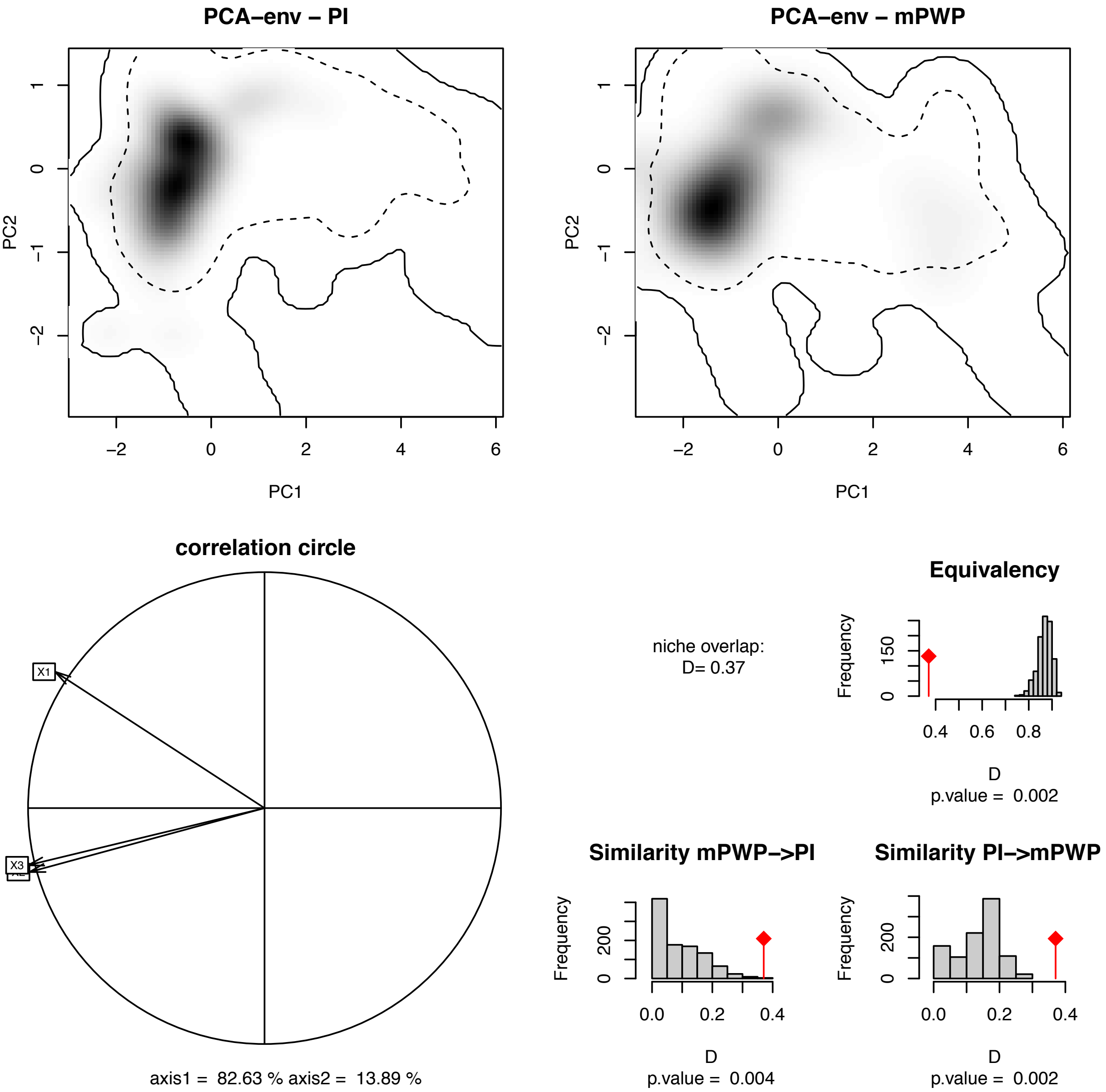
correlation circle

Equivalency

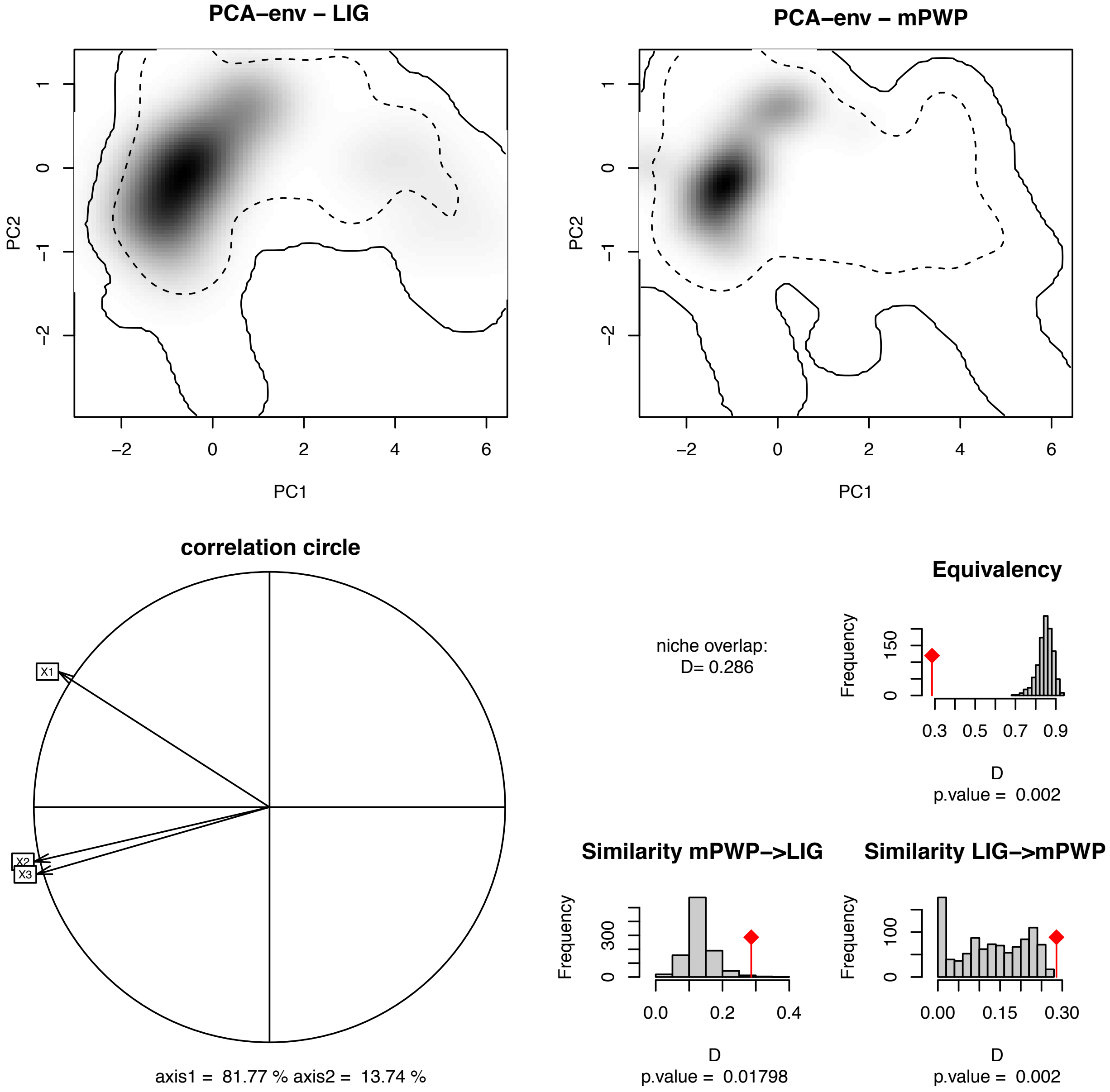
Similarity mPWP–>LIG

Similarity LIG–>mPWP

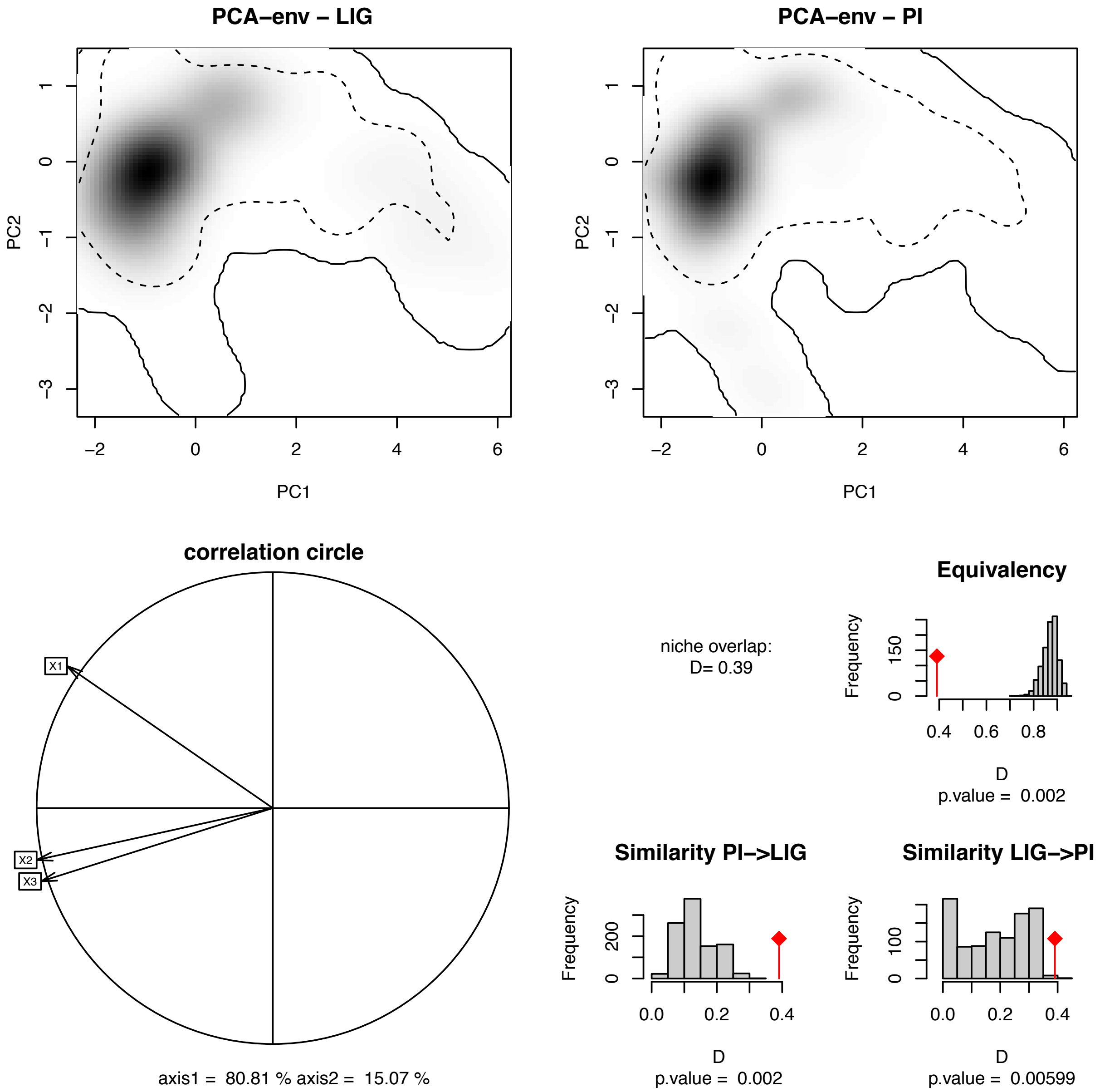
Oliva sayana: **PI—mPWP**



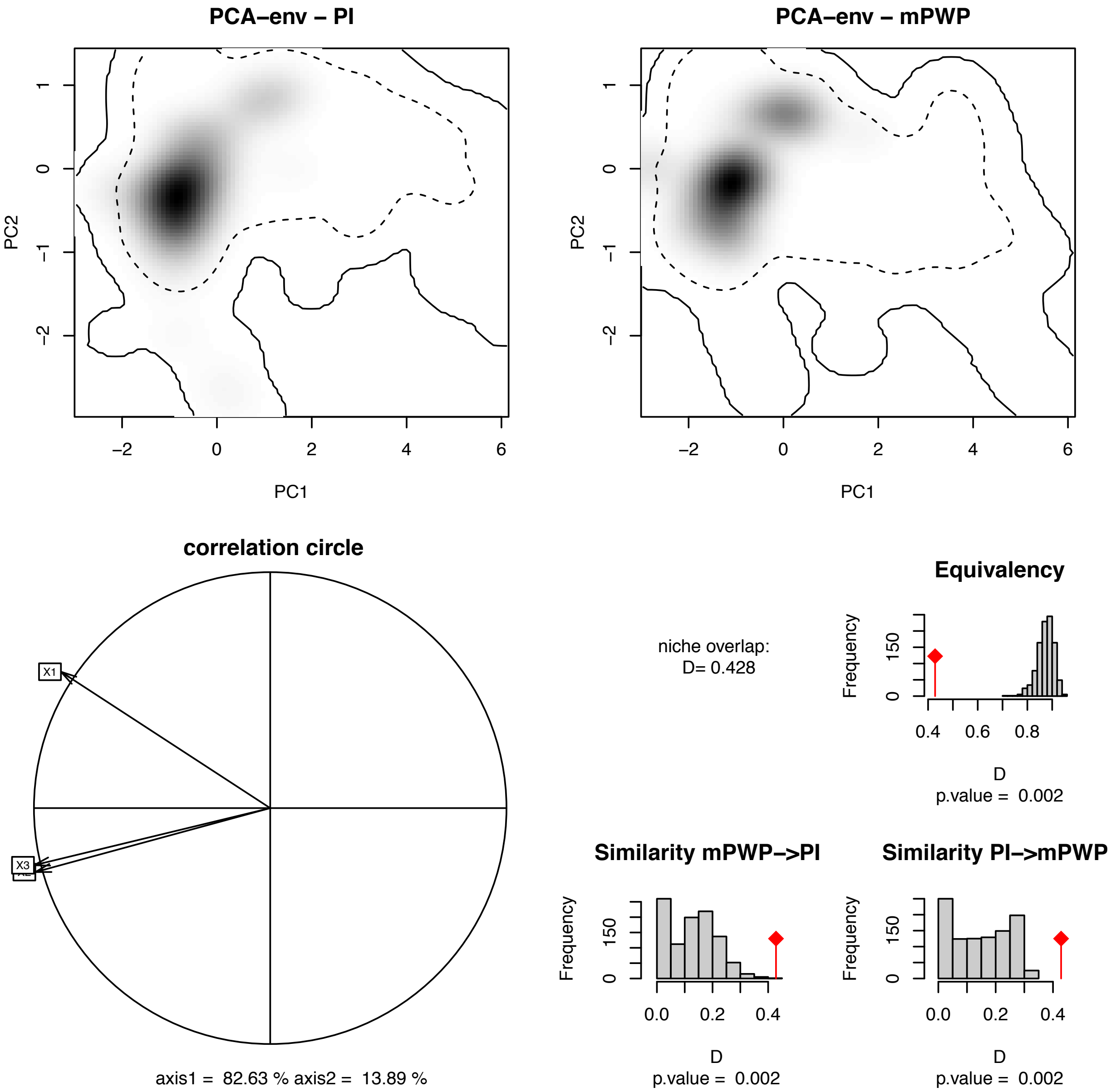
Terebra dislocata: **LIG—mPWP**



Terebra dislocata: **LIG—PI**

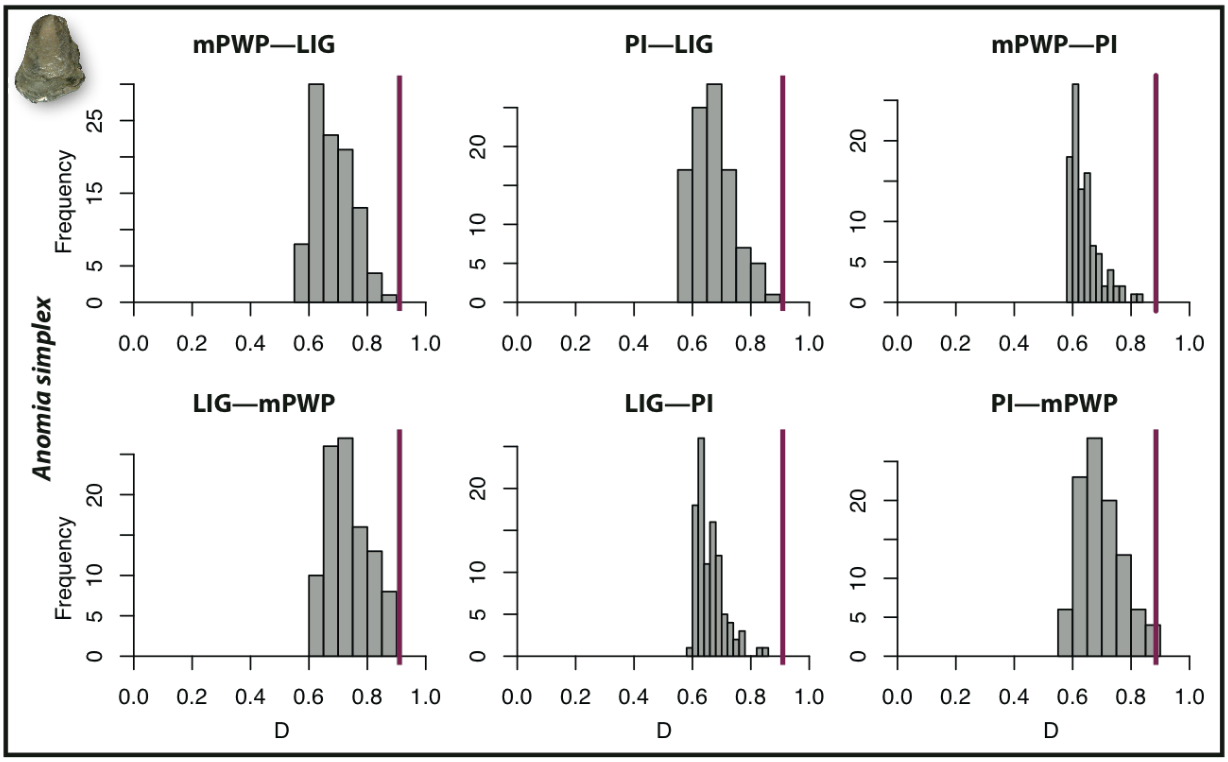


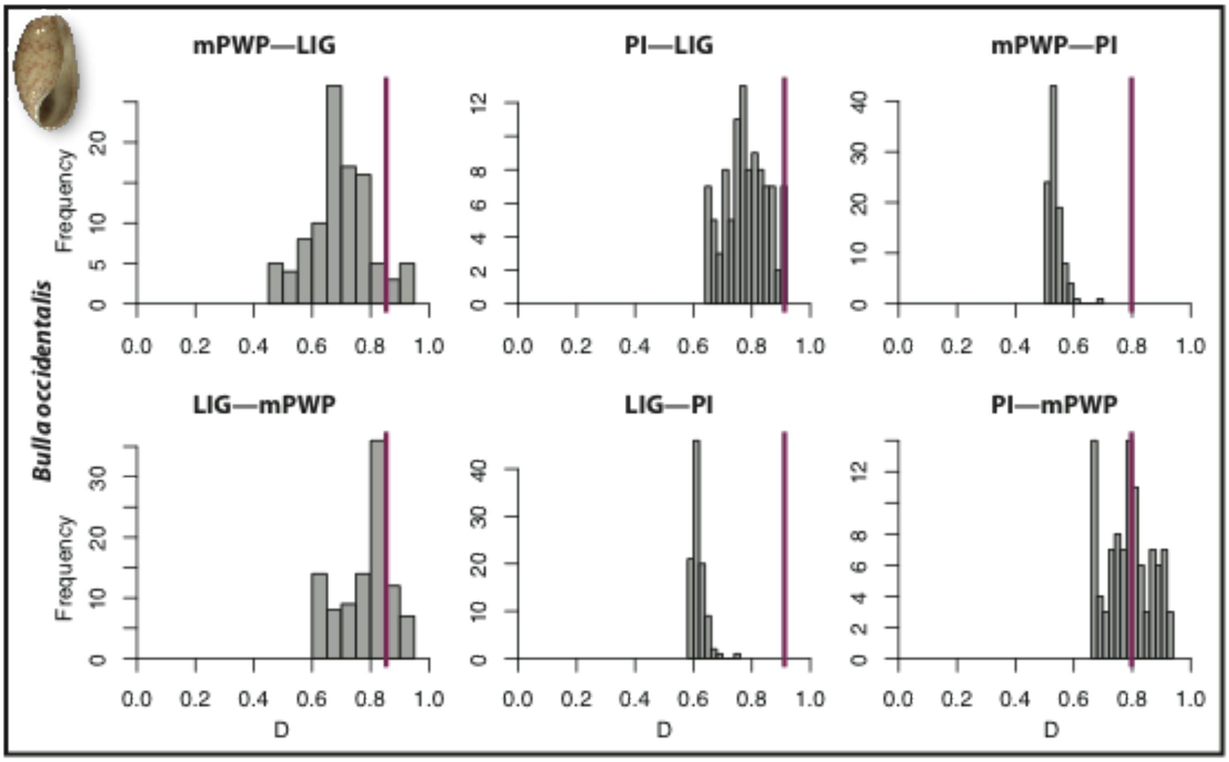
Terebra dislocata: **PI—mPWP**

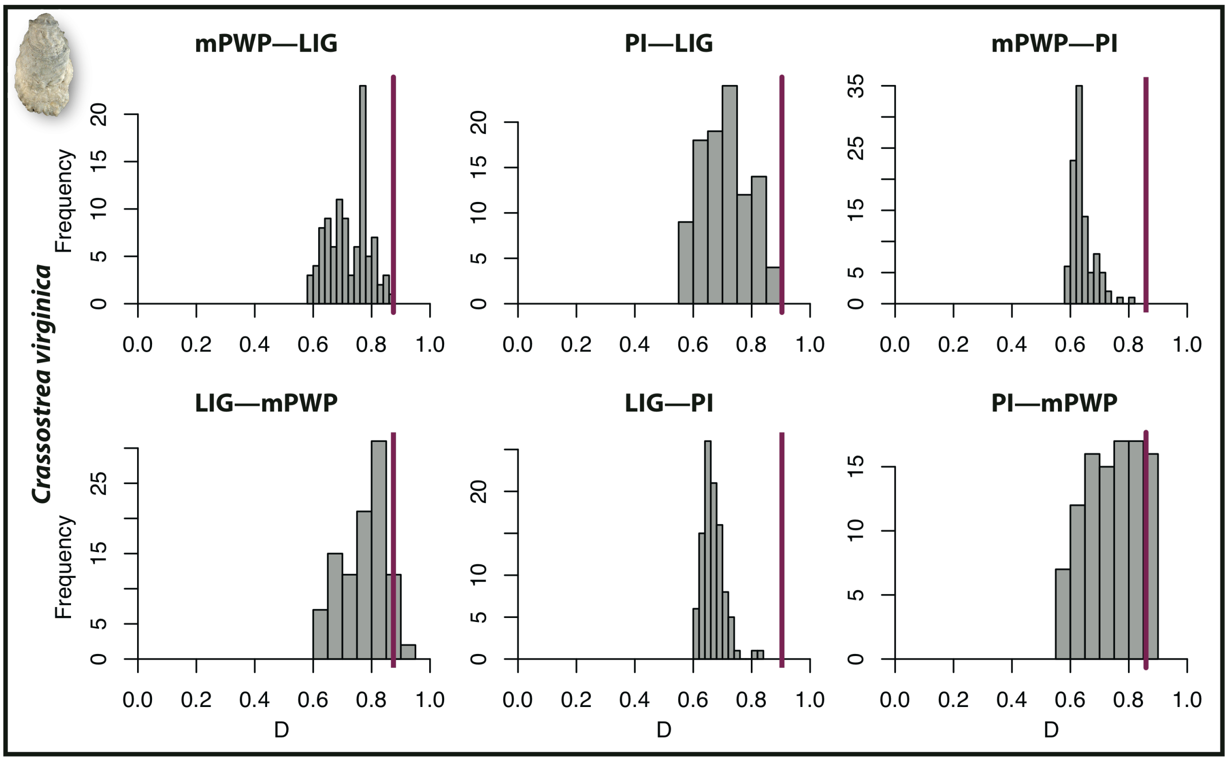


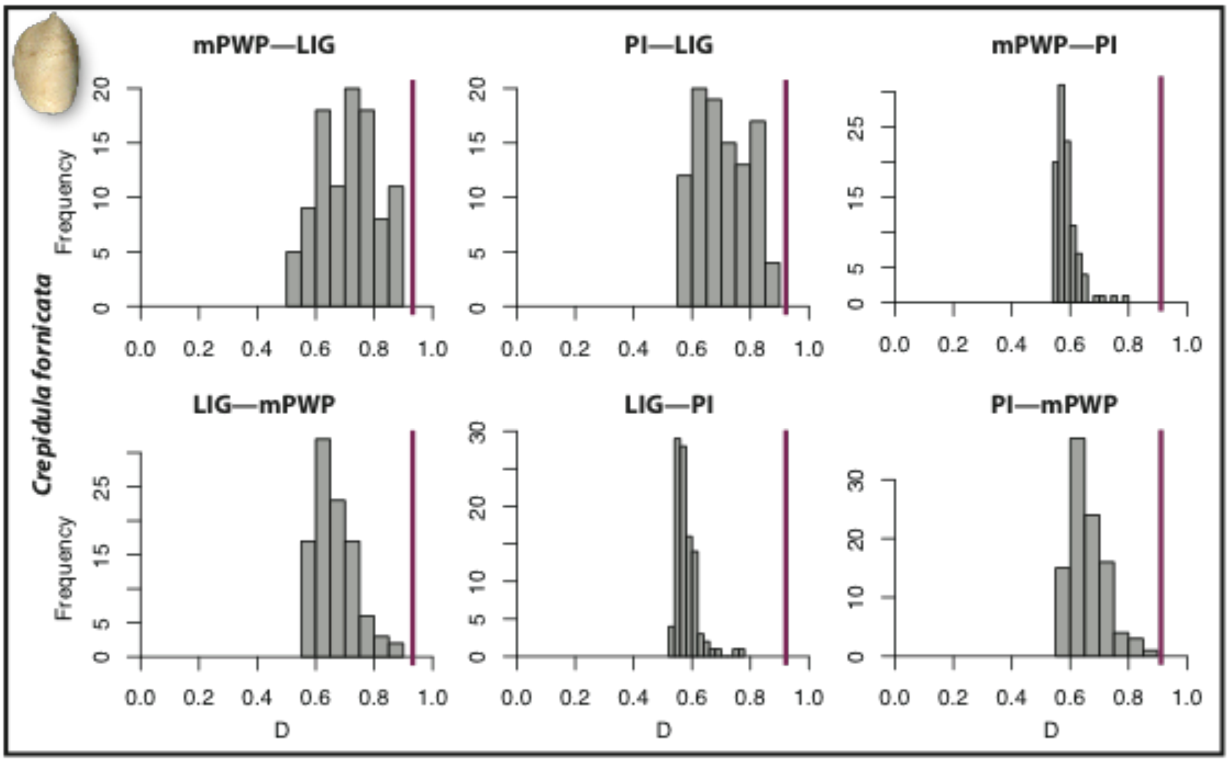
Appendix S2.3c. Environmental comparisons using raw temperature variables

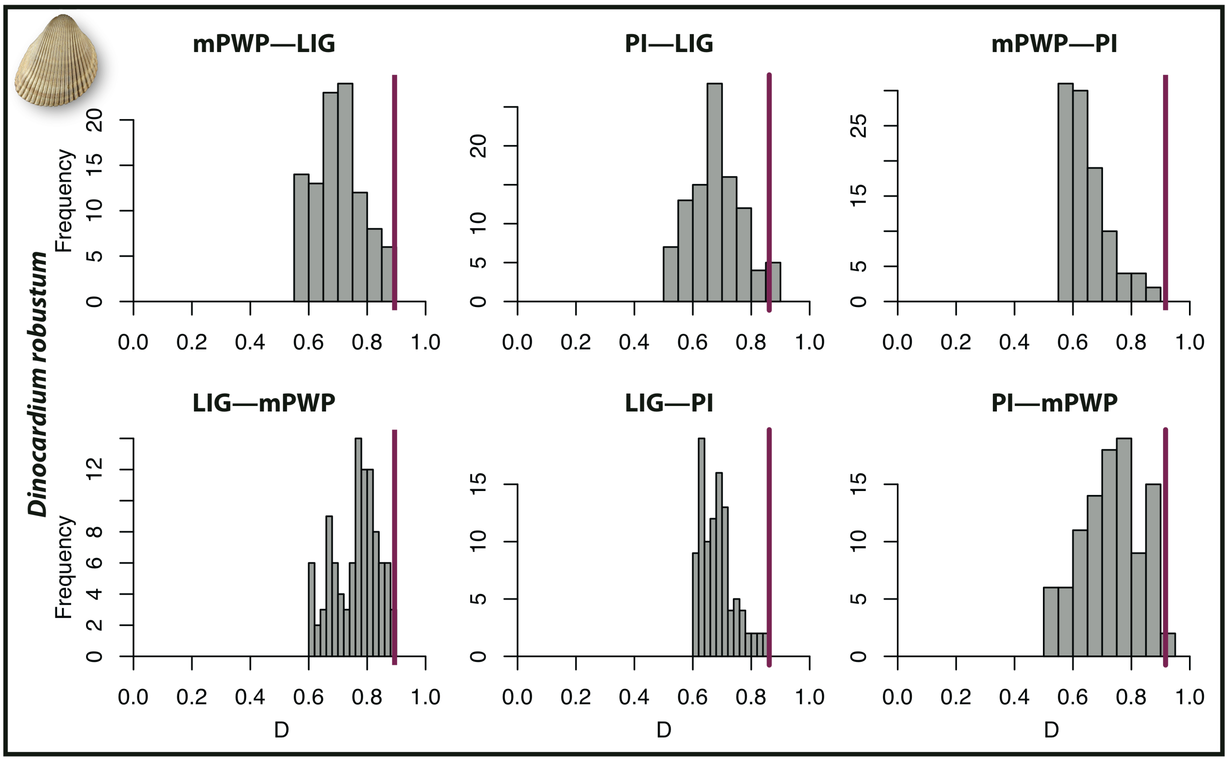
Results from niche comparison tests using raw average bottom temperature and maximum surface temperature conducted with a modified script of Broennimann *et al.* (2012). The histograms are the simulated and observed (red bar) similarity values (D). Observed values falling within the null distribution 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.

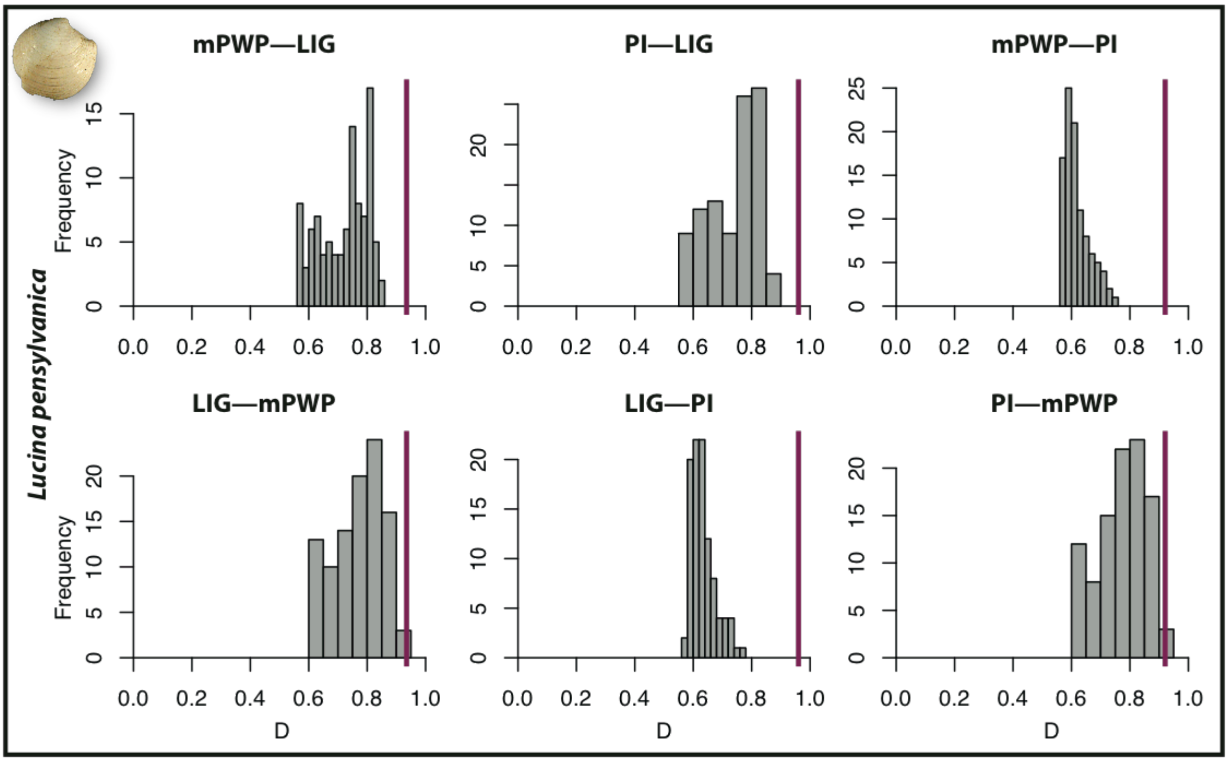


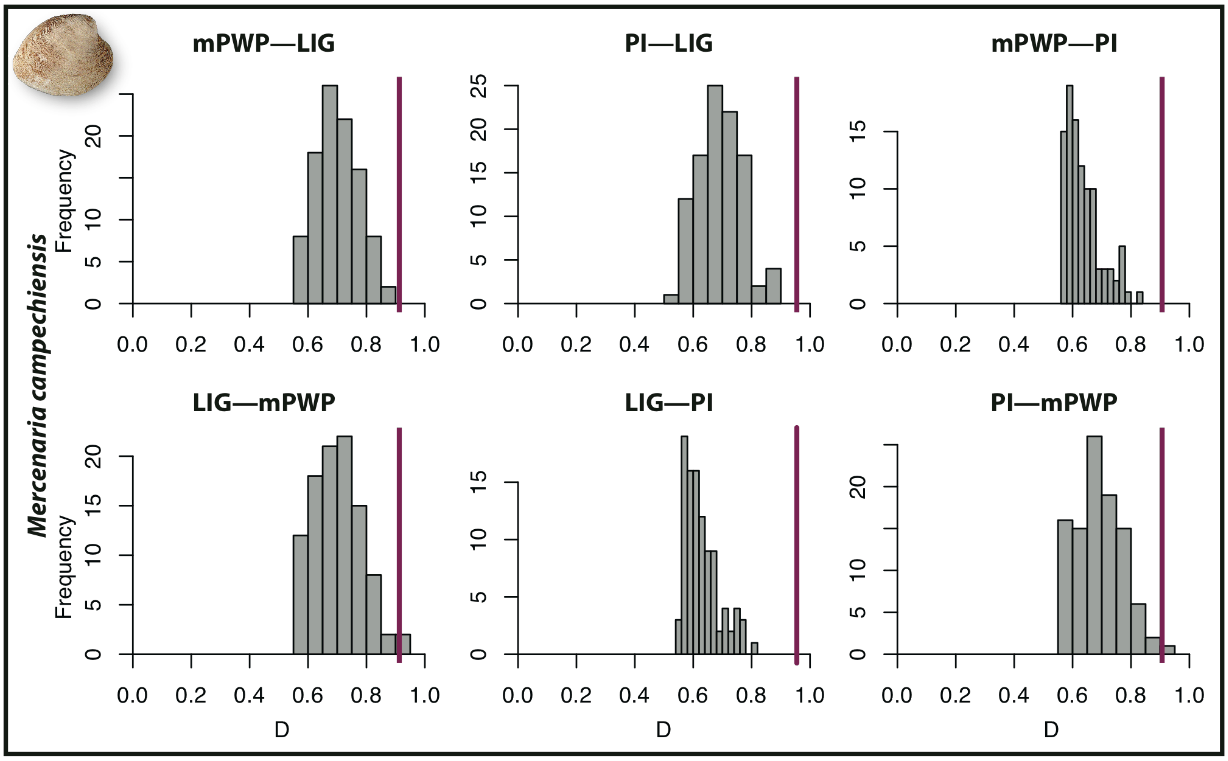

Bulla occidentalis
mPWP—LIG
PI—LIG
mPWP—PI
LIG—mPWP
LIG—PI
PI—mPWP
Frequency
Frequency
D
D
D
0.0
0.2
0.4
0.6
0.8
1.0

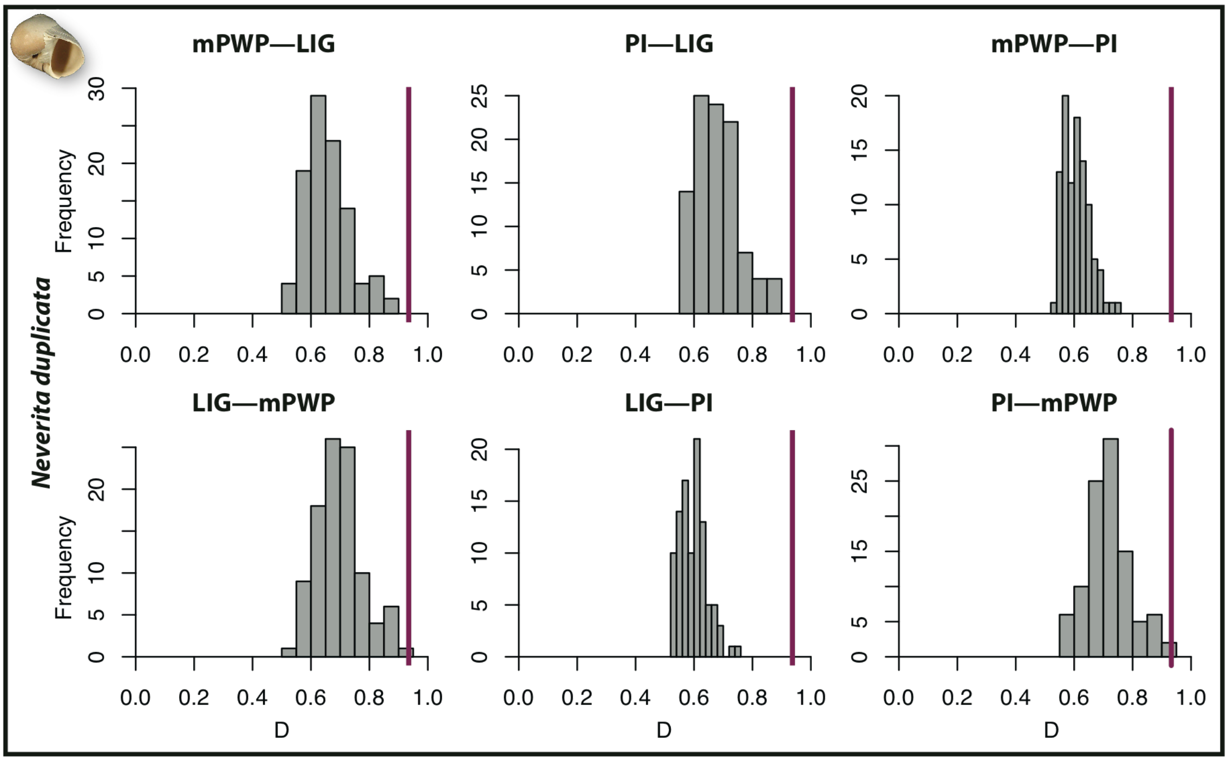

Crassostrea virginica
mPWP—LIG
PI—LIG
mPWP—PI
LIG—mPWP
LIG—PI
PI—mPWP
Frequency
Frequency
D
D
D
0.0
0.2
0.4
0.6
0.8
1.0

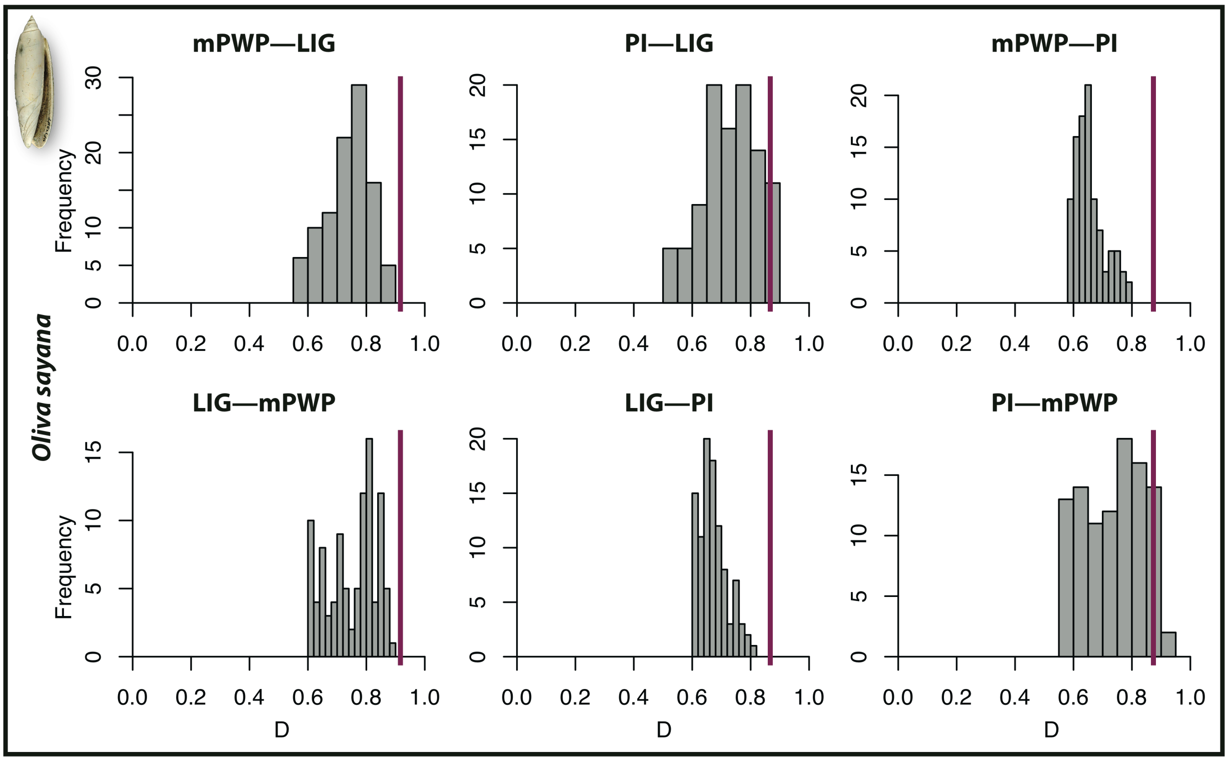

Crepidula fornicata
mPWP—LIG
PI—LIG
mPWP—PI
LIG—mPWP
LIG—PI
PI—mPWP
Frequency
Frequency
0 5 10 15 20
0 5 10 15 20
0 5 15 25
0 5 15 25
0 5 10 20 30
0 10 20 30
0.0 0.2 0.4 0.6 0.8 1.0
D
D
D

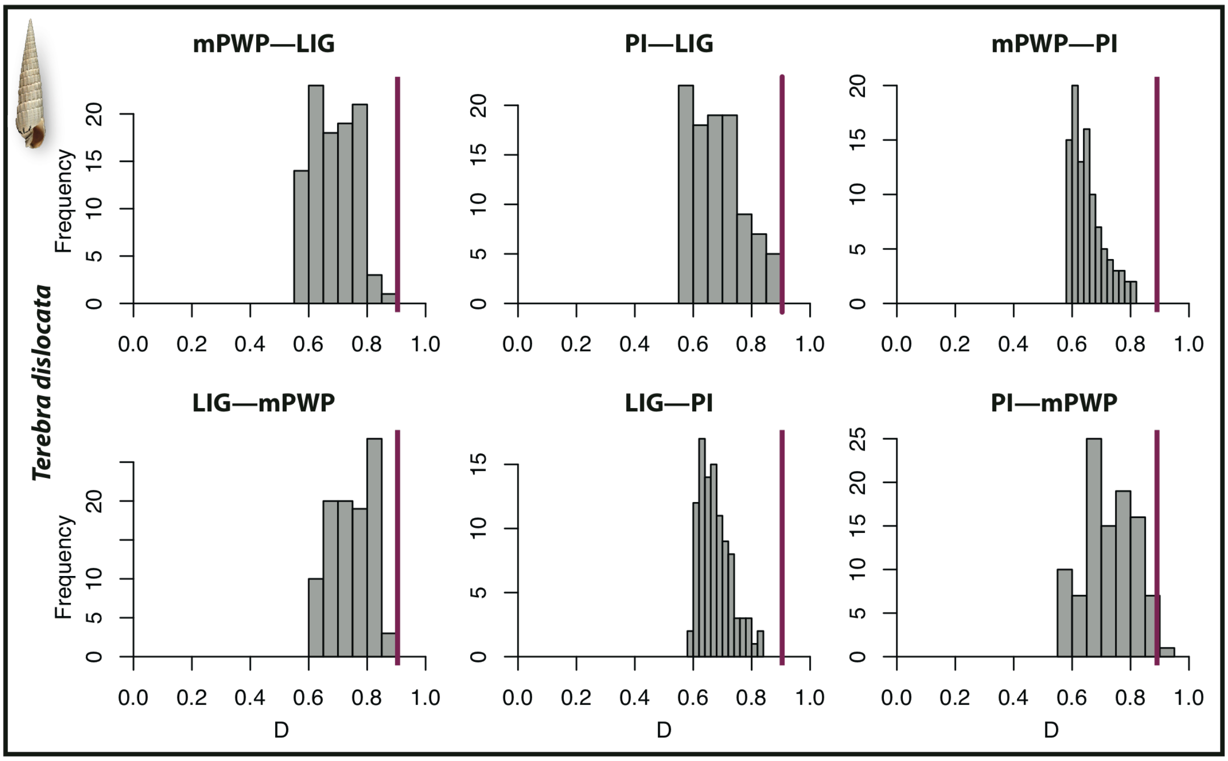

Dinocardium robustum
mPWP—LIG
PI—LIG
mPWP—PI
LIG—mPWP
LIG—PI
PI—mPWP
Frequency
Frequency
0 5 10 15 20
0 5 10 20
0 5 15 25
0 2 4 6 8 12
0 5 10 15
0 5 10 15
0.0 0.2 0.4 0.6 0.8 1.0
D
D
D


Lucina pensylvanica
mPWP—LIG
PI—LIG
mPWP—PI
LIG—mPWP
LIG—PI
PI—mPWP
Frequency
Frequency
0
5
10
15
20
25
0.0
0.2
0.4
0.6
0.8
1.0
D
D
D


Mercenaria campechiensis
mPWP—LIG
PI—LIG
mPWP—PI
LIG—mPWP
LIG—PI
PI—mPWP
Frequency
Frequency
0
5
10
15
20
25
0.0
0.2
0.4
0.6
0.8
1.0
D
D
D

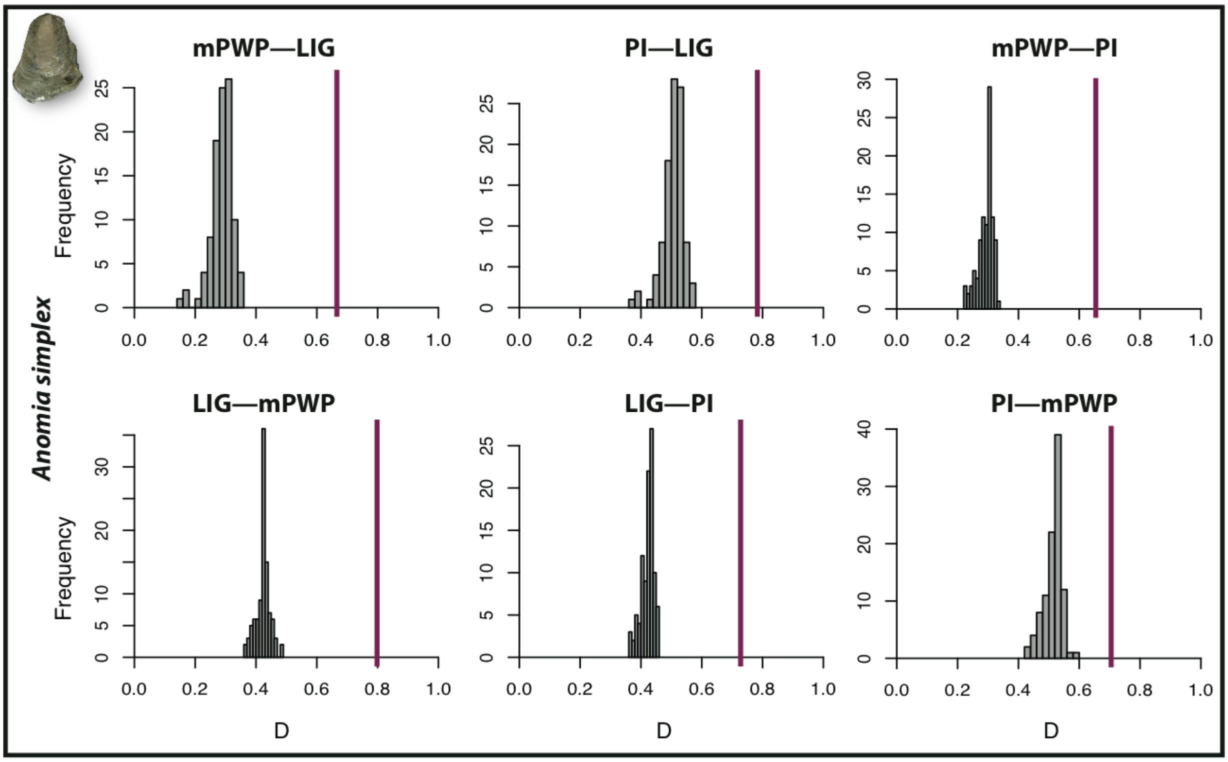

Neverita duplicata
mPWP—LIG
PI—LIG
mPWP—PI
LIG—mPWP
LIG—PI
PI—mPWP
Frequency
D
0.0 0.2 0.4 0.6 0.8 1.0

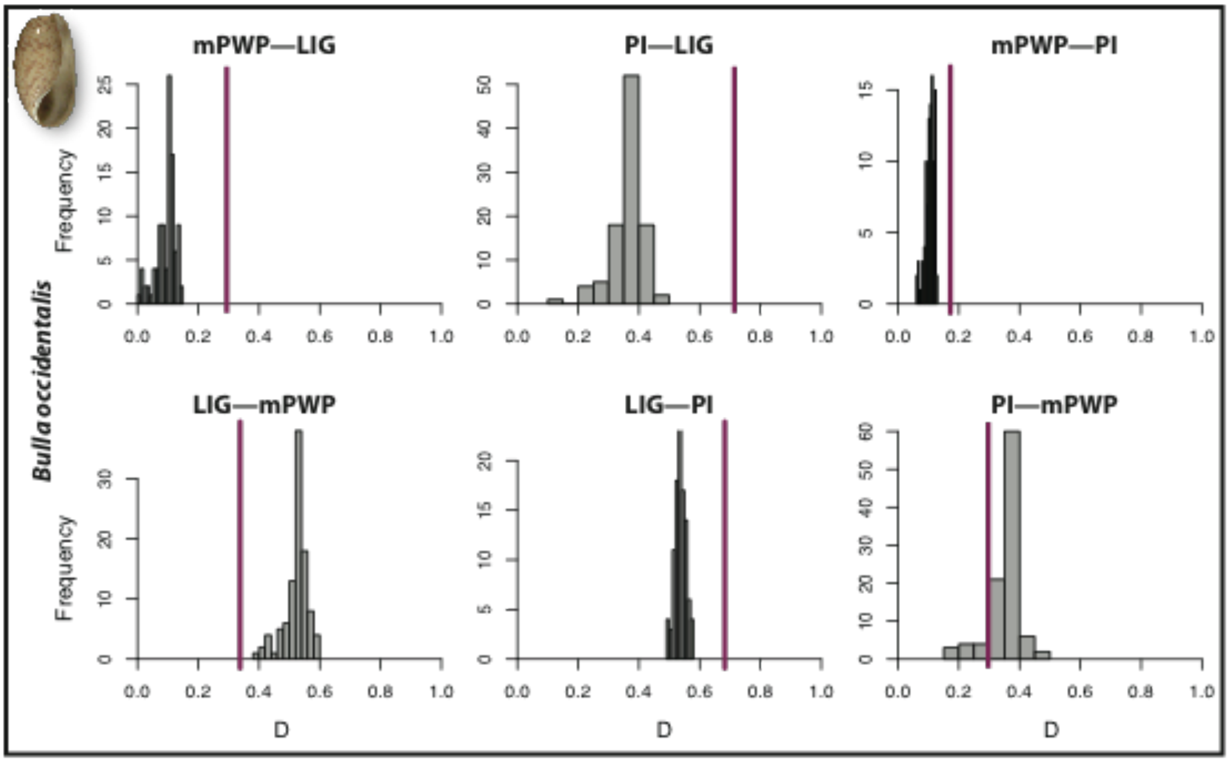

Oliva sayana
mPWP—LIG
PI—LIG
mPWP—PI
LIG—mPWP
LIG—PI
PI—mPWP
Frequency
D
0.0 0.2 0.4 0.6 0.8 1.0

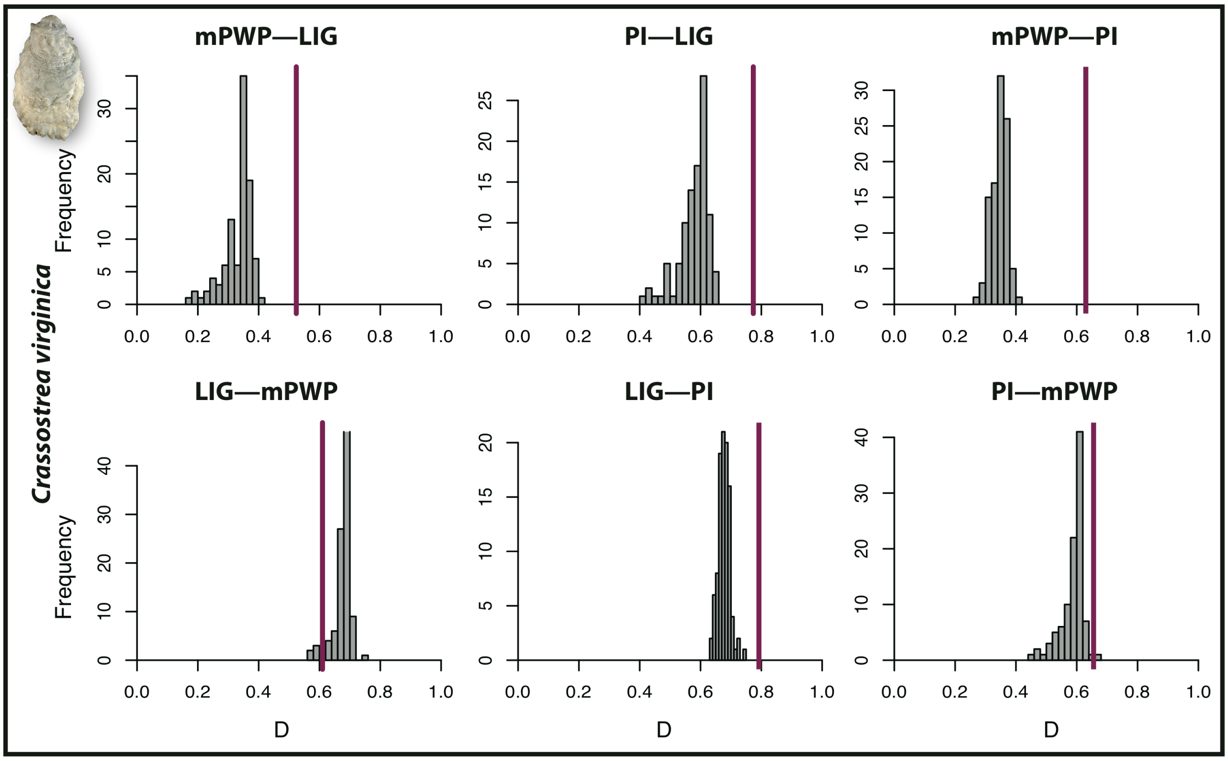

Terebra dislocata
mPWP—LIG
PI—LIG
mPWP—PI
LIG—mPWP
LIG—PI
PI—mPWP
Frequency
0
5
10
15
20
25
0.0
0.2
0.4
0.6
0.8
1.0
D

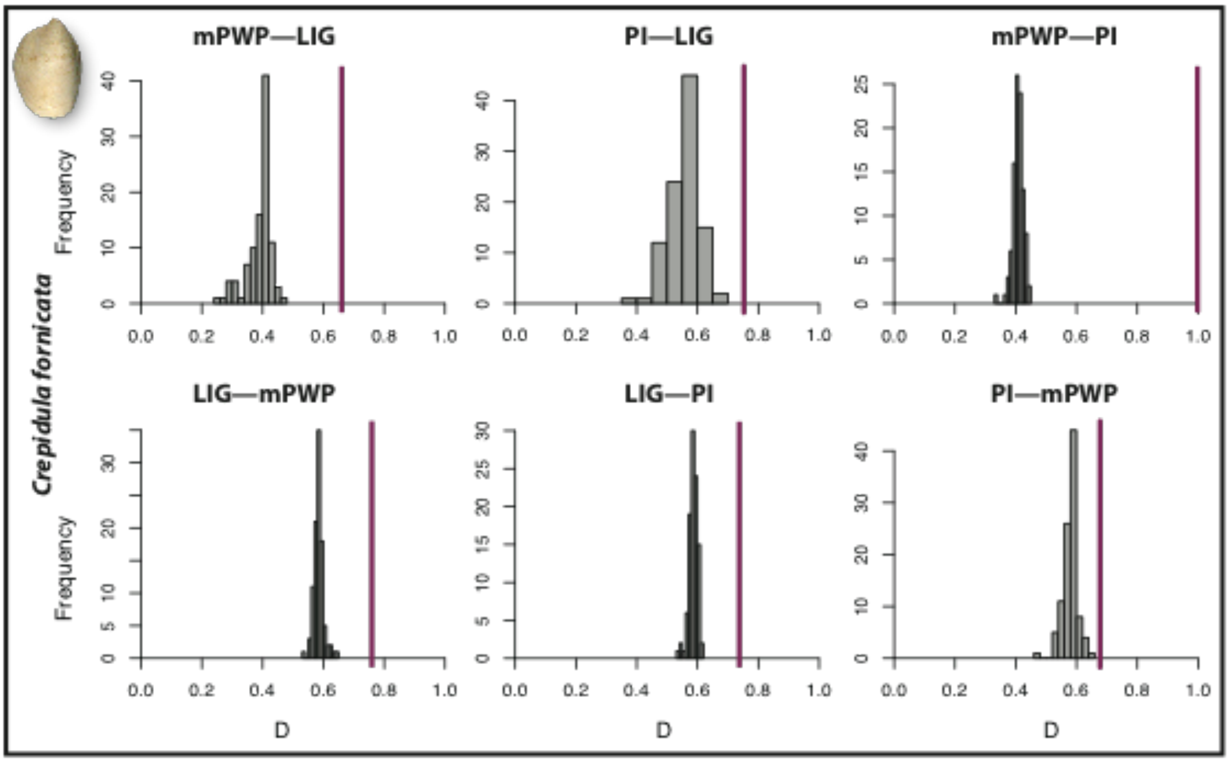
Appendix S2.3d. Geographic comparisons using projections from ecological niche models

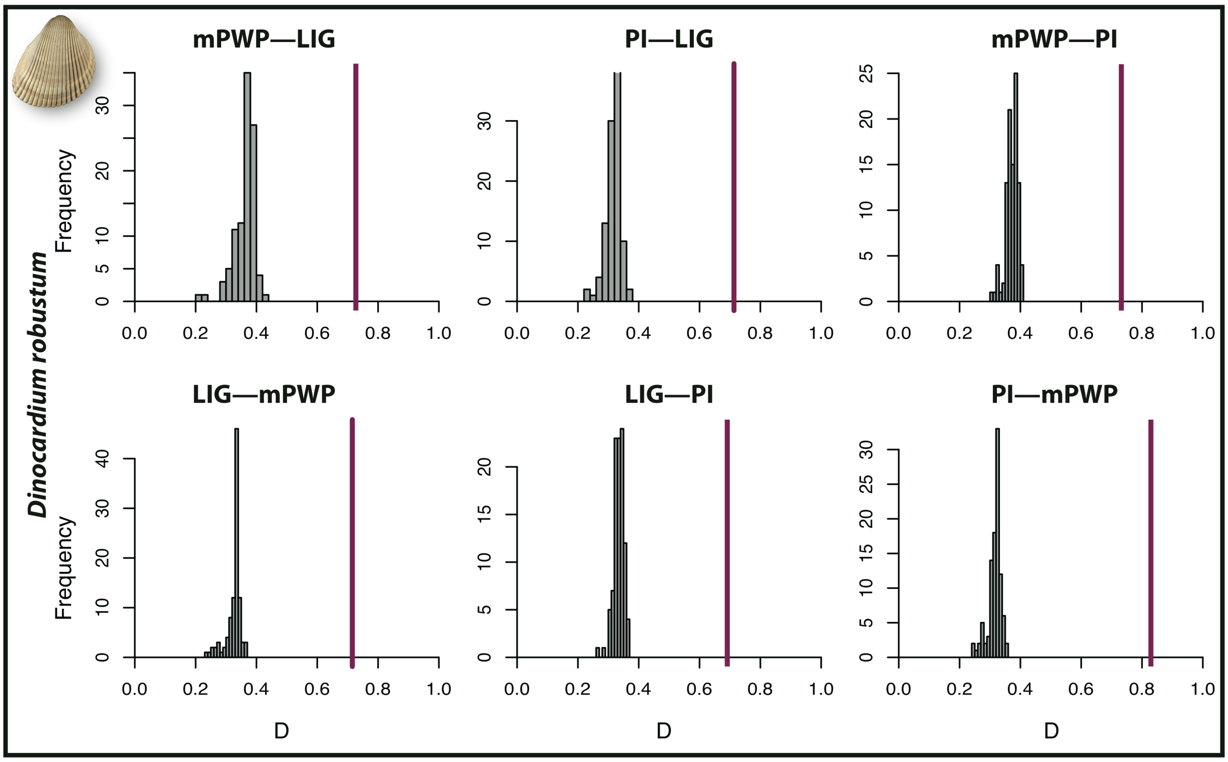
Results from niche comparison tests using ENMTools (Warren *et al.*, 2008, 2010) on projections of ecological niche models. The histograms are the simulated and observed (red bar) similarity values (D). Observed values falling within the null distribution do not allow for discrimination of similarity 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.

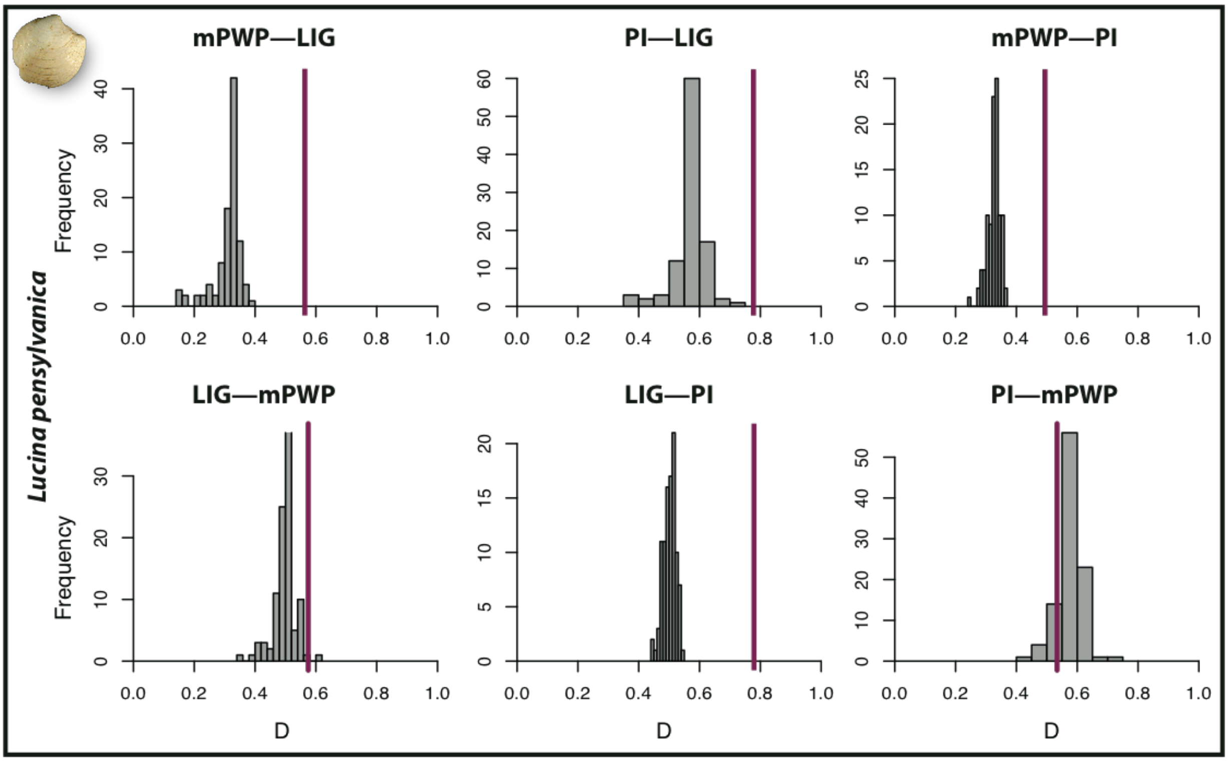


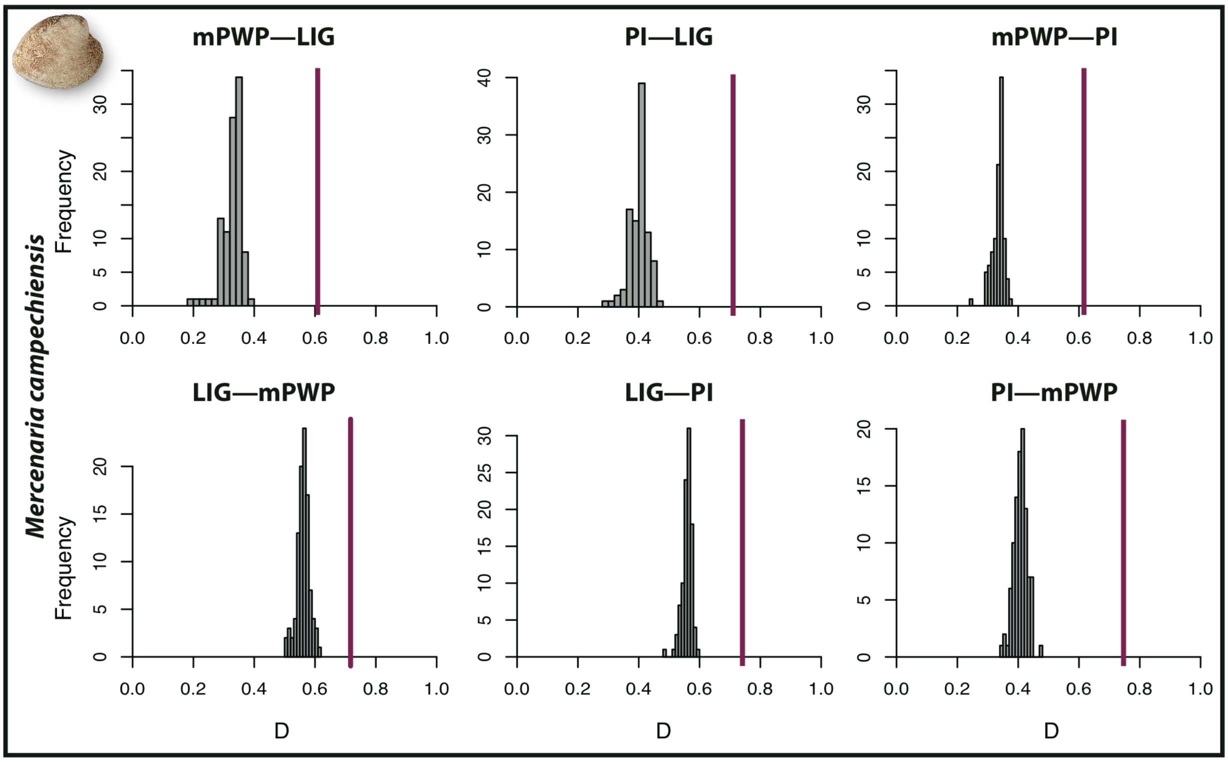

Bulla occidentalis
mPWP—LIG
PI—LIG
mPWP—PI
LIG—mPWP
LIG—PI
PI—mPWP
Frequency
D
0.0
0.2
0.4
0.6
0.8
1.0

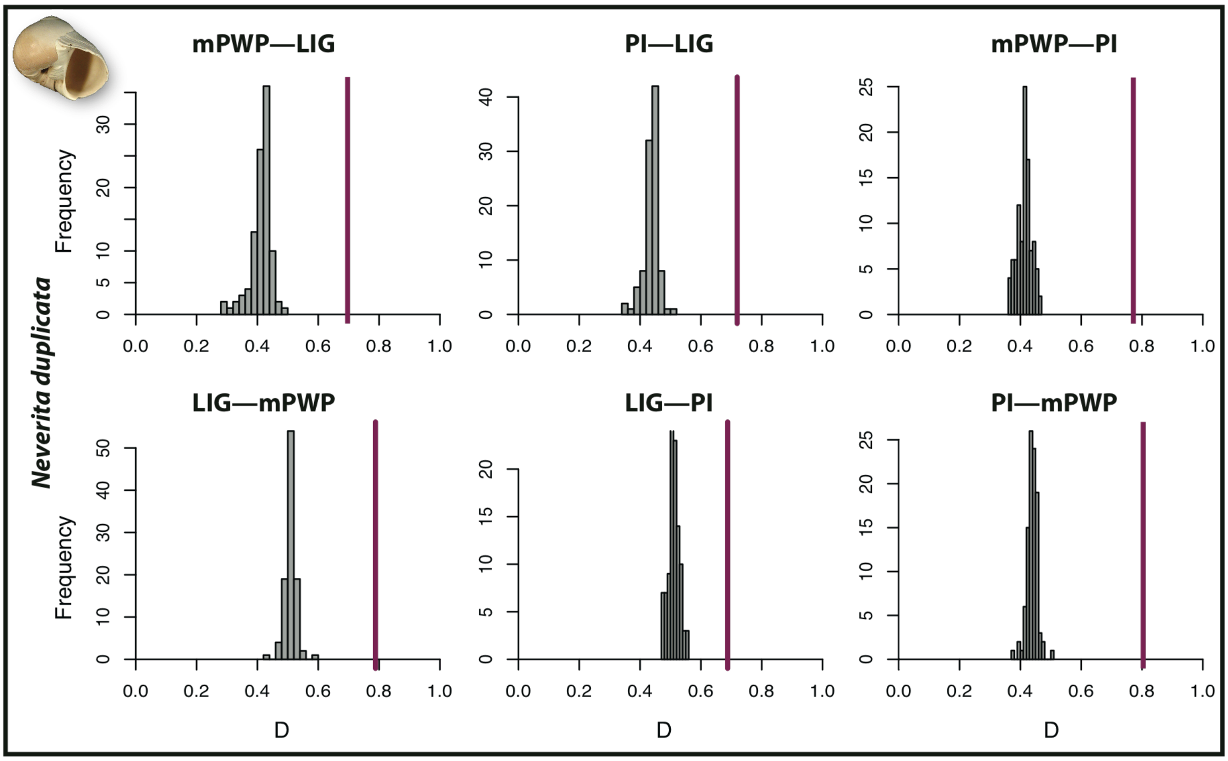

Crassostrea virginica
mPWP—LIG
PI—LIG
mPWP—PI
LIG—mPWP
LIG—PI
PI—mPWP
Frequency
D
0.0
0.2
0.4
0.6
0.8
1.0

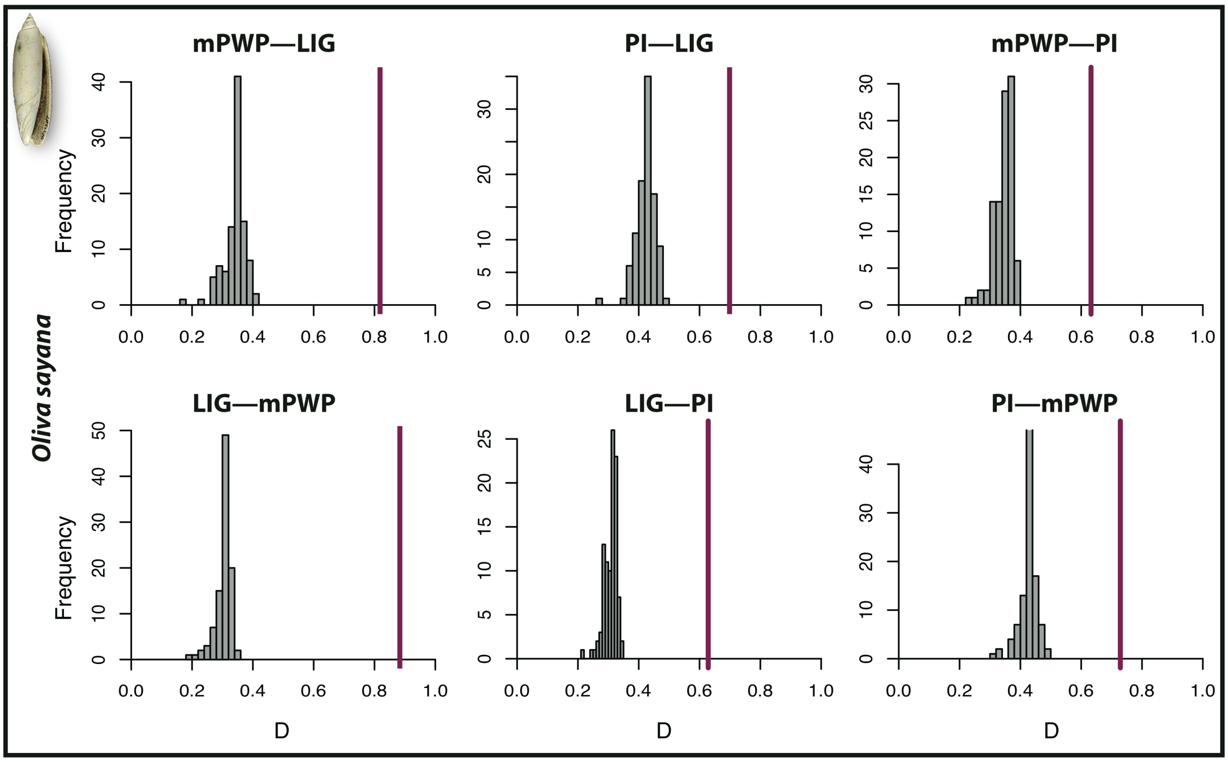

Crepidula fornicata
mPWP—LIG
PI—LIG
mPWP—PI
LIG—mPWP
LIG—PI
PI—mPWP
Frequency
Frequency
D
D
D
0.0
0.2
0.4
0.6
0.8
1.0

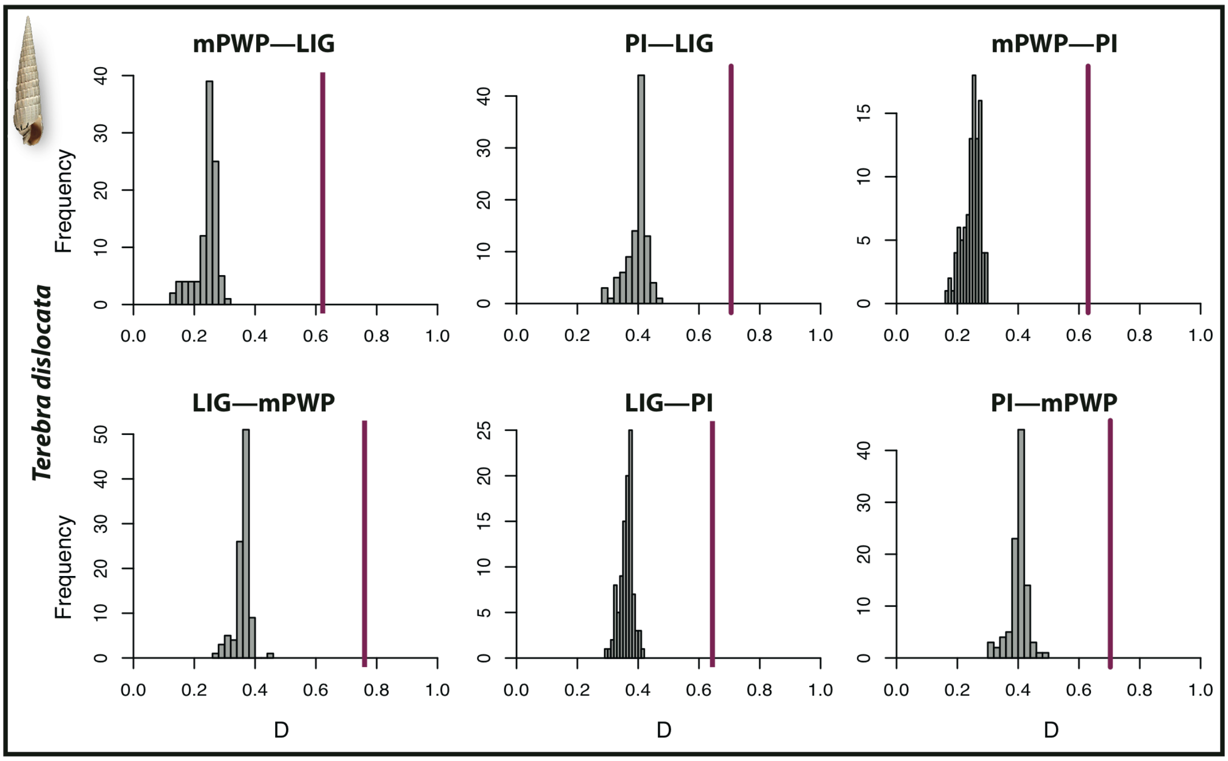

Dinocardium robustum
mPWP—LIG
PI—LIG
mPWP—PI
LIG—mPWP
LIG—PI
PI—mPWP
Frequency
Frequency
D
D
D
0.0
0.2
0.4
0.6
0.8
1.0


Lucina pensylvanica
mPWP—LIG
PI—LIG
mPWP—PI
LIG—mPWP
LIG—PI
PI—mPWP
Frequency
Frequency
0
10
20
30
40
50
60
0.0
0.2
0.4
0.6
0.8
1.0
D
D
D


Mercenaria campechiensis
mPWP—LIG
PI—LIG
mPWP—PI
LIG—mPWP
LIG—PI
PI—mPWP
Frequency
Frequency
0
5
10
15
20
25
30
40
0.0
0.2
0.4
0.6
0.8
1.0
D
D
D


Neverita duplicata
mPWP—LIG
PI—LIG
mPWP—PI
LIG—mPWP
LIG—PI
PI—mPWP
Frequency
D
0.0
0.2
0.4
0.6
0.8
1.0

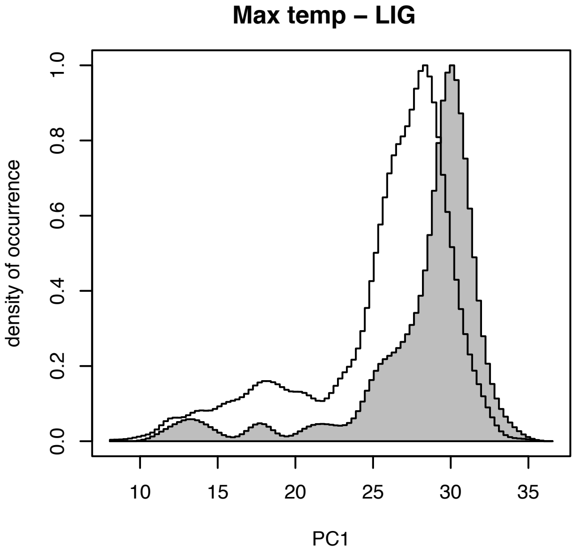

Oliva sayana
mPWP—LIG
PI—LIG
mPWP—PI
LIG—mPWP
LIG—PI
PI—mPWP
Frequency
D
0.0
0.2
0.4
0.6
0.8
1.0

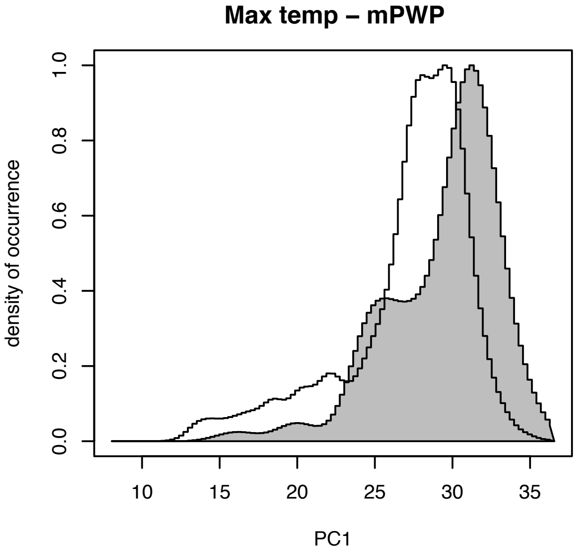

Terebra dislocata
mPWP—LIG
PI—LIG
mPWP—PI
LIG—mPWP
LIG—PI
PI—mPWP
Frequency
Frequency
0.0
0.2
0.4
0.6
0.8
1.0
D
D
D

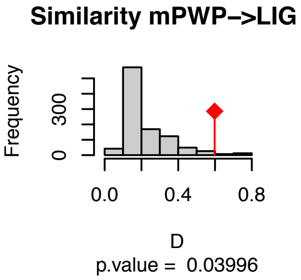
Appendix S2.3e. Maximum temperature comparisons

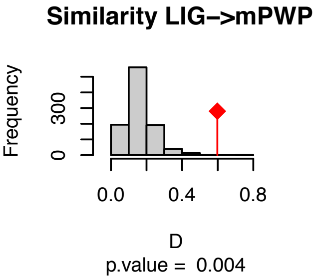
Results from comparison of maximum temperature tolerances using script of Broennimann *et al.* (2012). The right histogram is the simulated similarity values (D) and observed similarity value (red bar) for the niche equivalency test. The left two histograms are the simulated and observed (red bar) similarity 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**

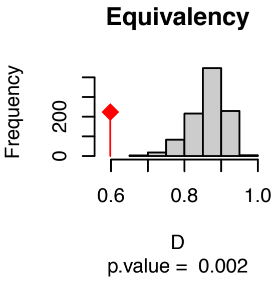




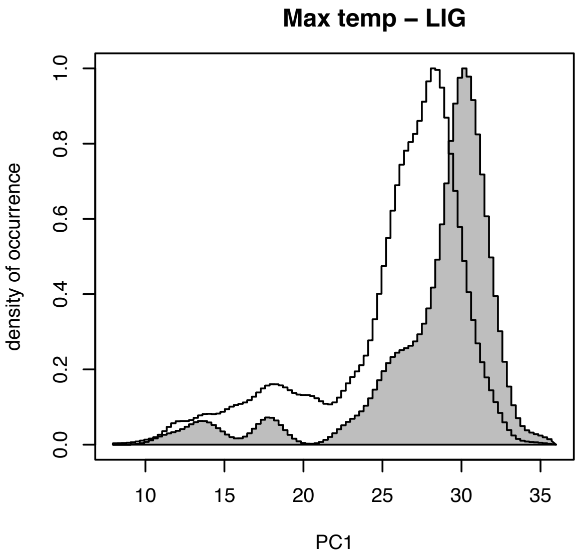


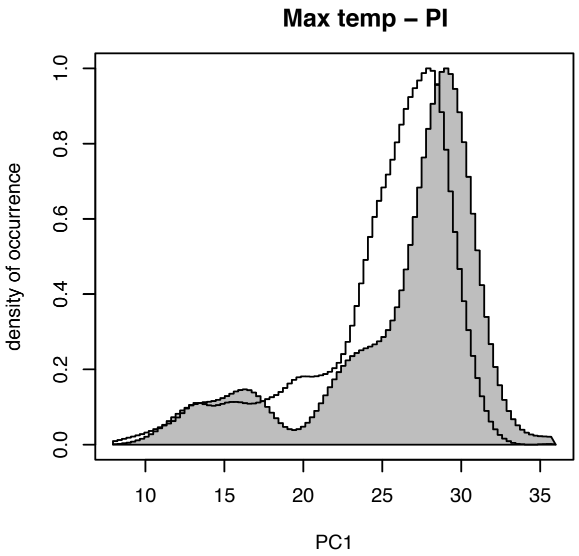


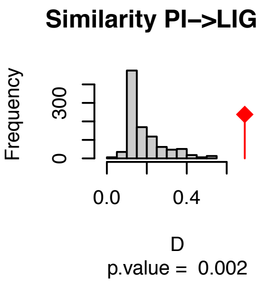
niche overlap:
D= 0.598

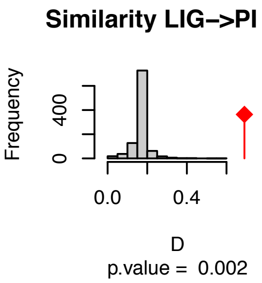


Anomia simplex: **LIG—PI**

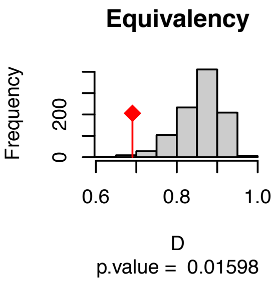




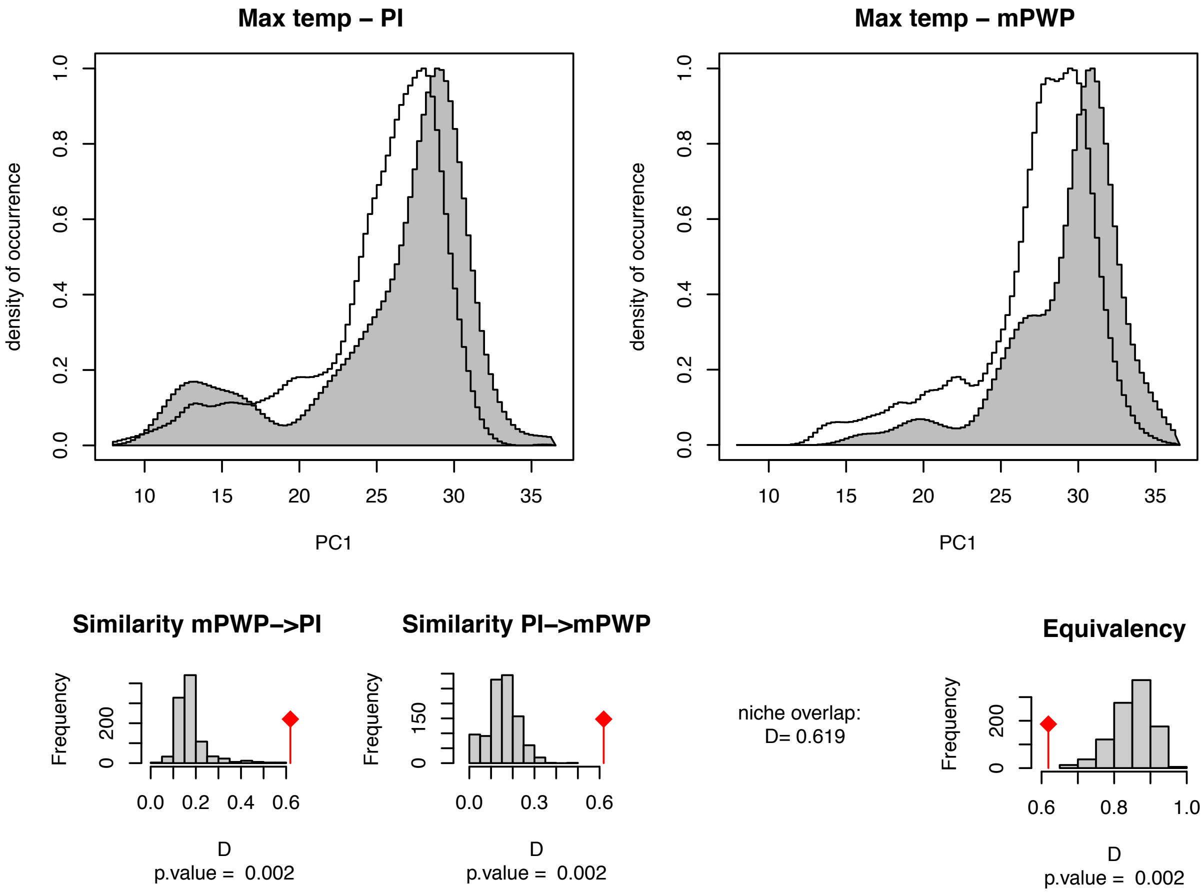




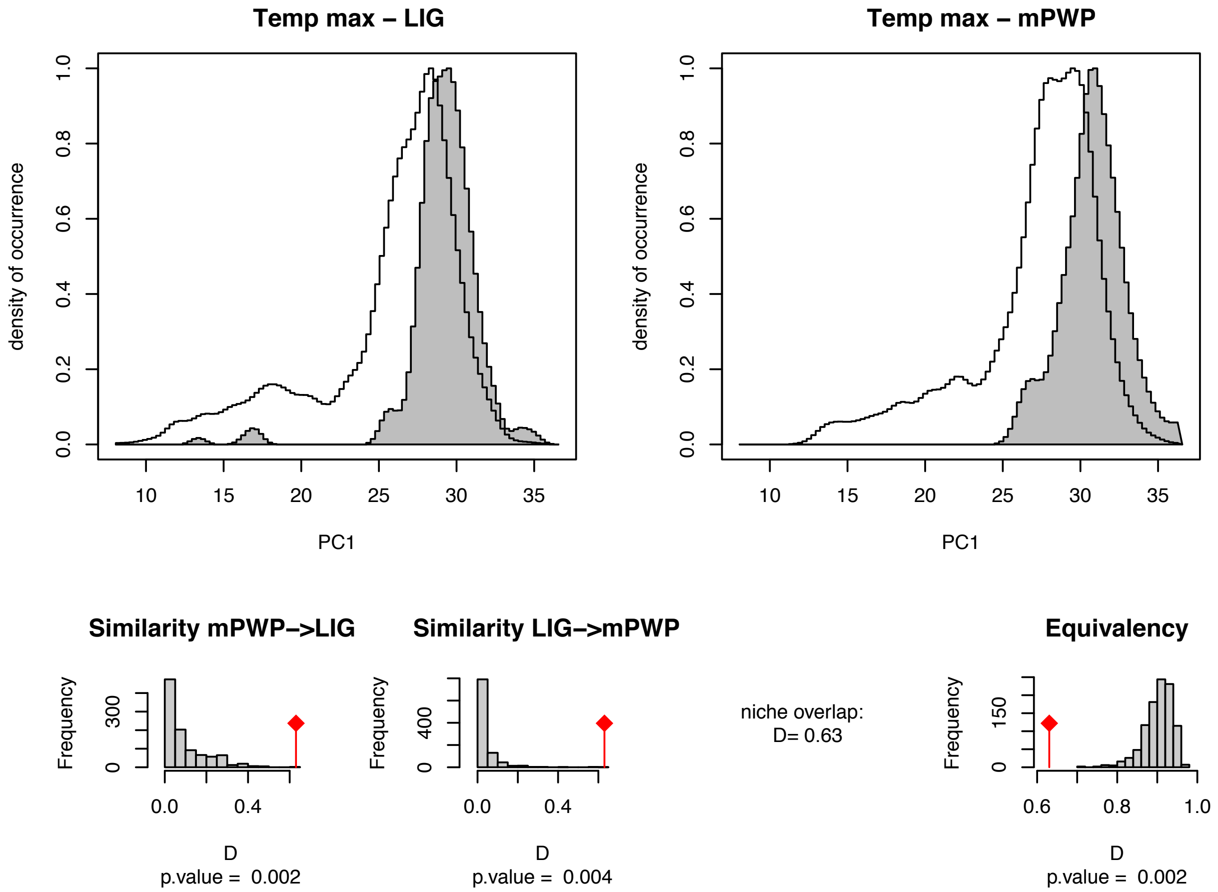
niche overlap:
D= 0.69



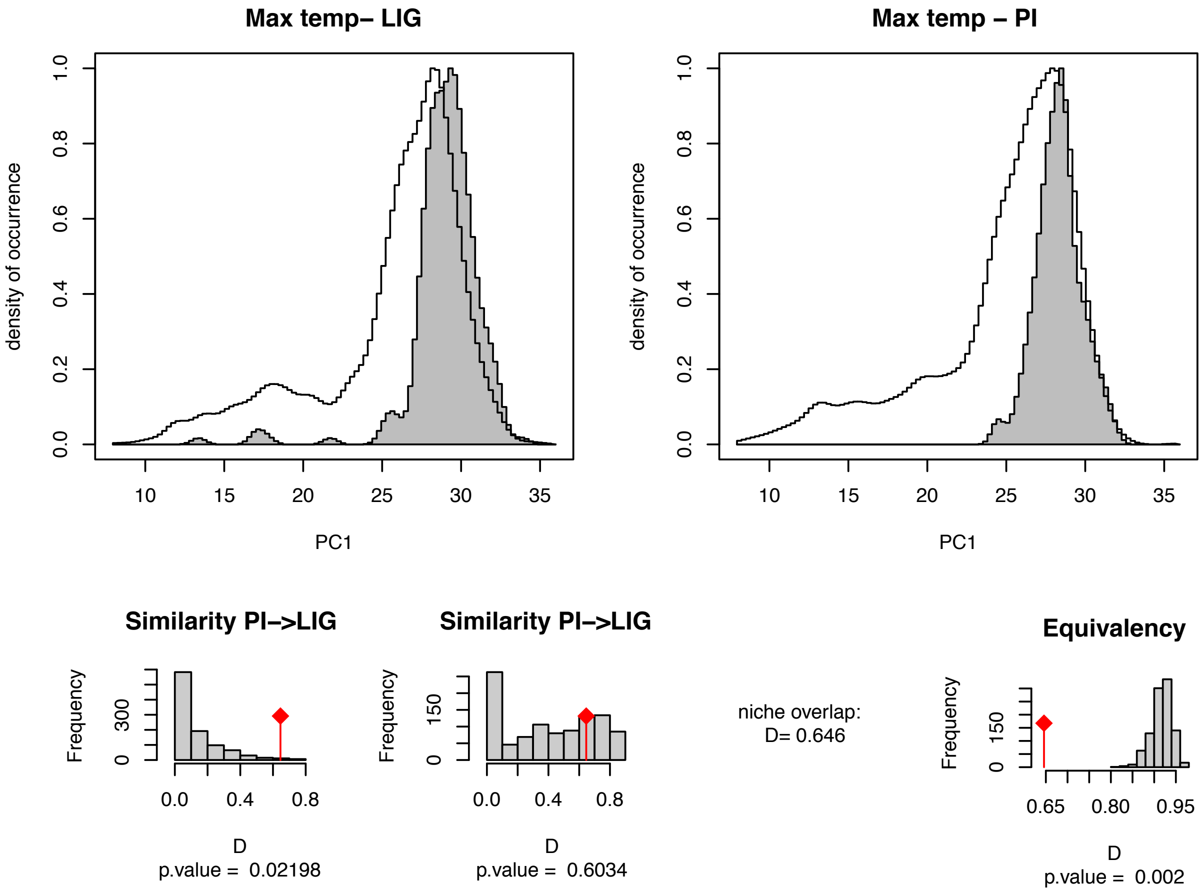
Anomia simplex: **PI—mPWP**



Bulla occidentalis: **LIG—mPWP**



Bulla occidentalis: **LIG—PI**



Max temp- LIG

Max temp – PI

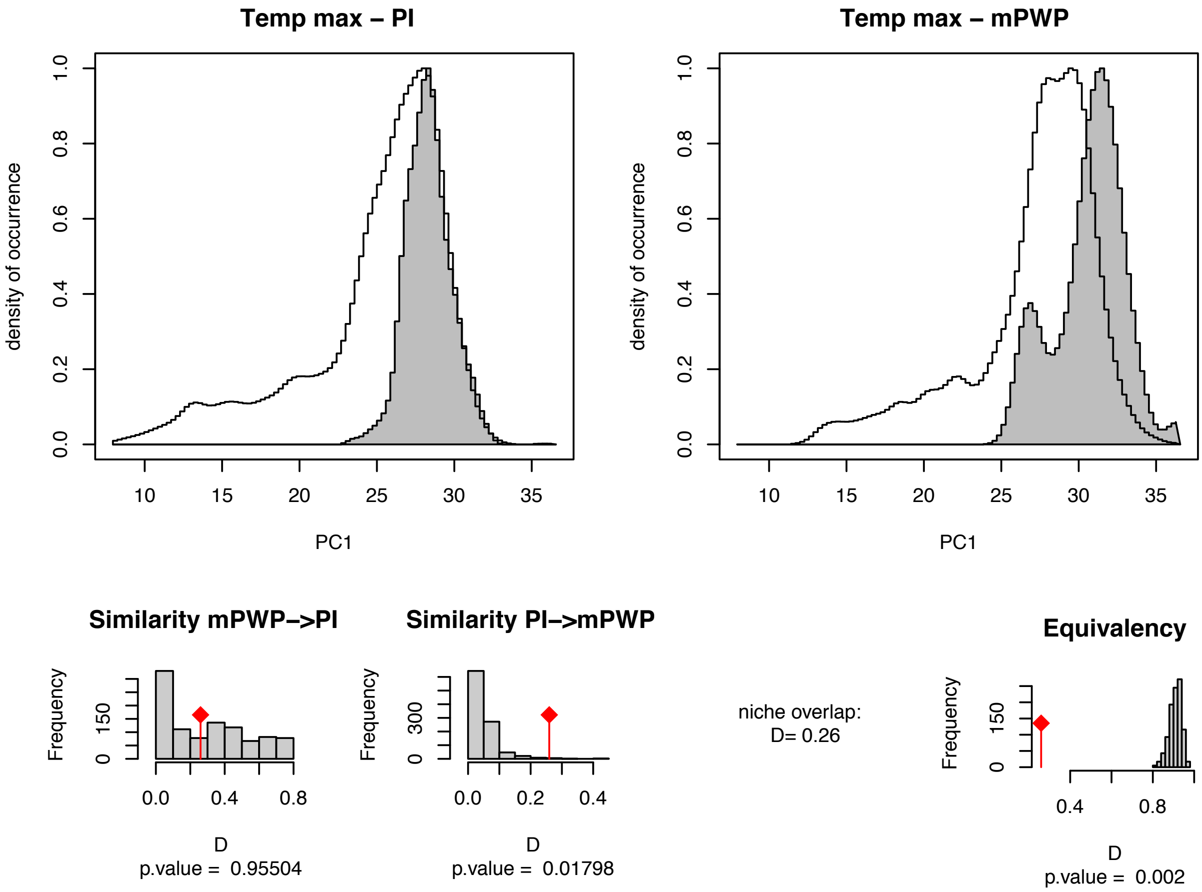
Similarity PI->LIG

Similarity PI->LIG

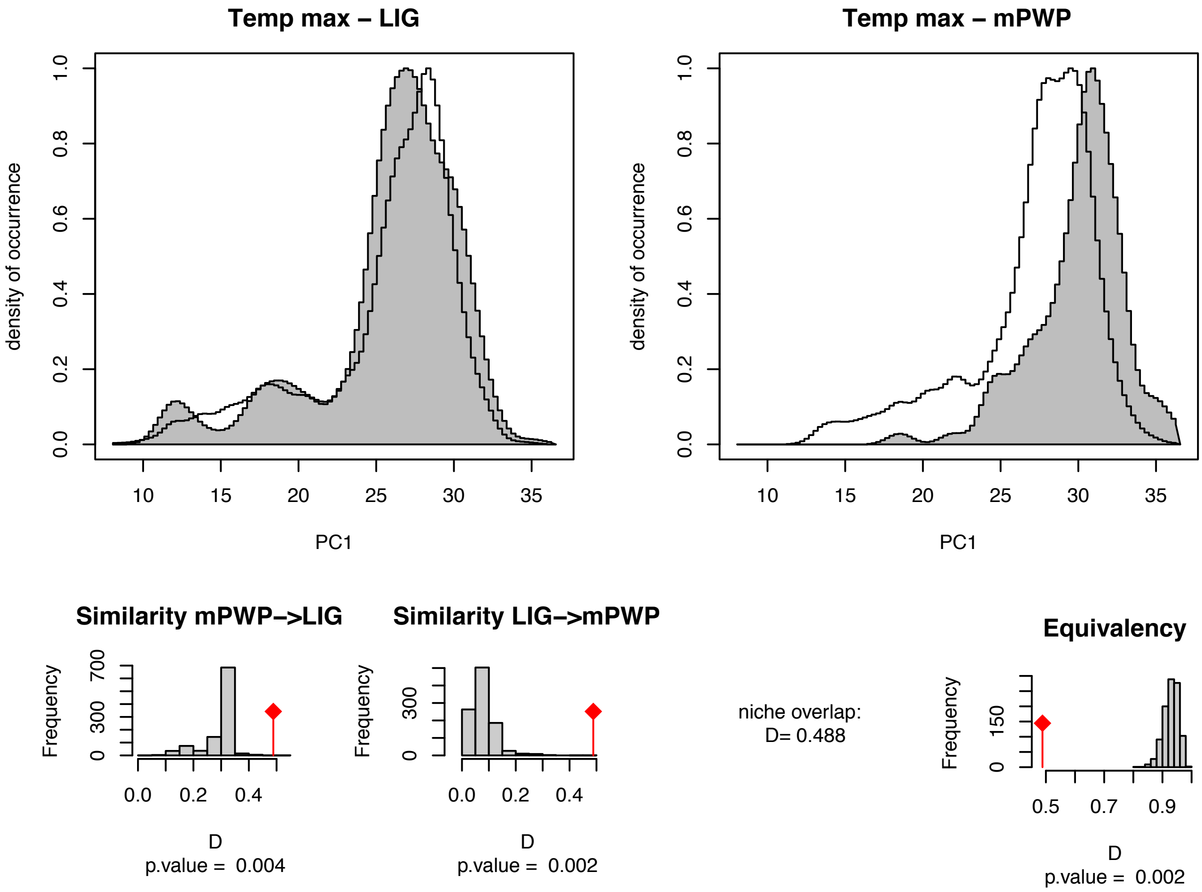
Equivalency

niche overlap:
D= 0.646

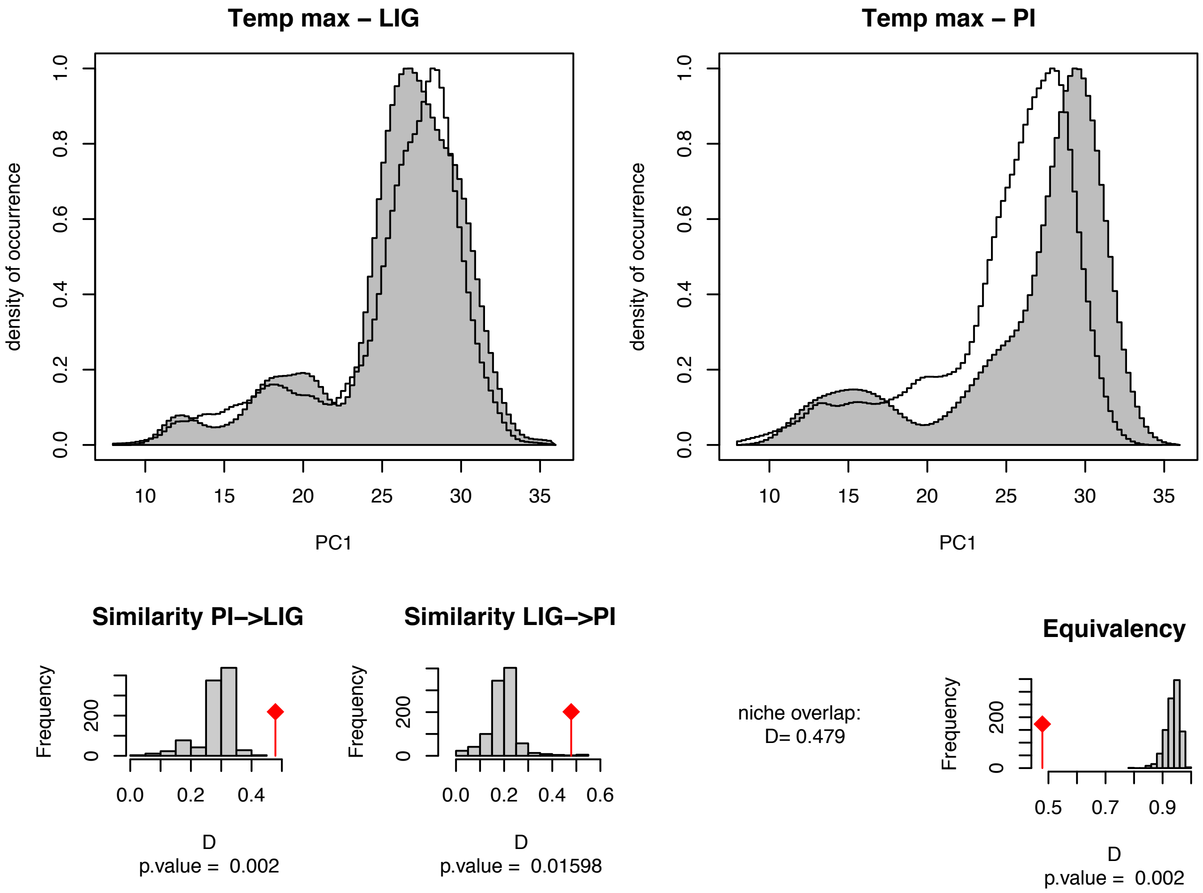
Bulla occidentalis: **PI—mPWP**



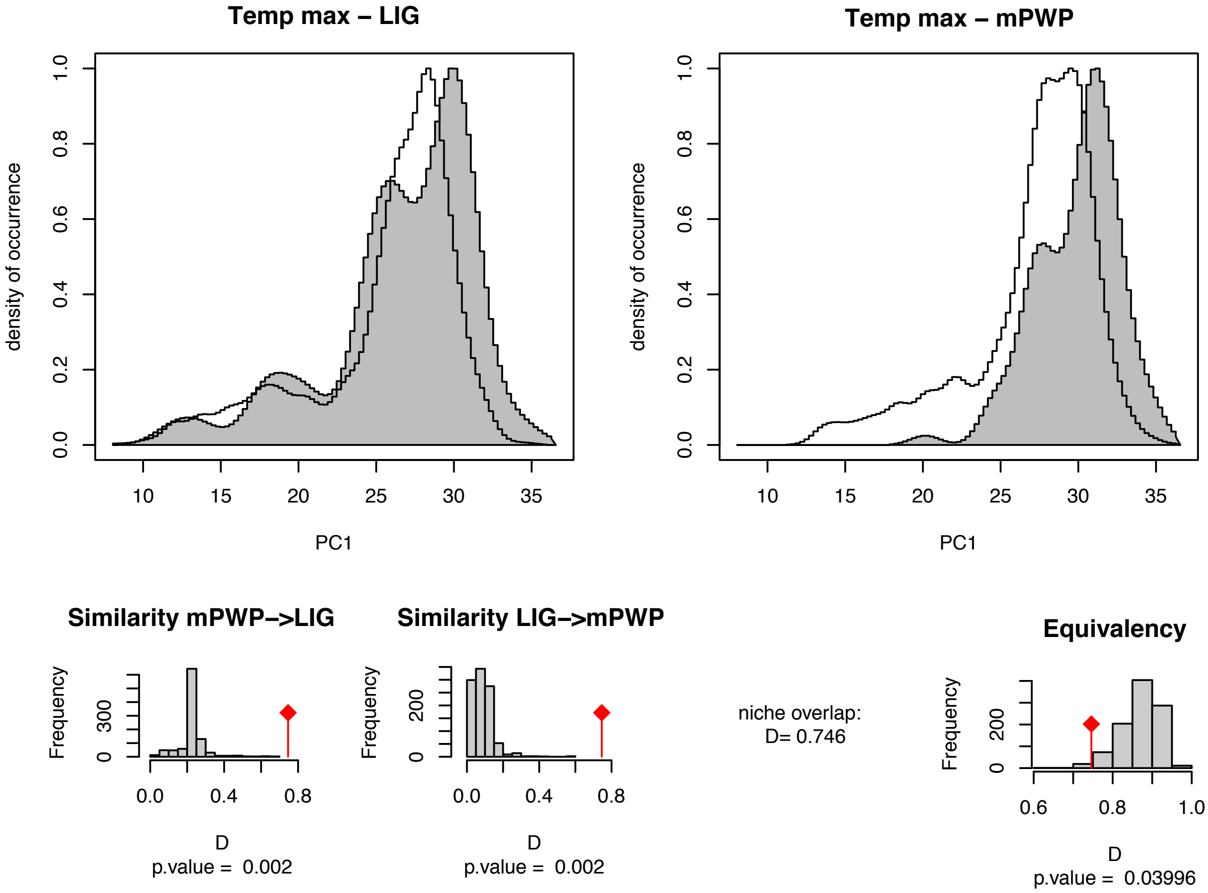
Crassostrea virginica: **LIG—mPWP**



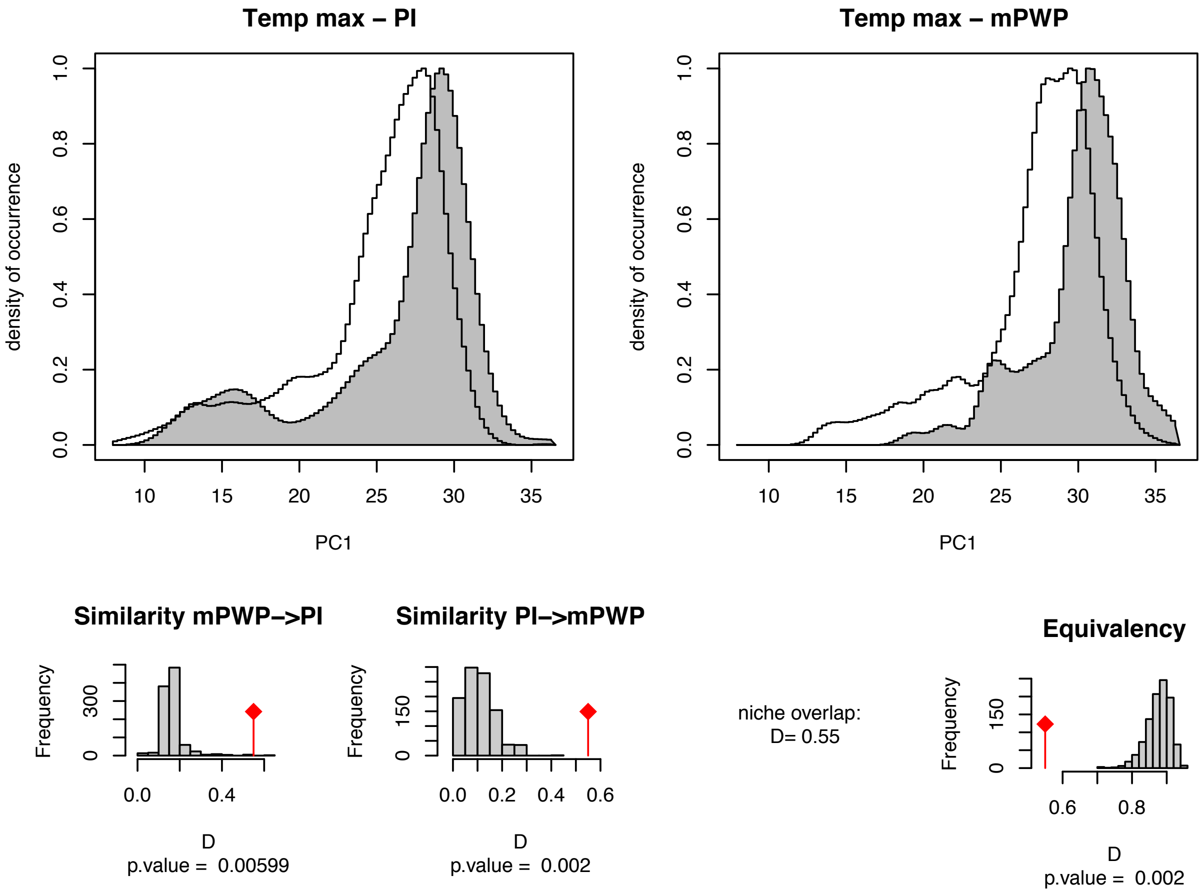
Crassostrea virginica: **LIG—PI**



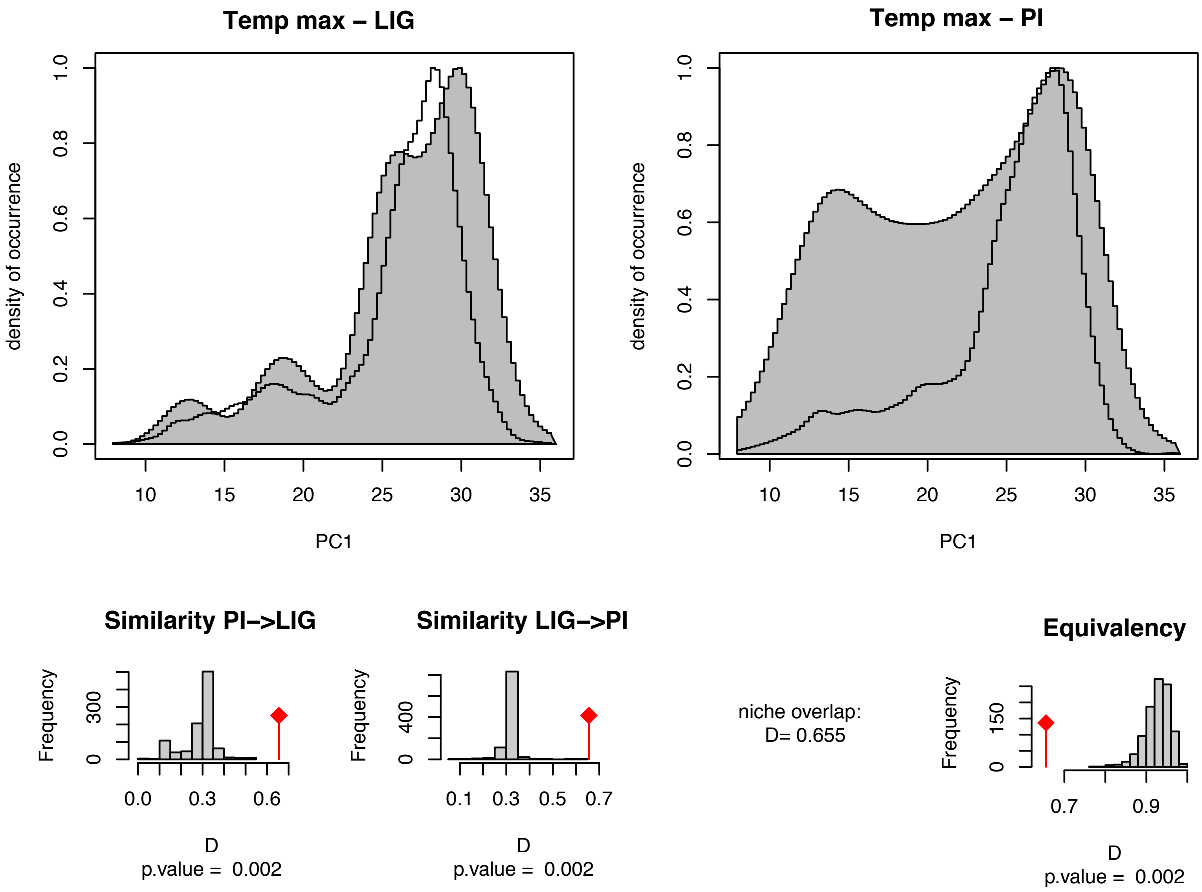
Crepidula fornicata: **LIG—mPWP**



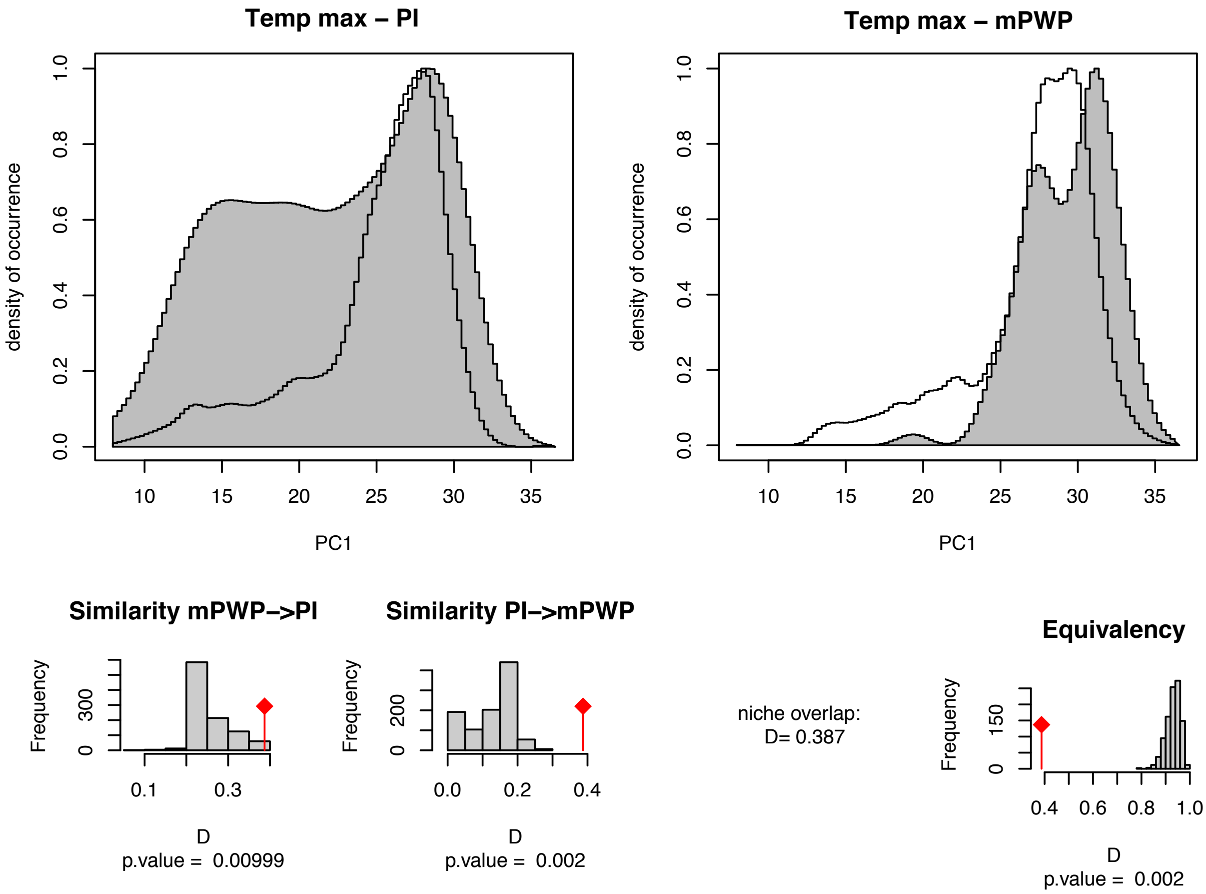
Crassostrea virginica: **PI—mPWP**



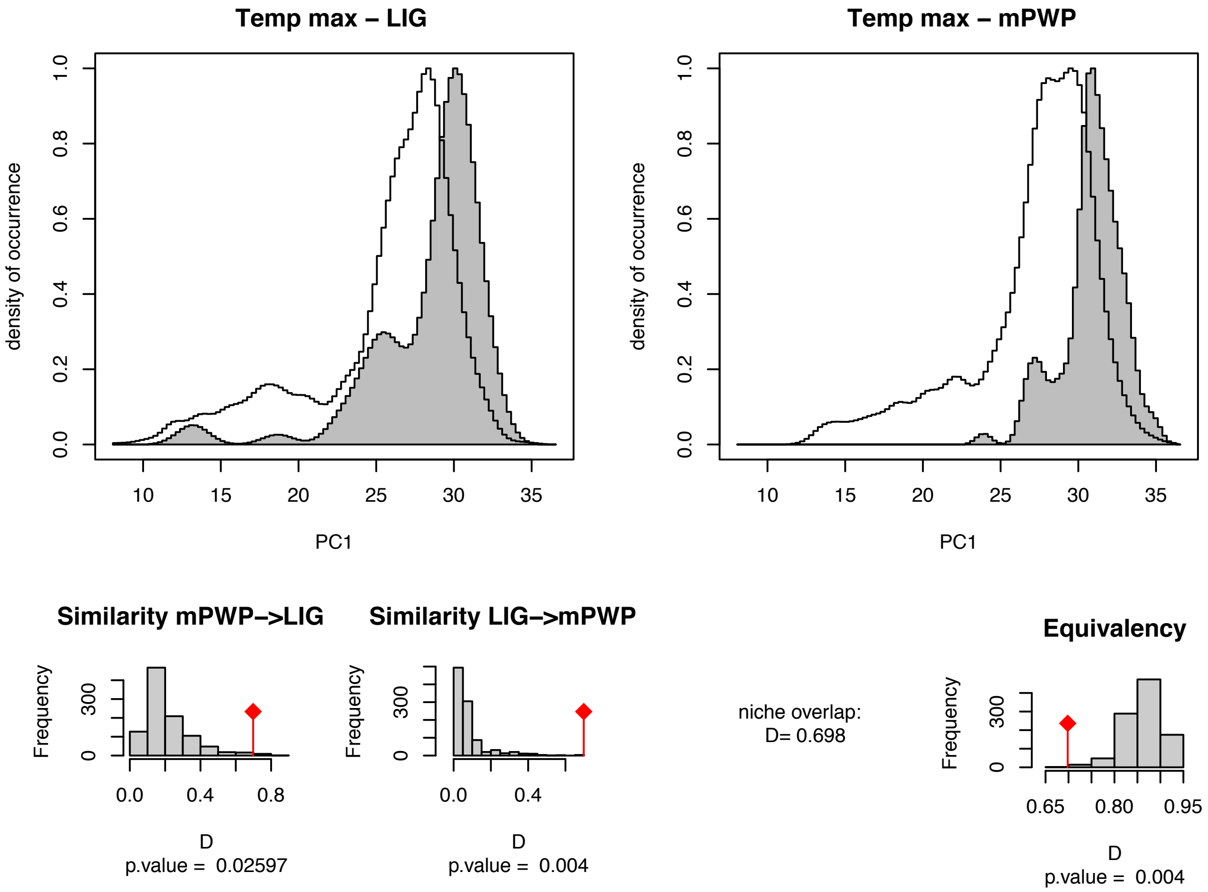
Crepidula fornicata: **LIG—PI**



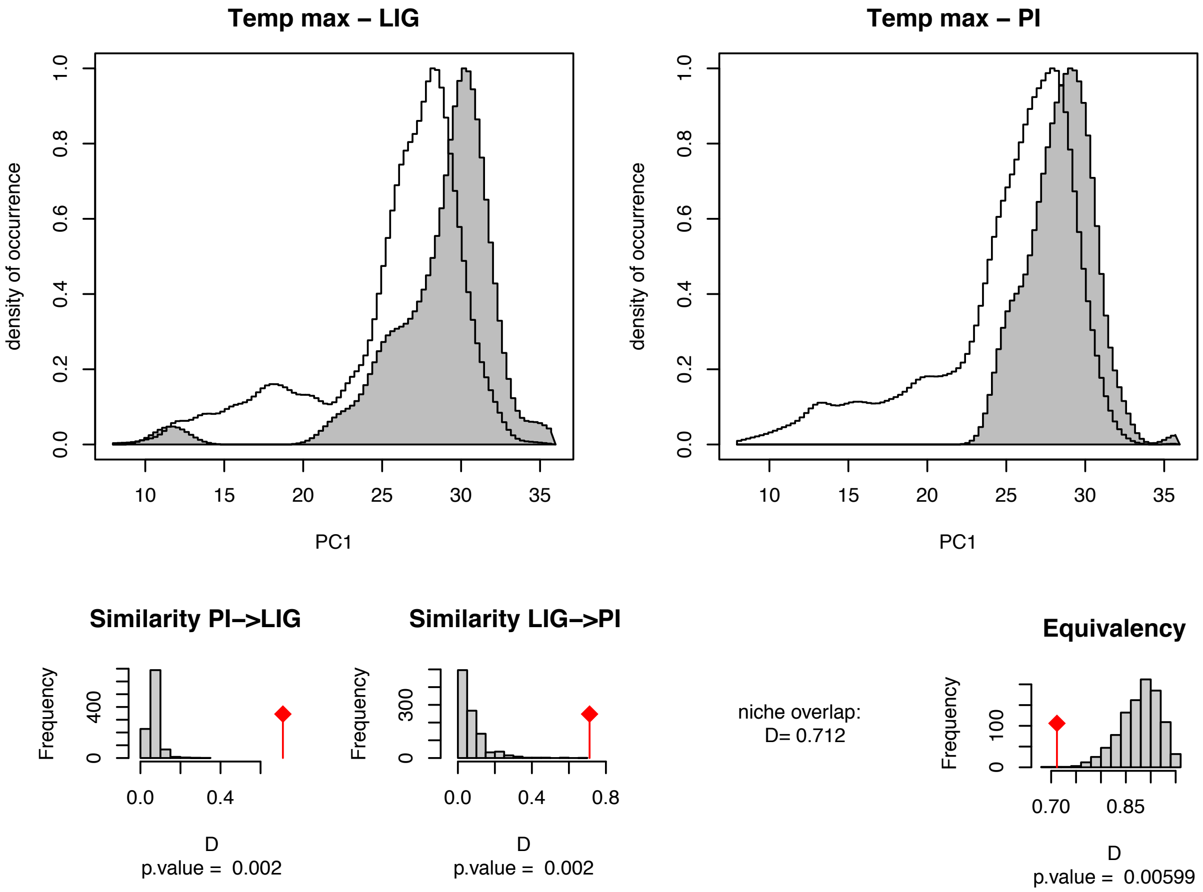
Crepidula fornicata: **PI—mPWP**



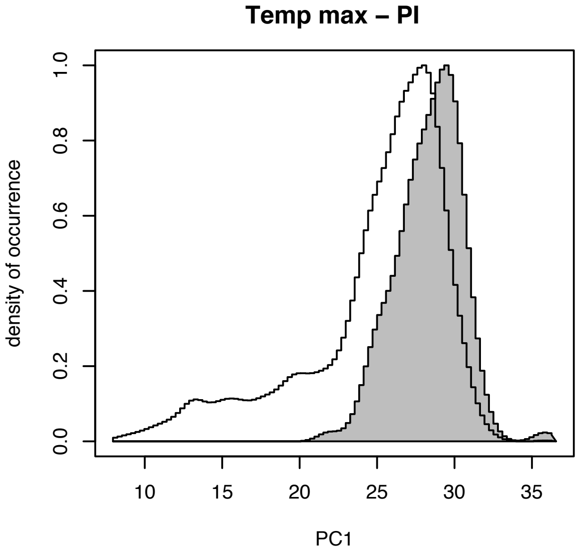
Dinocardium robustum: **LIG—mPWP**

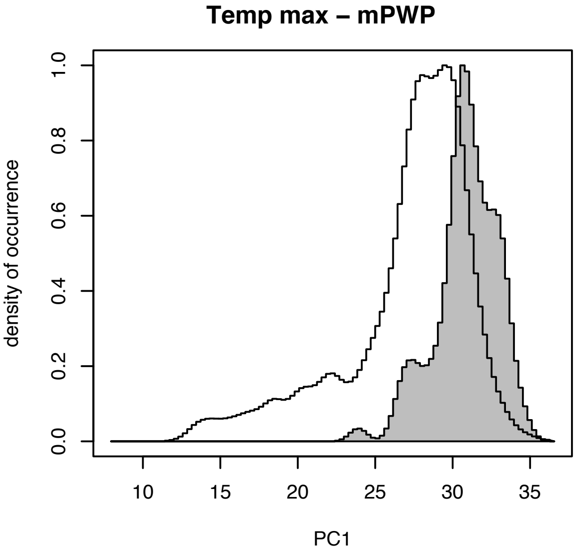


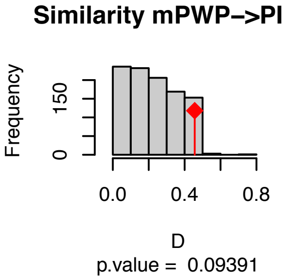
Dinocardium robustum: **LIG—PI**

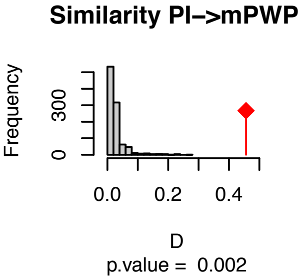


Dinocardium robustum: **PI—mPWP**

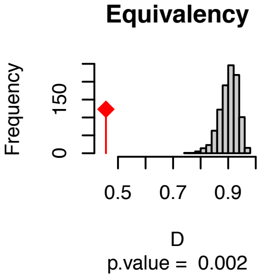




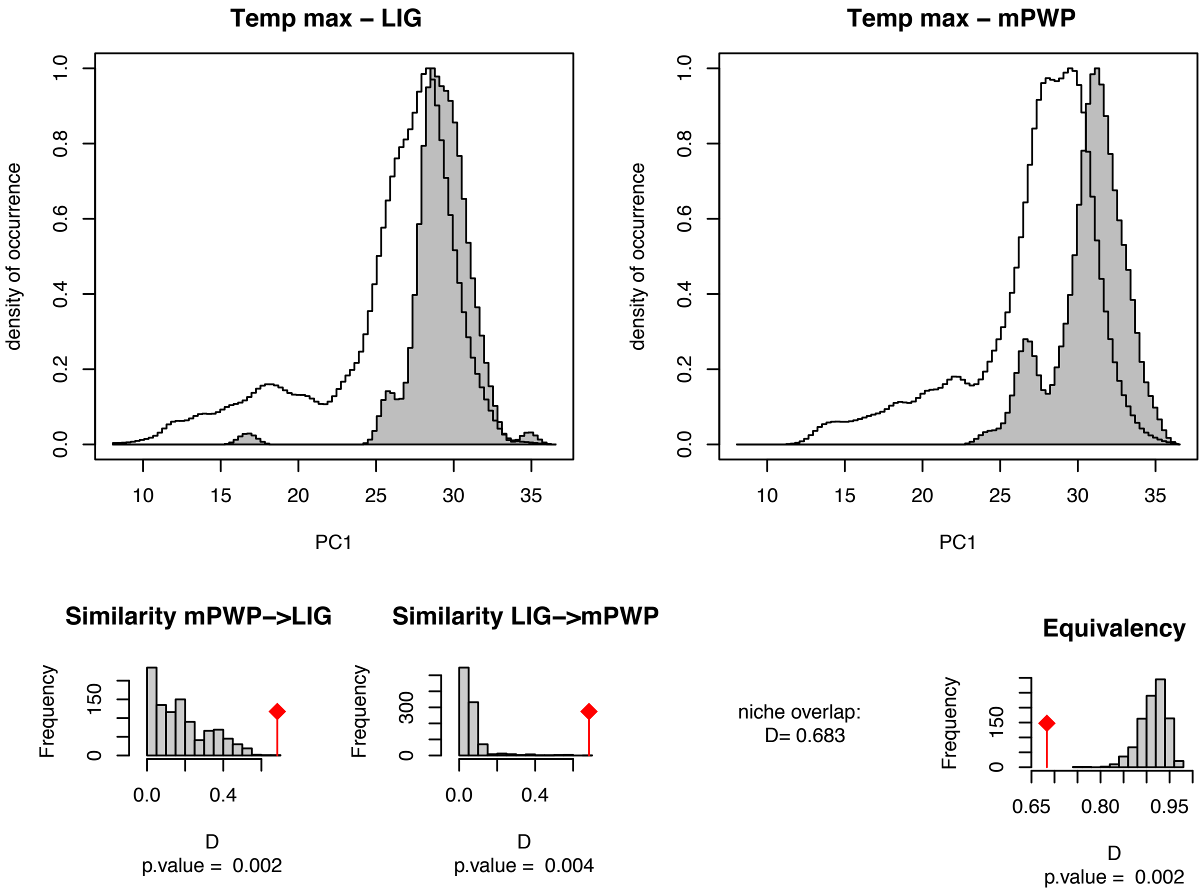




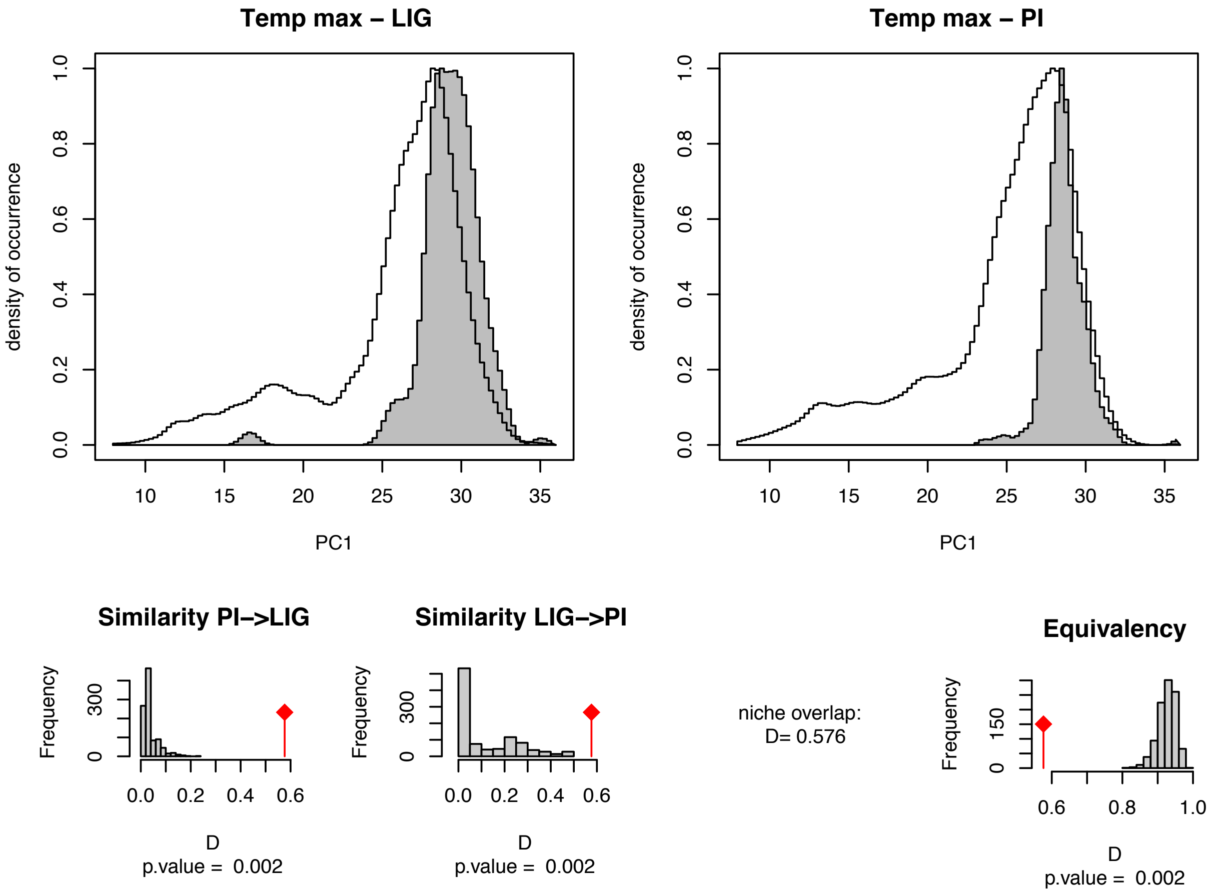
niche overlap:
D= 0.456



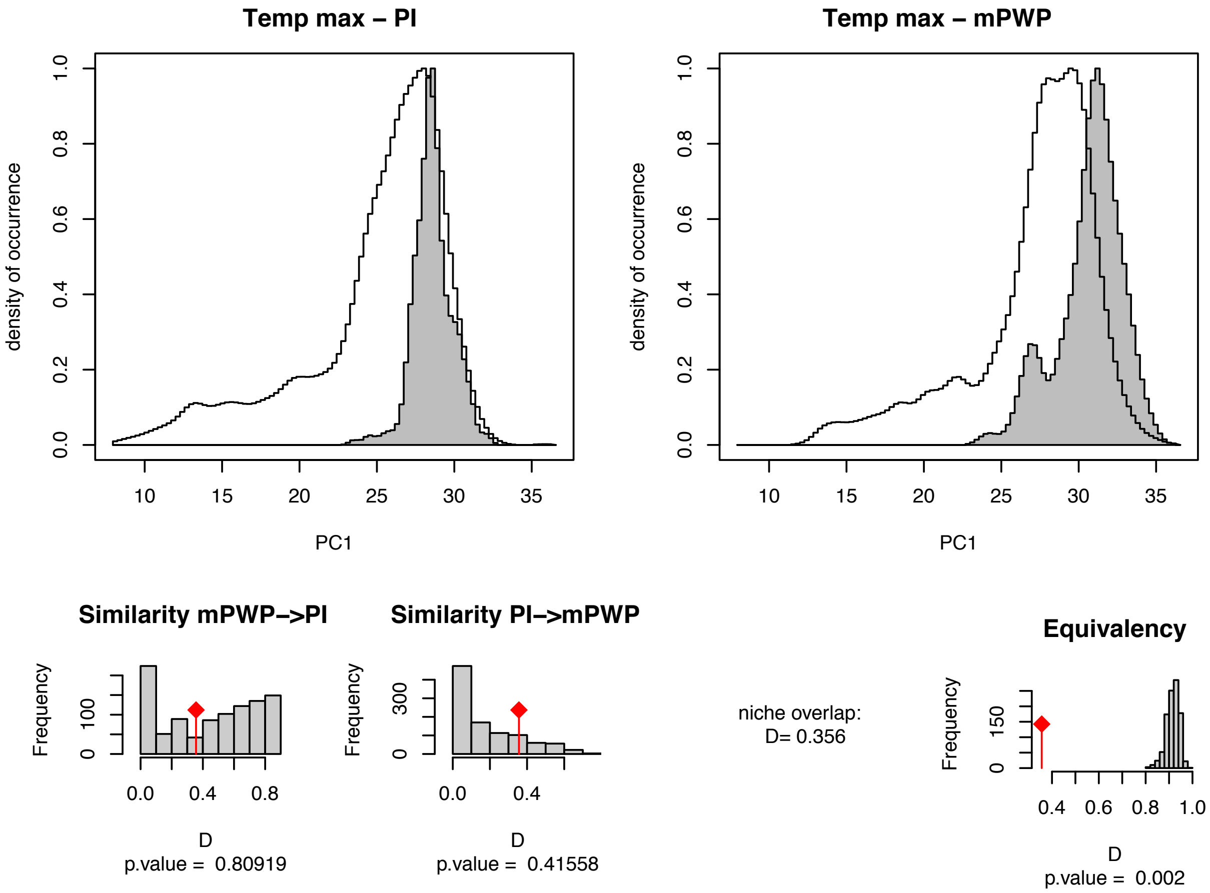
Lucina pensylvanica: **LIG—mPWP**



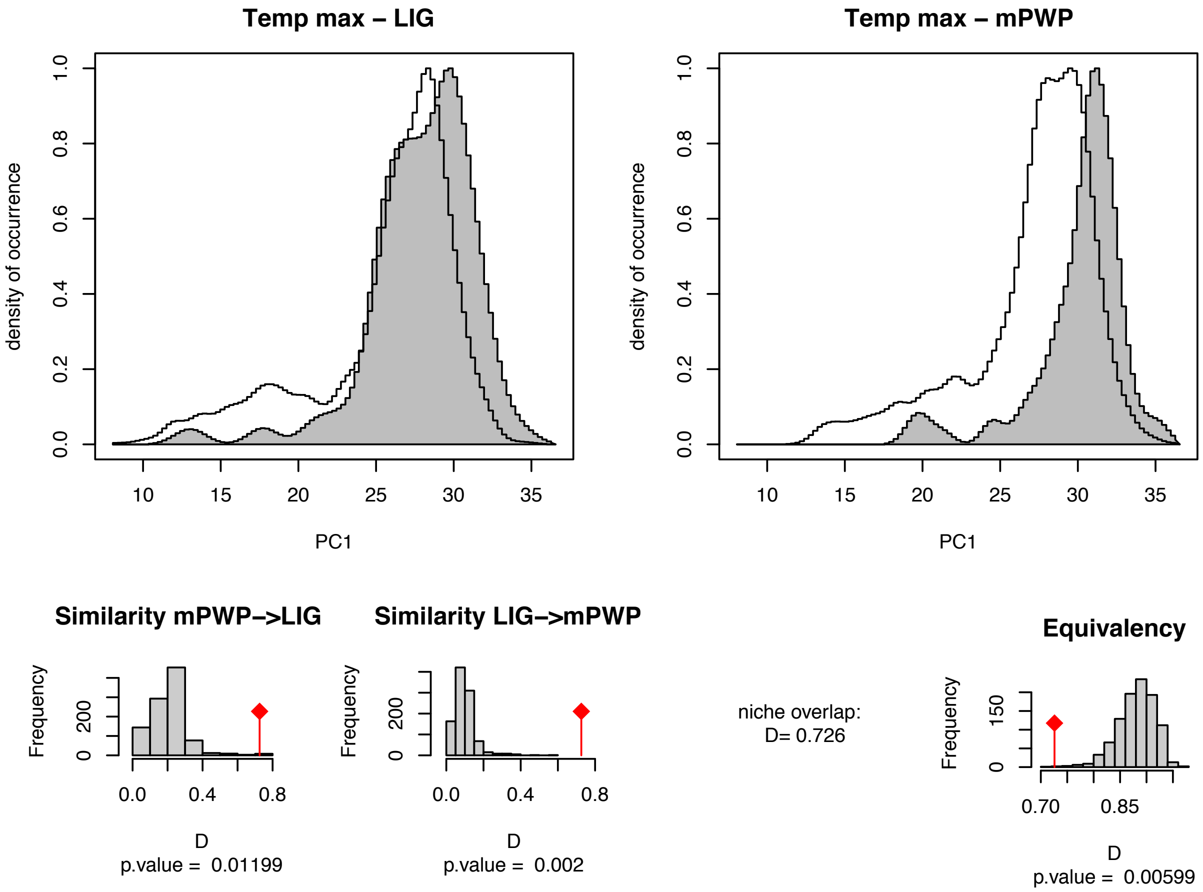
Lucina pensylvanica: **LIG—PI**



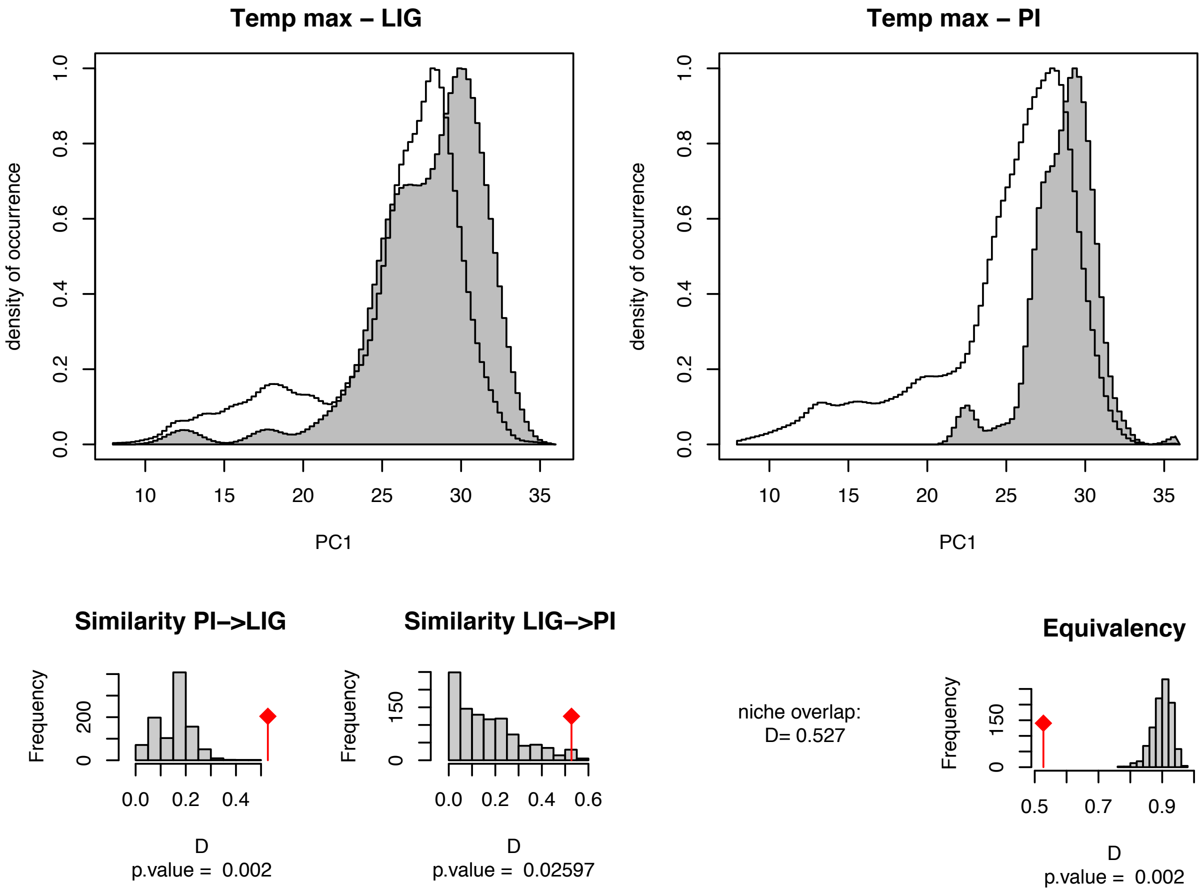
Lucina pensylvanica: **PI—mPWP**



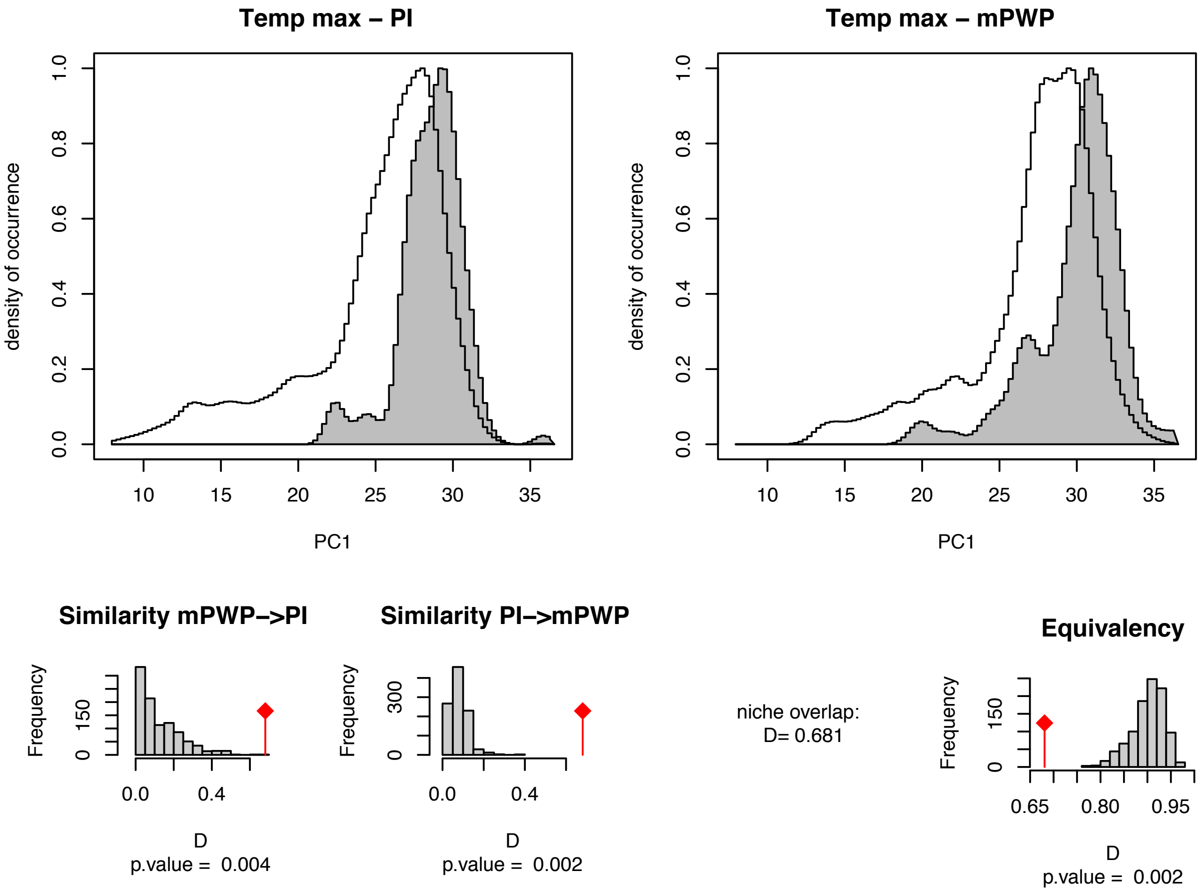
Mercenaria campechiensis: **LIG—mPWP**



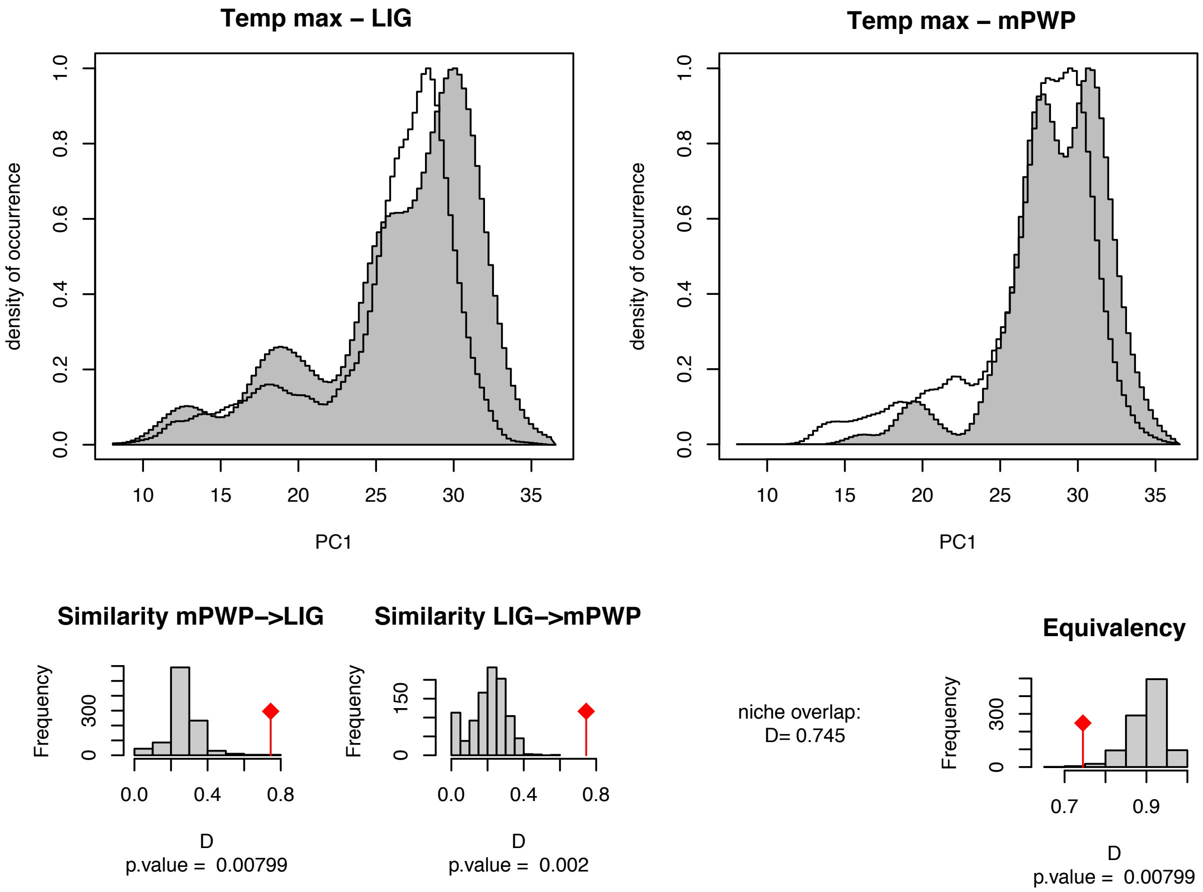
Mercenaria campechiensis: **LIG—PI**



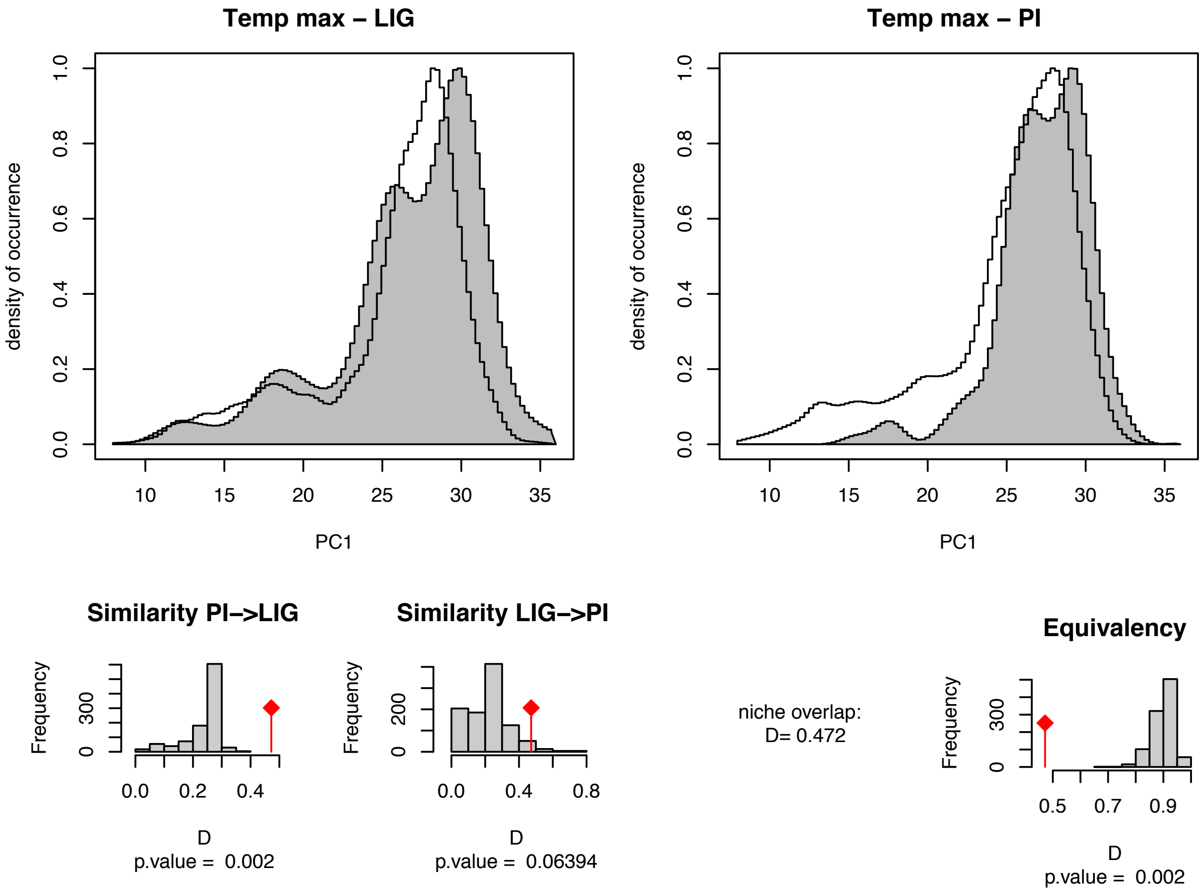
Mercenaria campechiensis: **PI—mPWP**



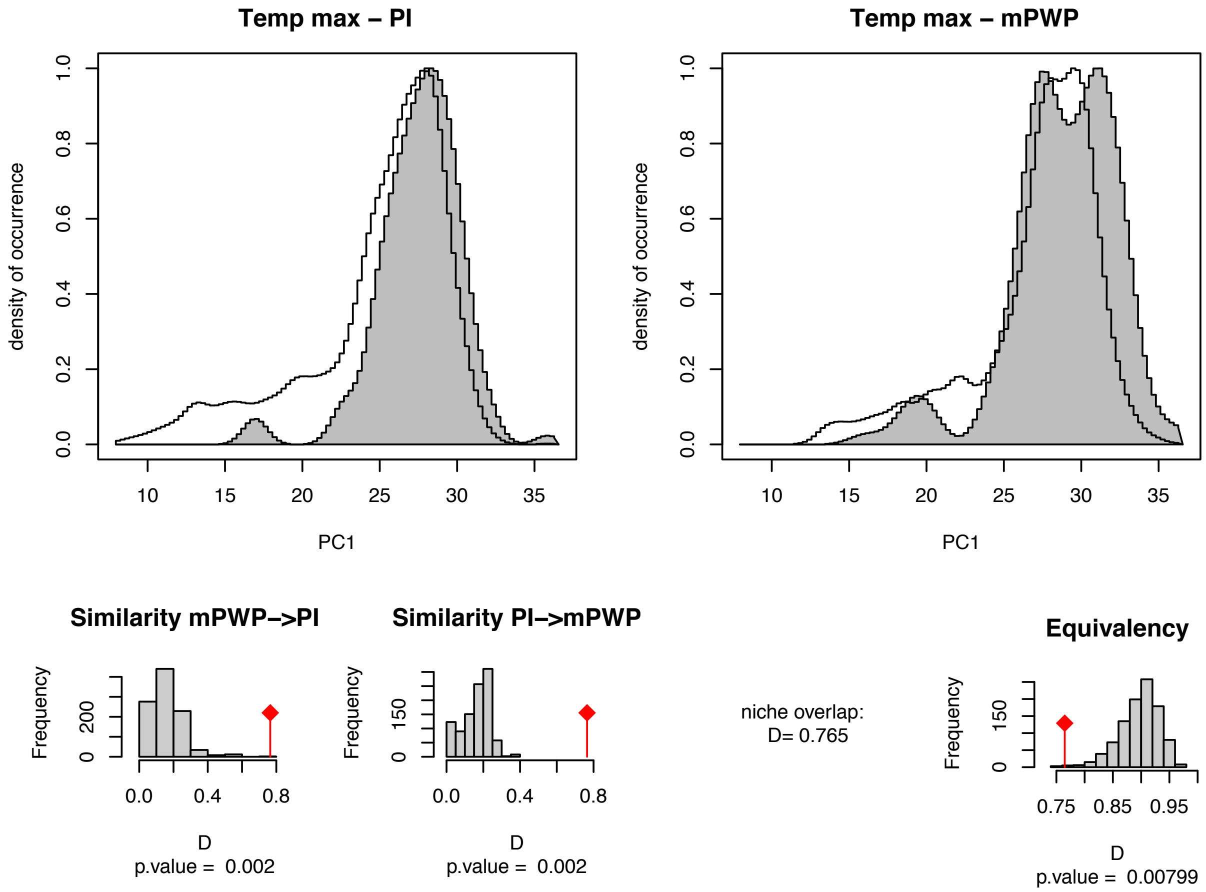
Neverita duplicata: **LIG—mPWP**



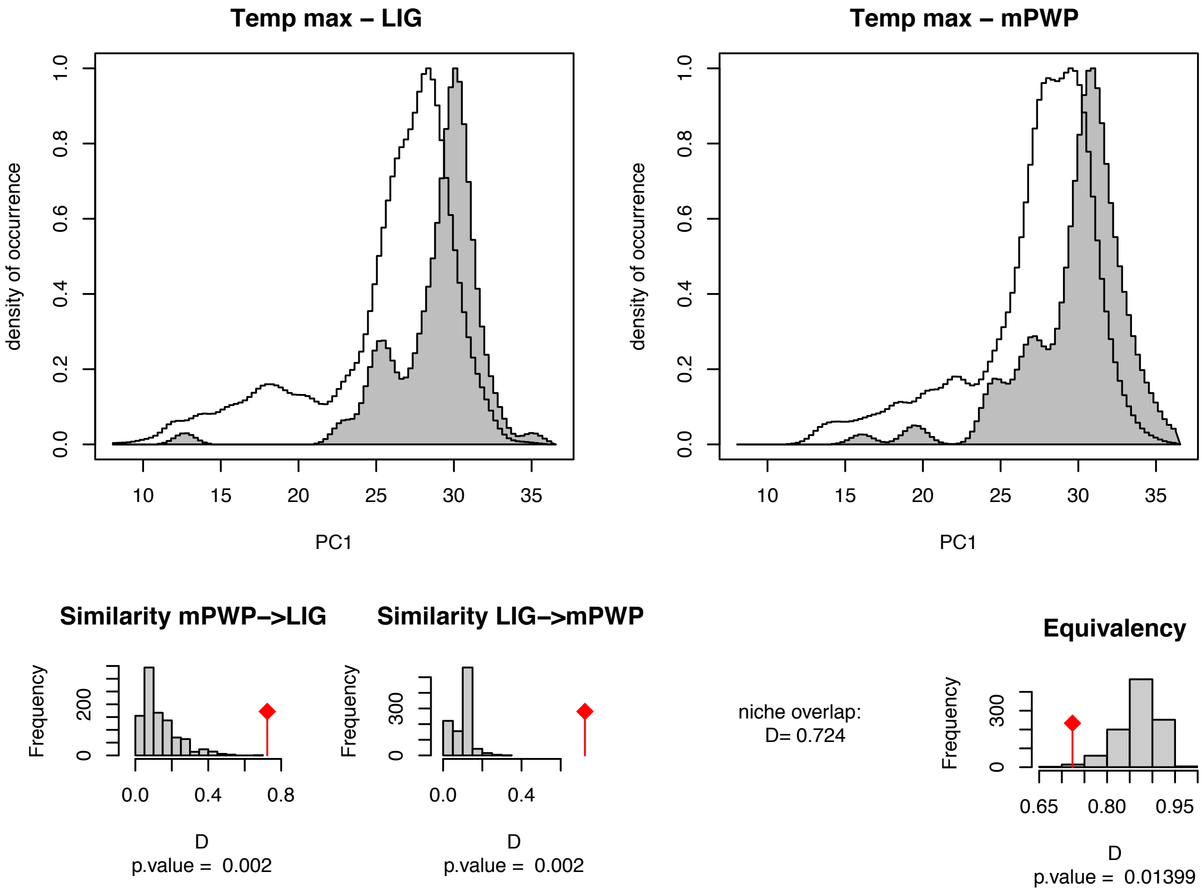
Neverita duplicata: **LIG—PI**



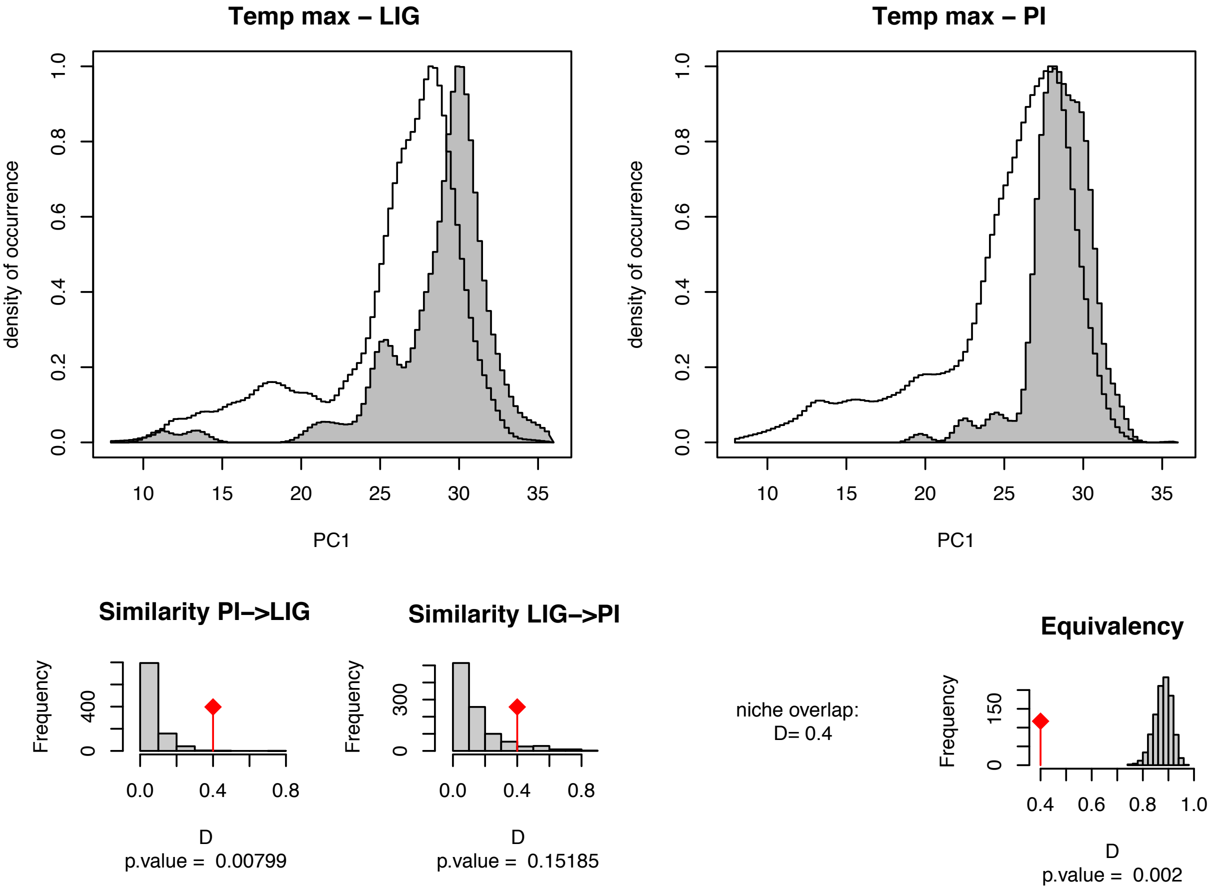
Neverita duplicata: **PI—mPWP**



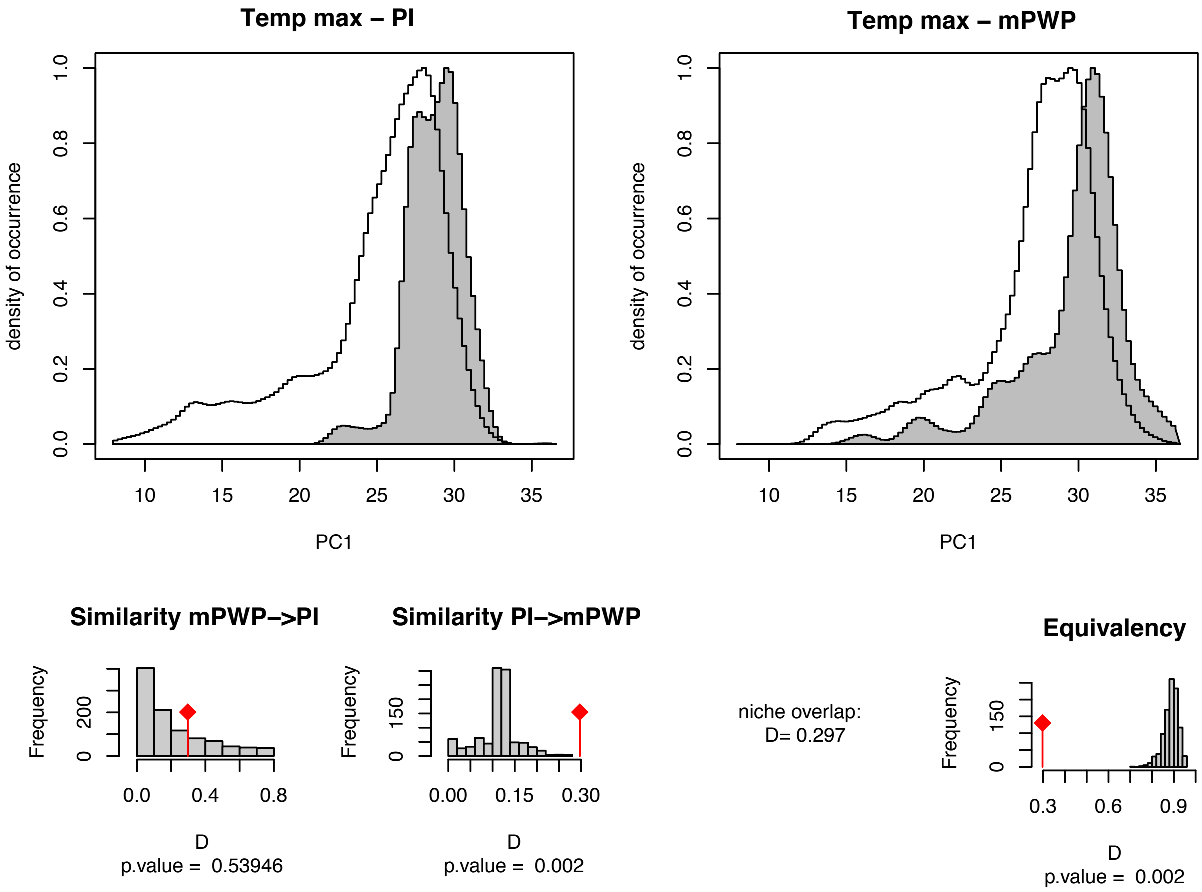
Oliva sayana: **LIG—mPWP**



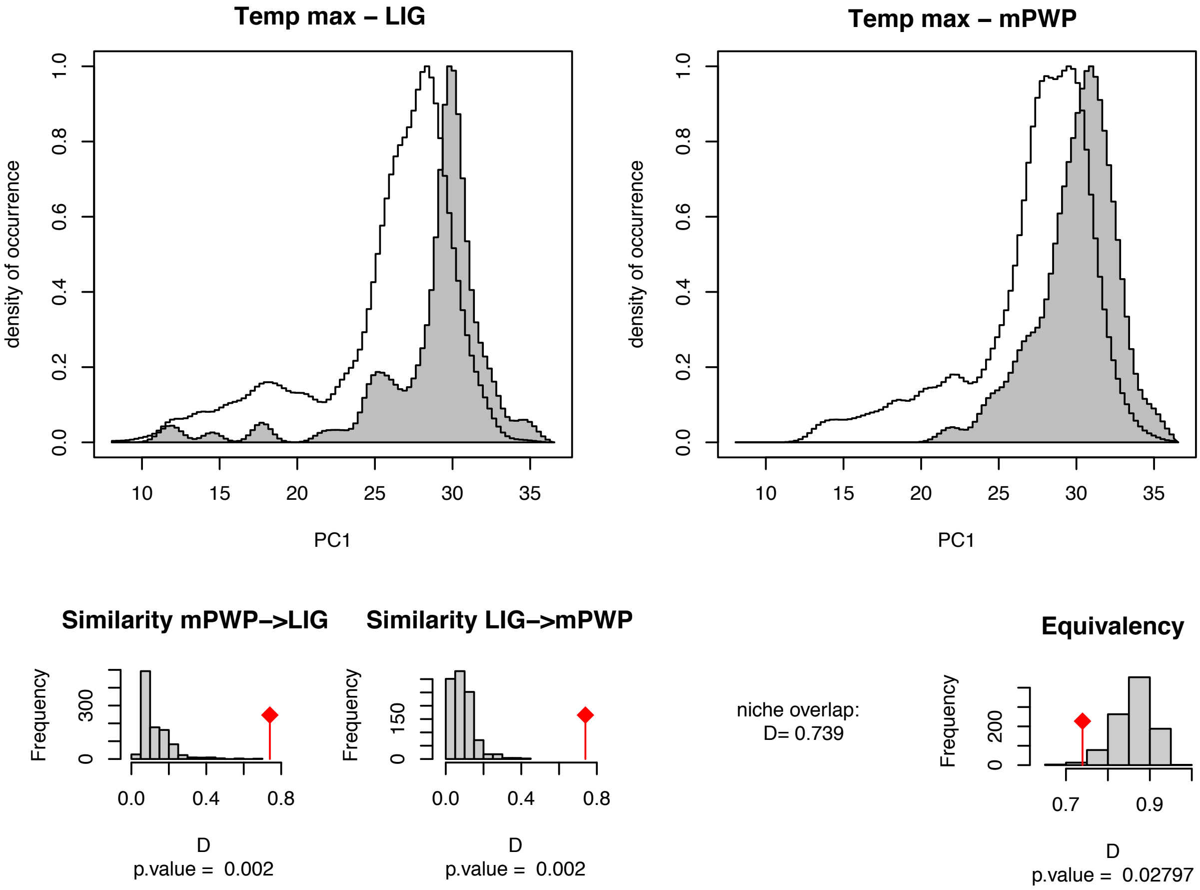
Oliva sayana: **LIG—PI**



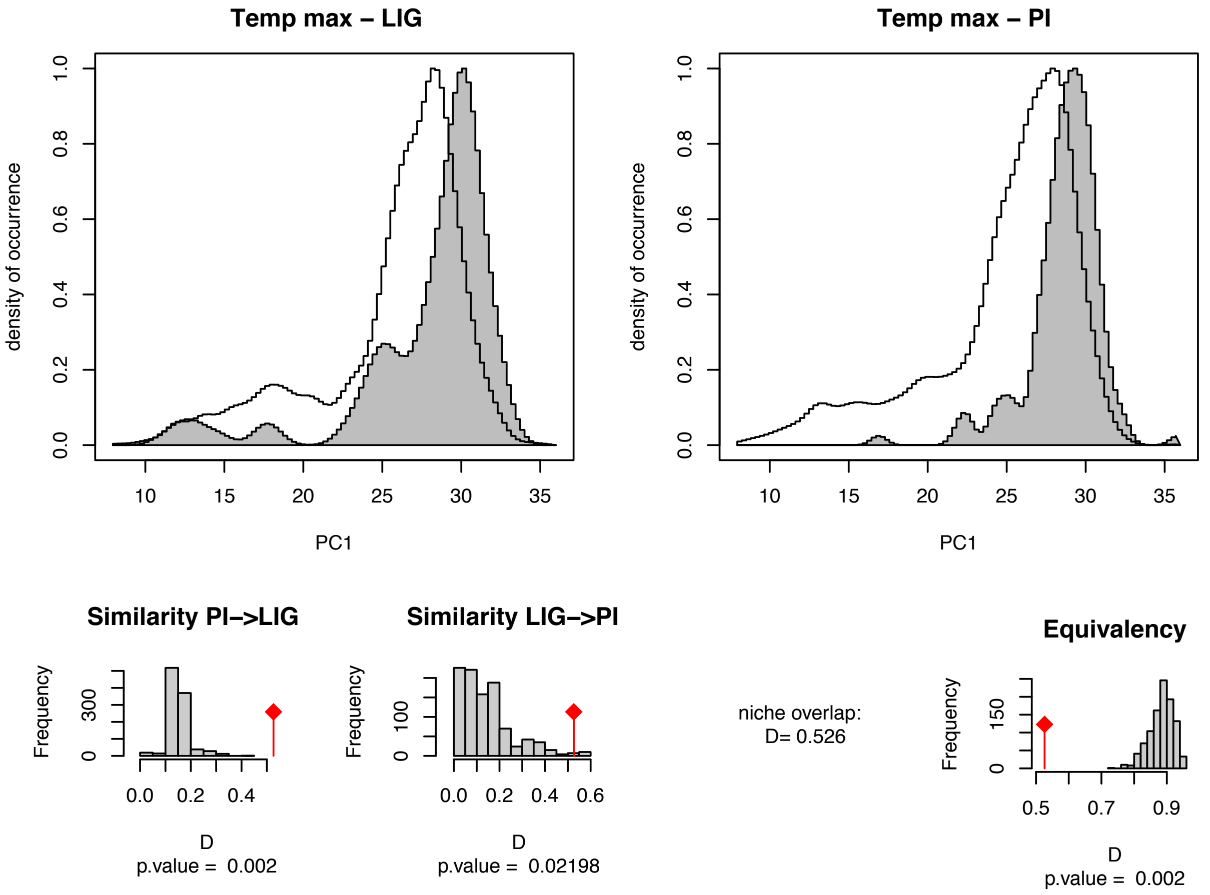
Oliva sayana: **PI—mPWP**



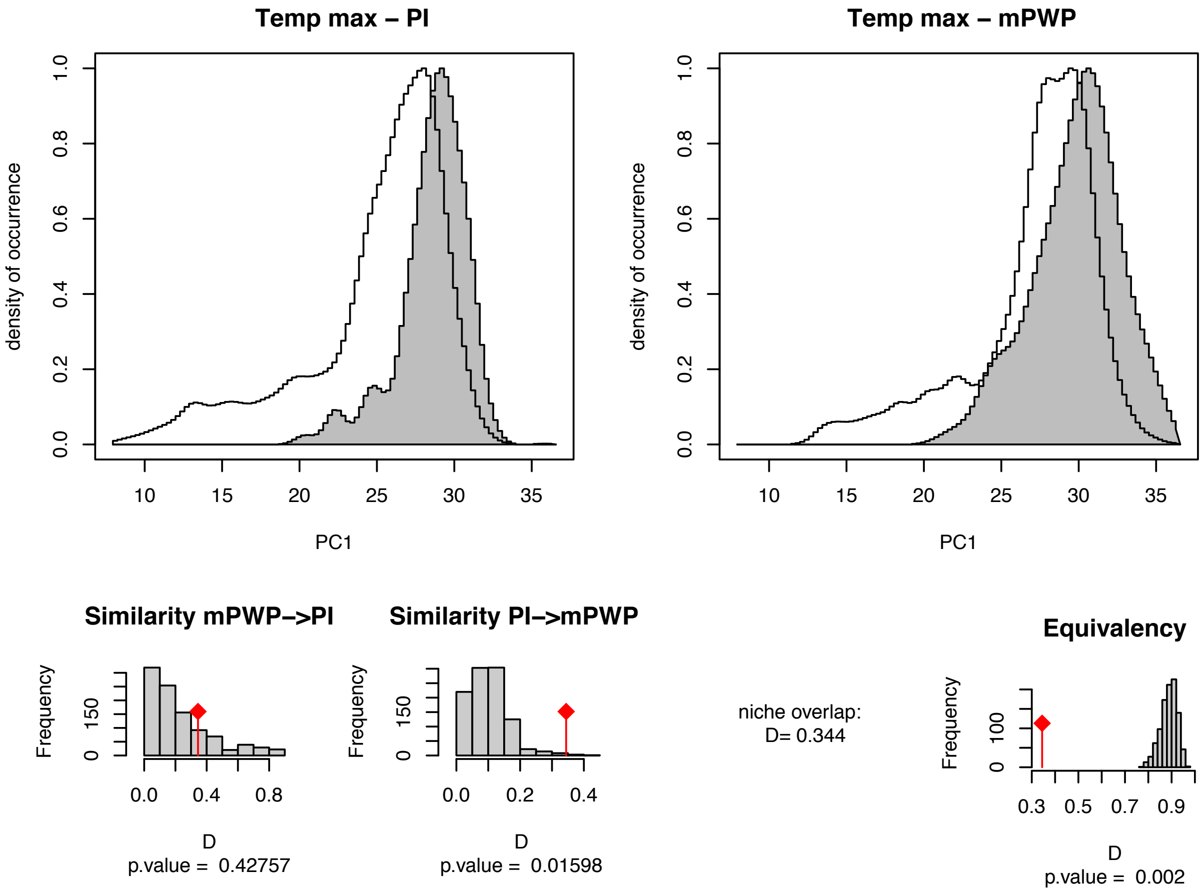
Terebra dislocata: **LIG—mPWP**



Terebra dislocata: **LIG—PI**



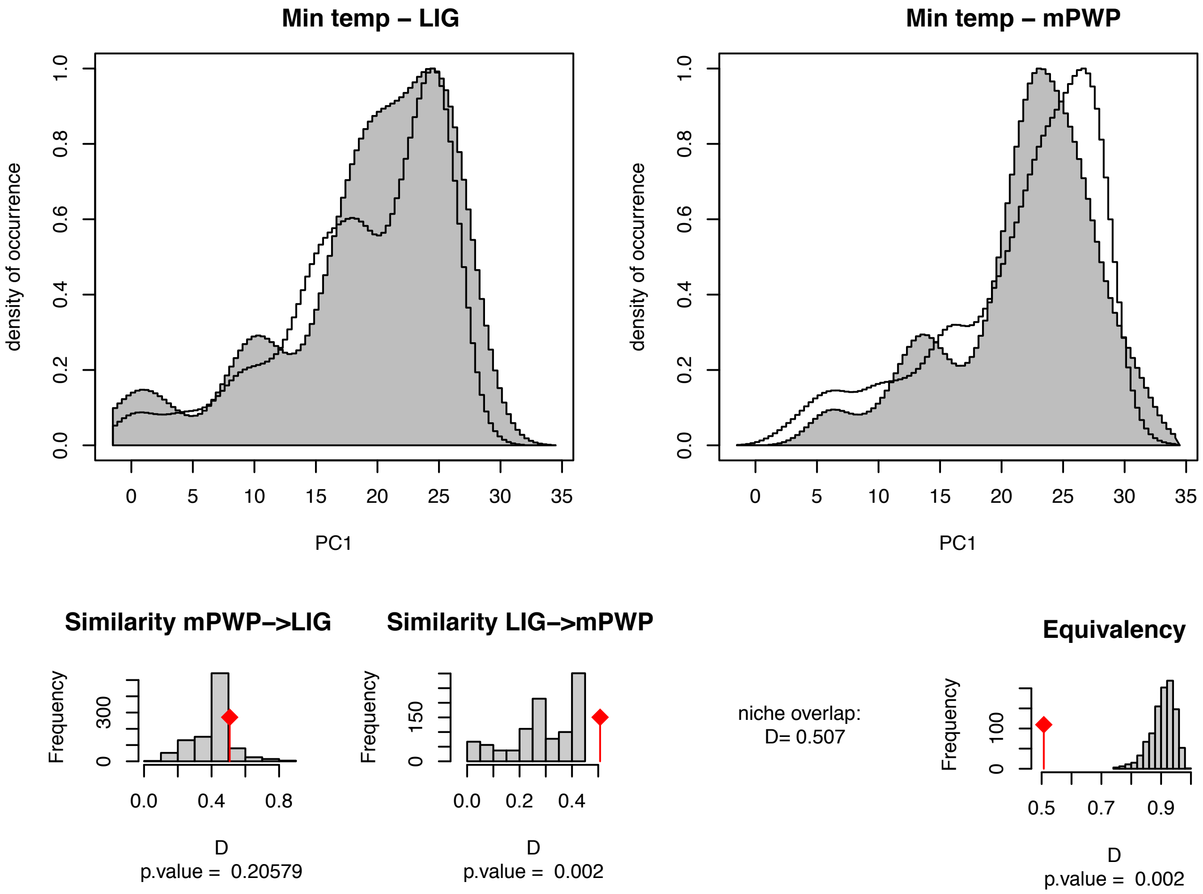
Terebra dislocata: **PI—mPWP**



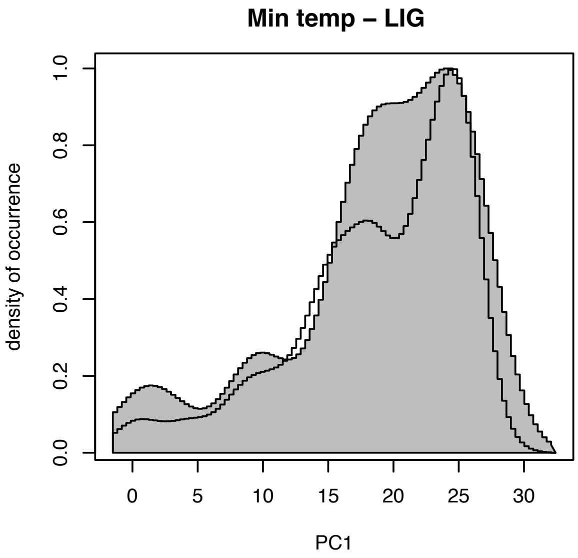
Appendix S2.3f. Minimum temperature comparisons

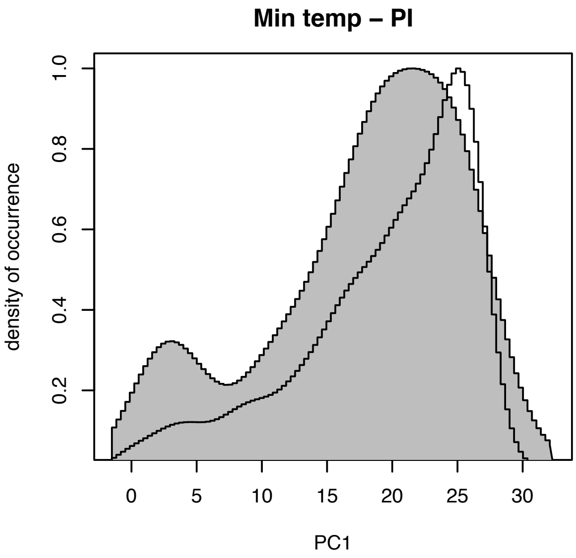
Results from comparison of minimum temperature tolerances using script of Broennimann *et al.* (2012). The right histogram is the simulated similarity values (D) and observed similarity value (red bar) for the niche equivalency test. The left two histograms are the simulated and observed (red bar) similarity 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.

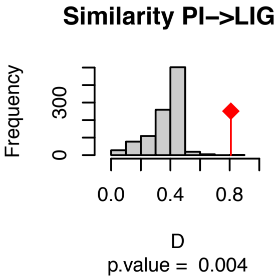
Anomia simplex: **LIG—mPWP**

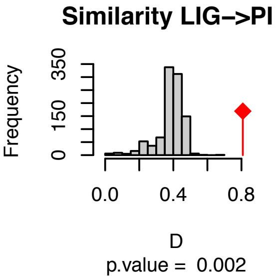


Anomia simplex: **LIG—PI**

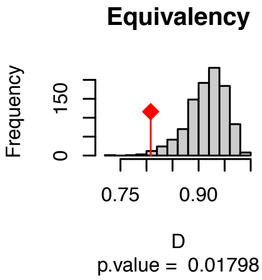




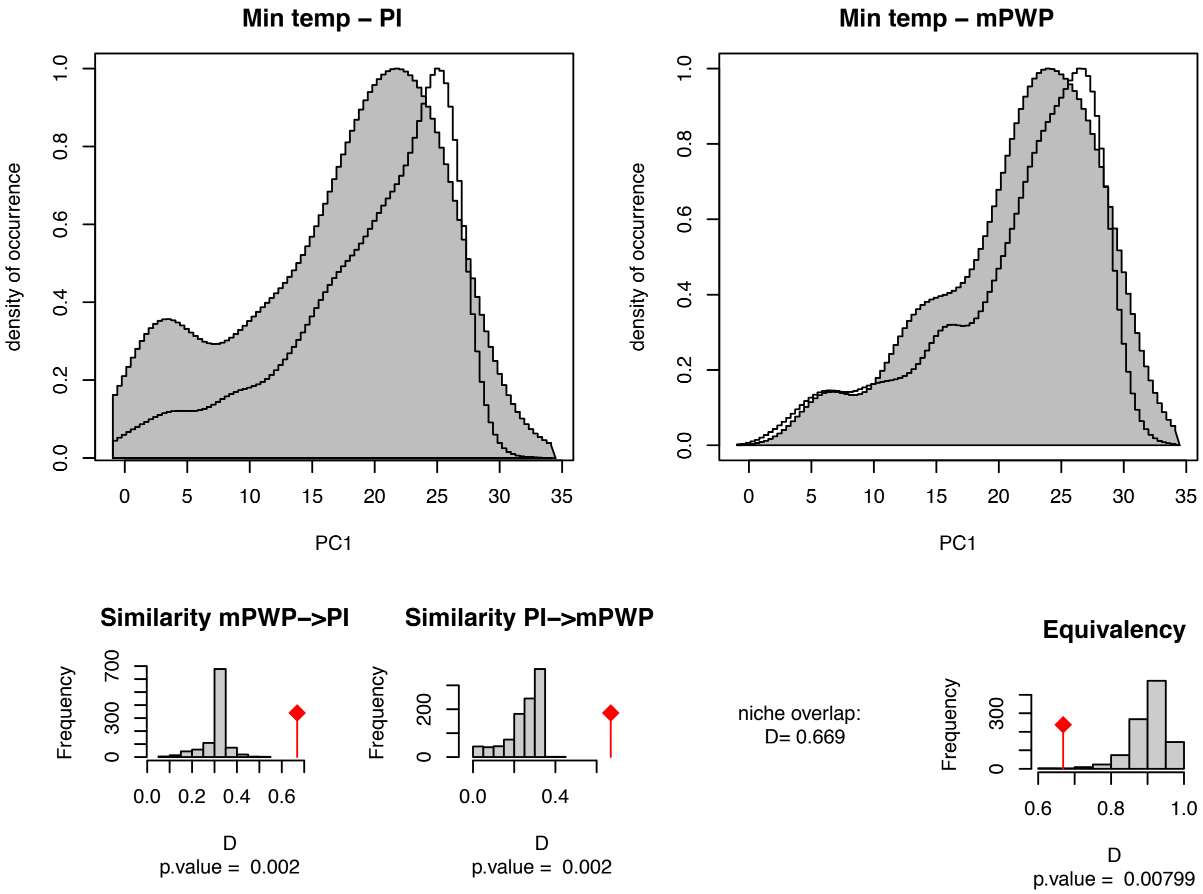




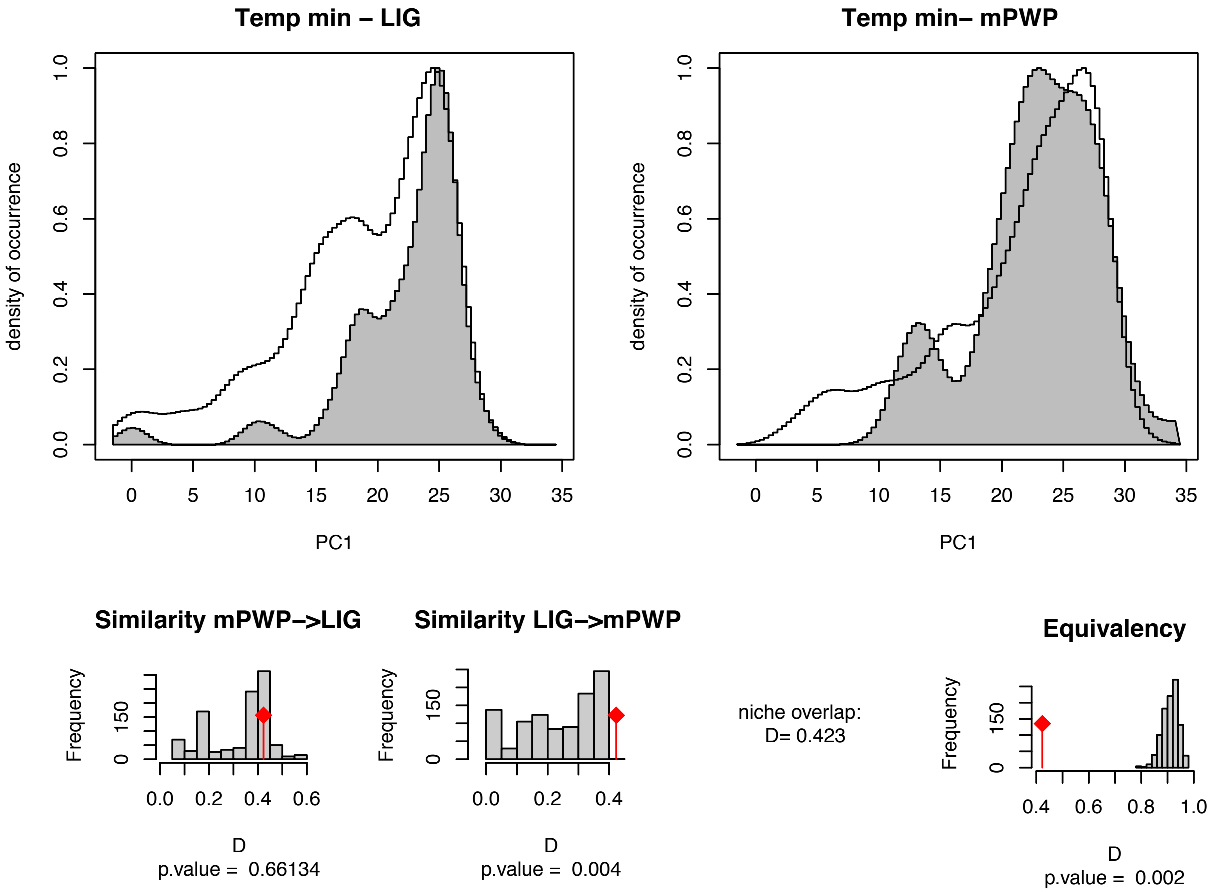
niche overlap:
D= 0.808



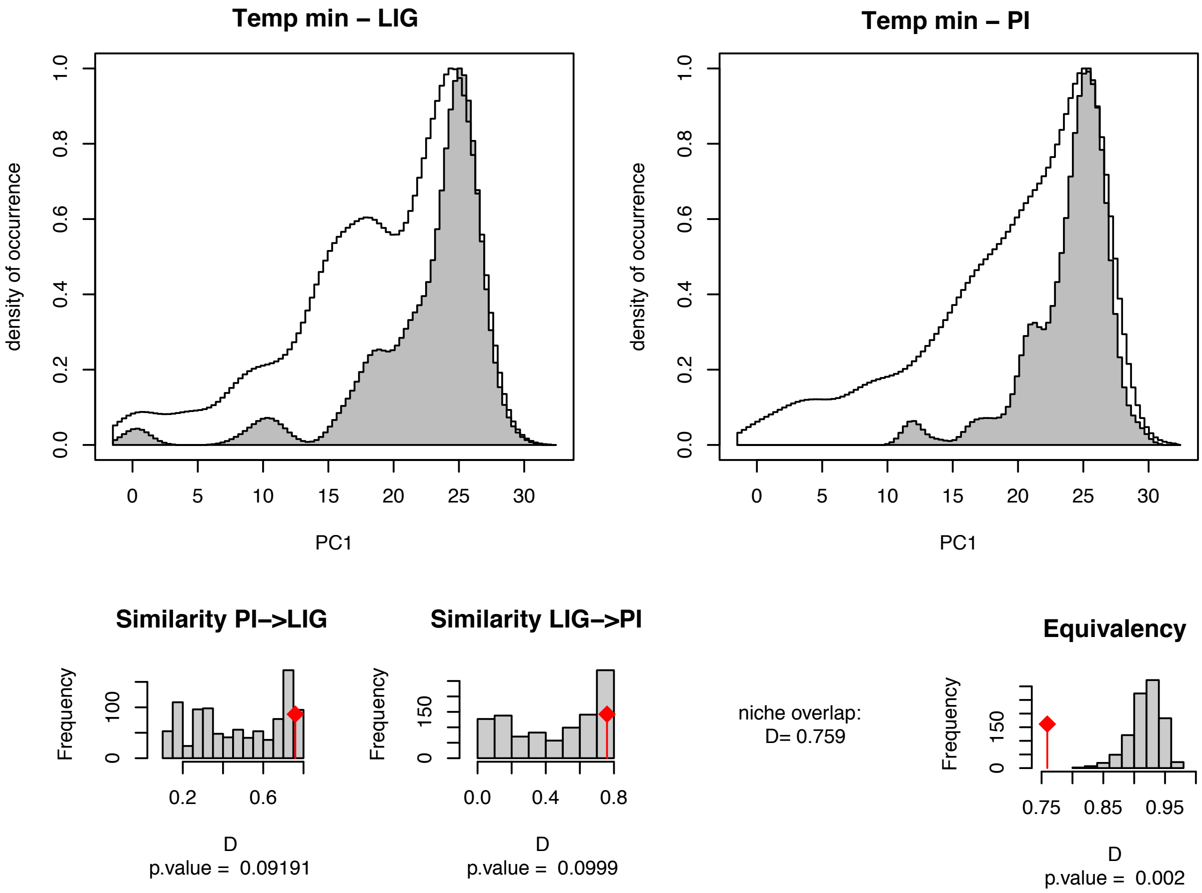
Anomia simplex: **PI—mPWP**



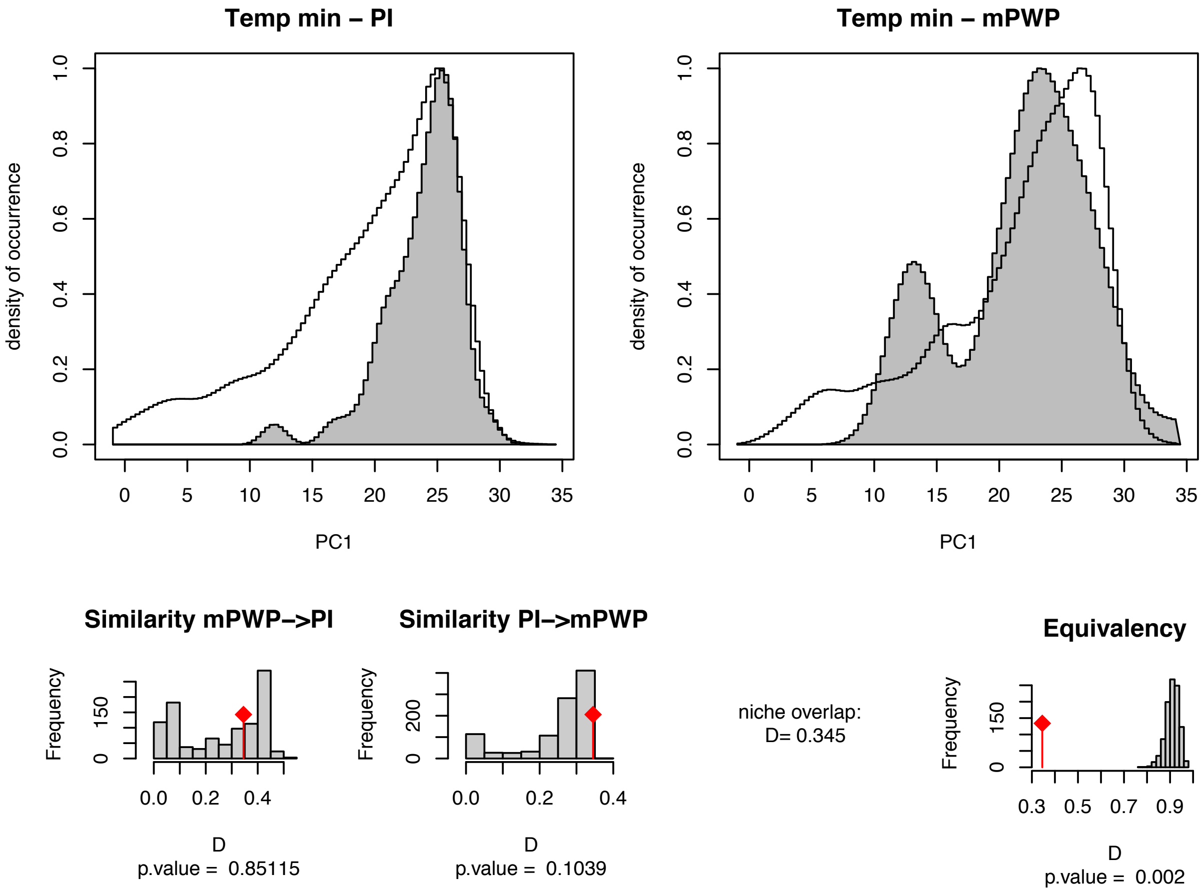
Bulla occidentalis: **LIG—mPWP**



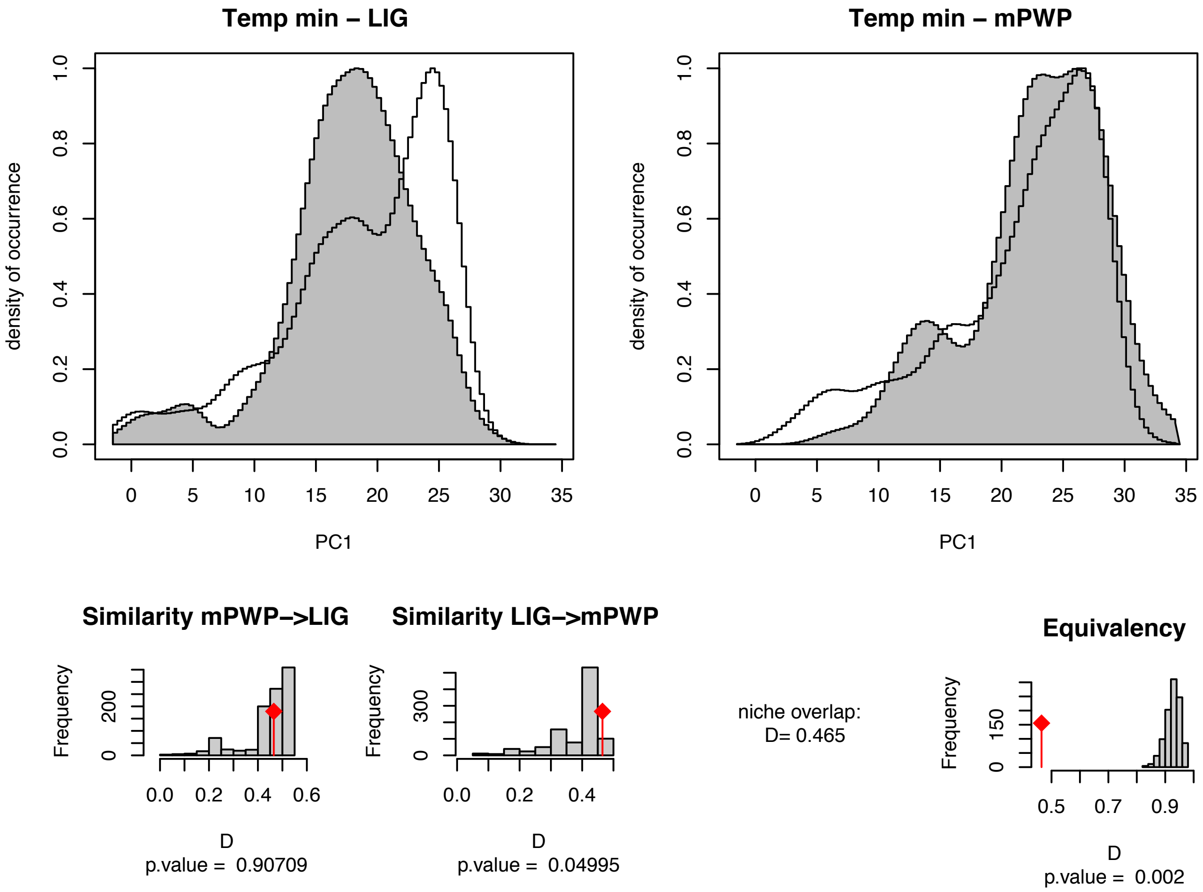
Bulla occidentalis: **LIG—PI**



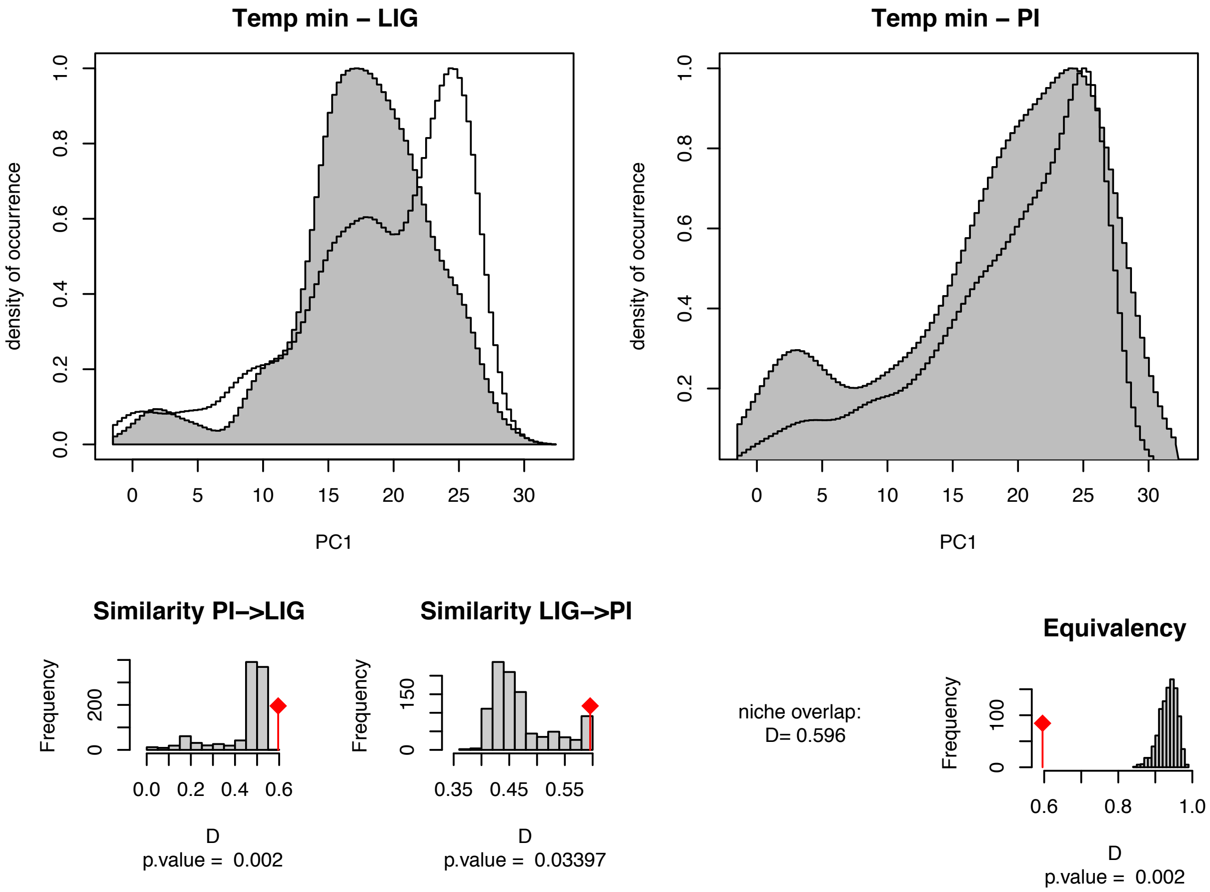
Bulla occidentalis: **PI—mPWP**



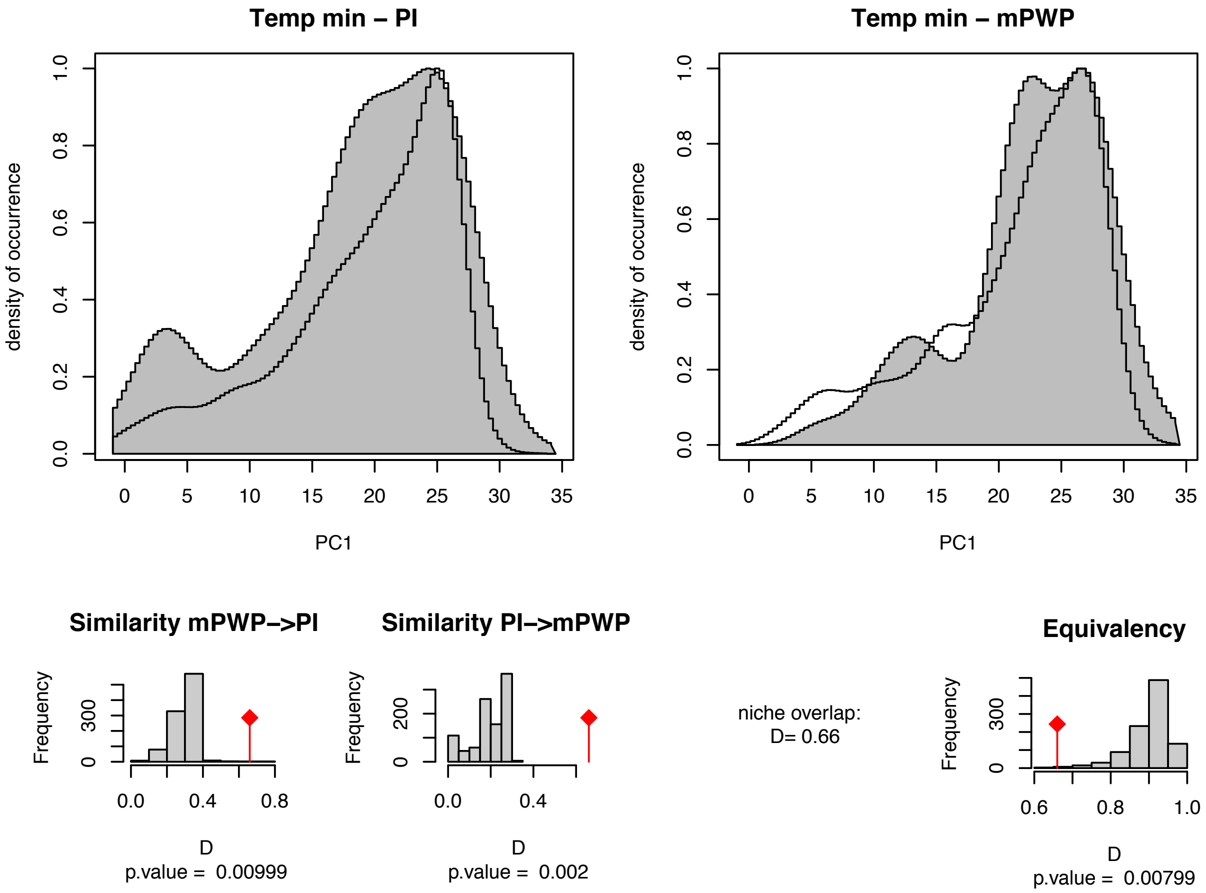
Crassostrea virginica: **LIG—mPWP**



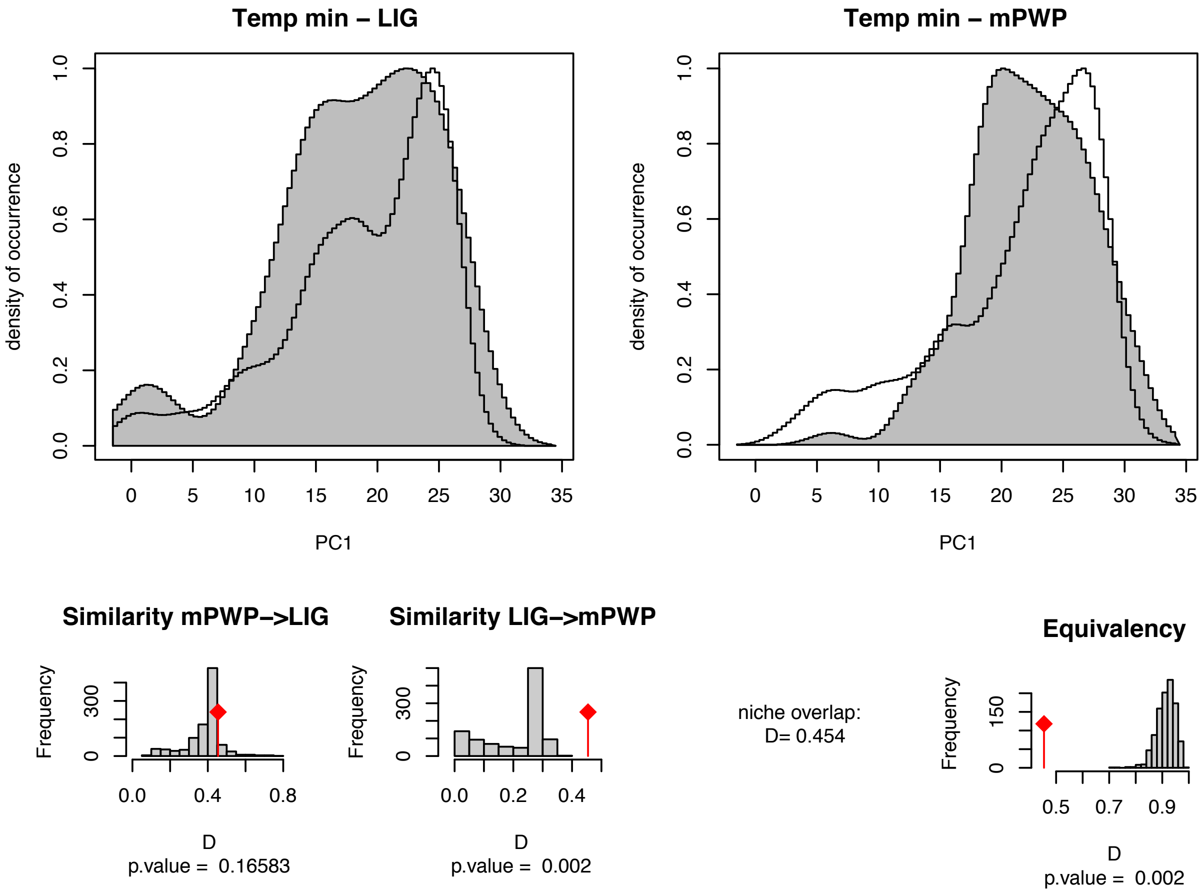
Crassostrea virginica: **LIG—PI**



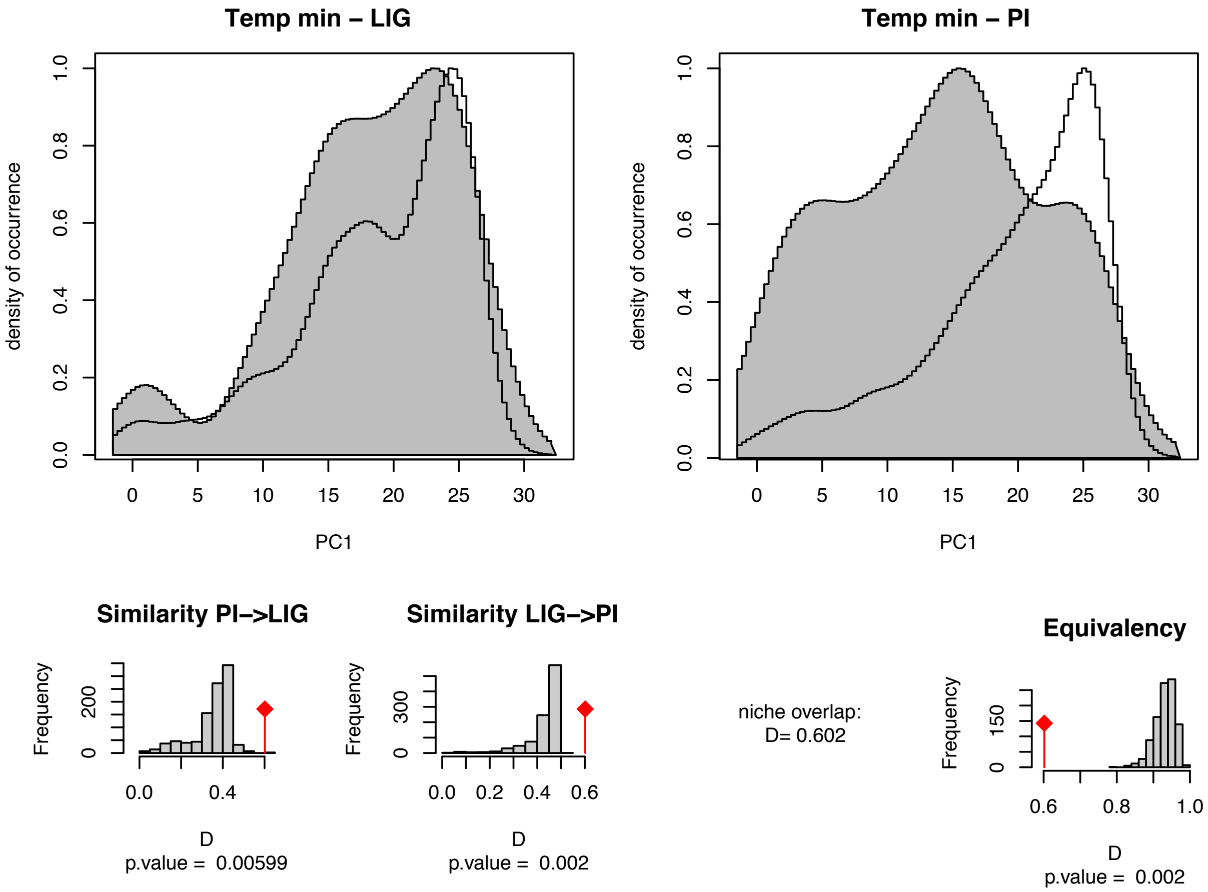
Crassostrea virginica: **PI—mPWP**



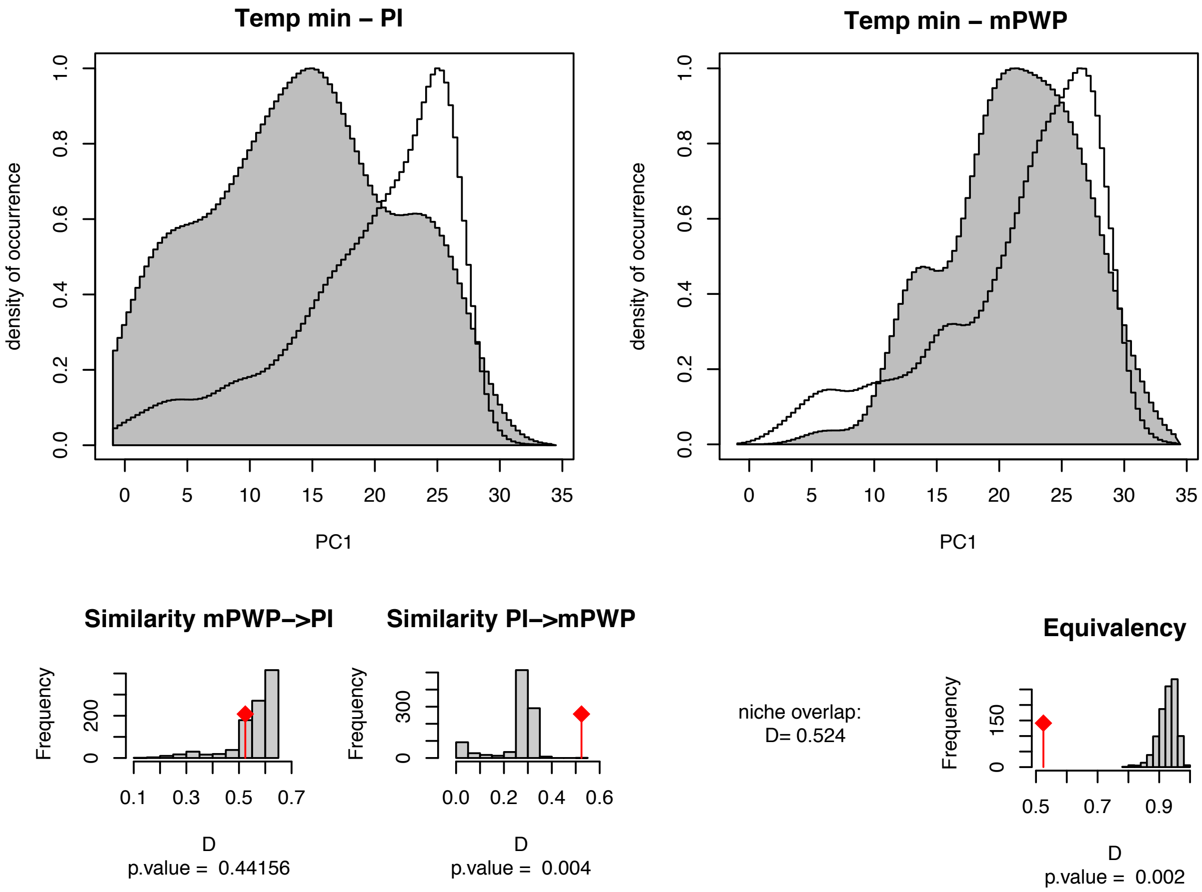
Crepidula fornicata: **LIG—mPWP**



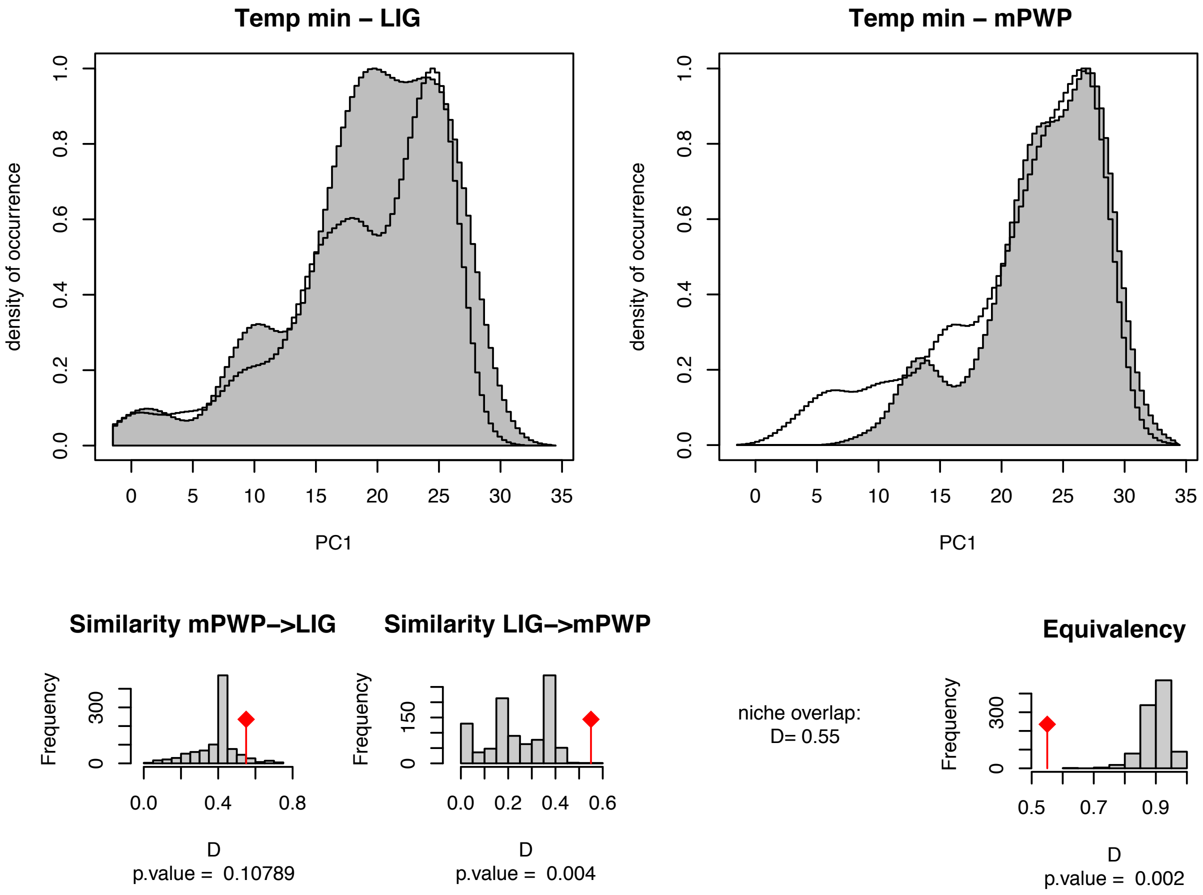
Crepidula fornicata: **LIG—PI**



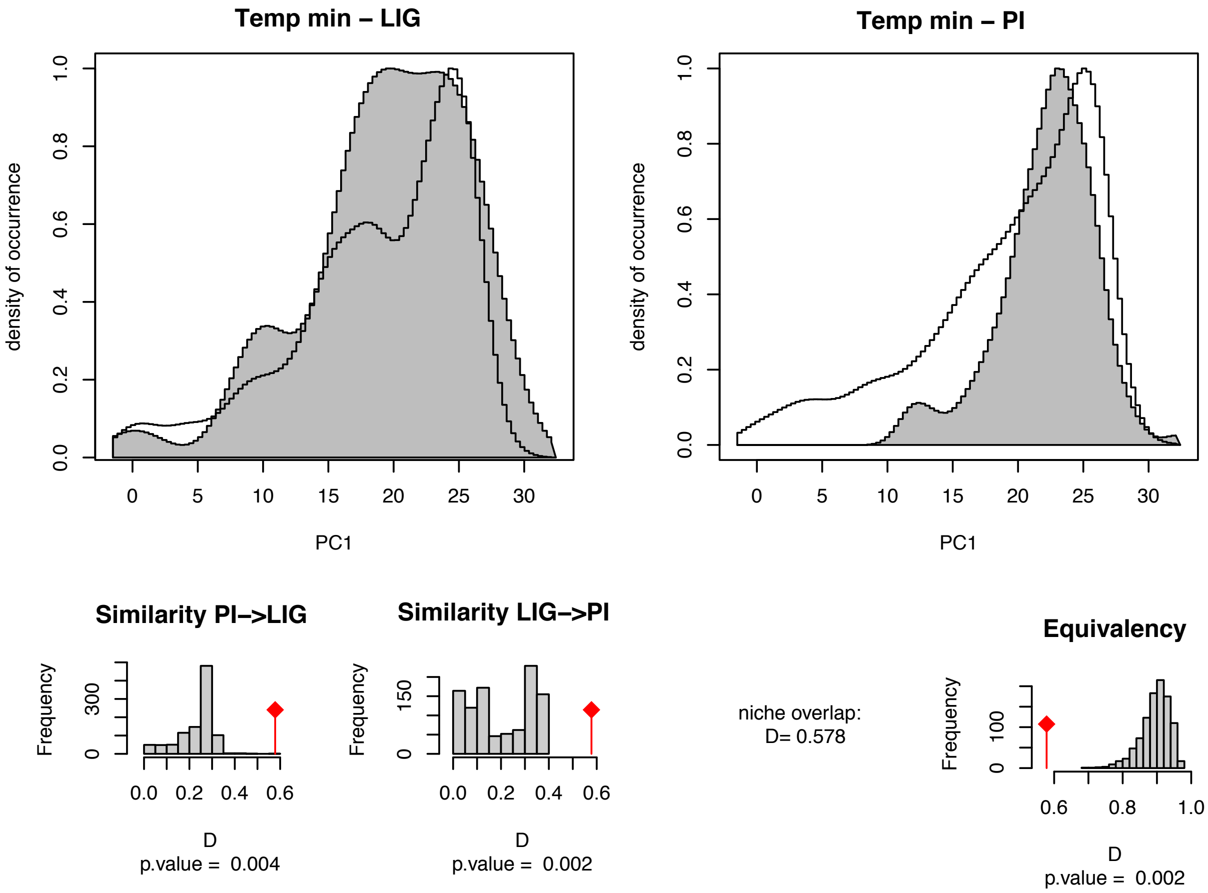
Crepidula fornicata: **PI—mPWP**



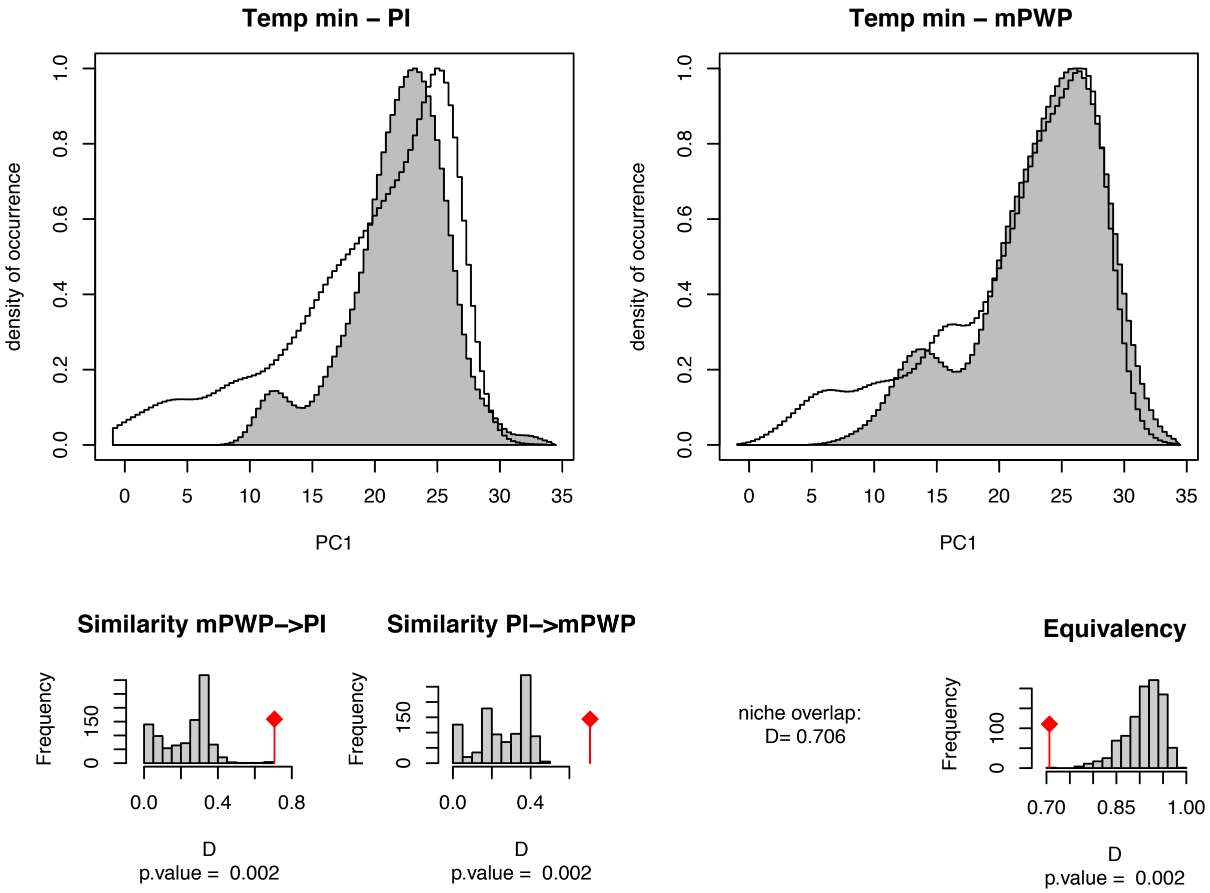
Dinocardium robustum: **LIG—mPWP**



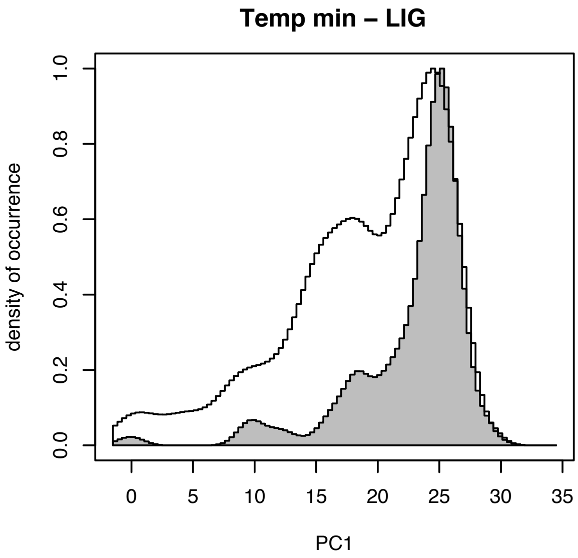
Dinocardium robustum: **LIG—PI**

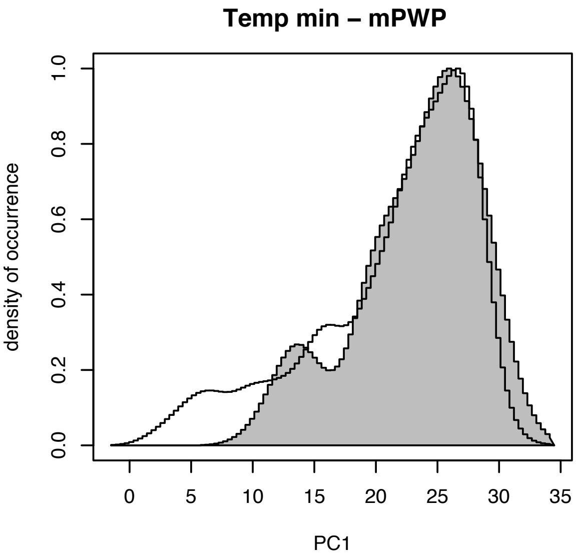


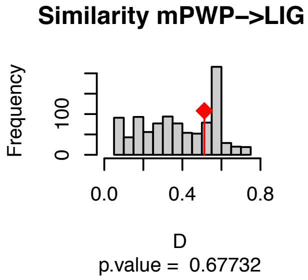
Dinocardium robustum: **PI—mPWP**



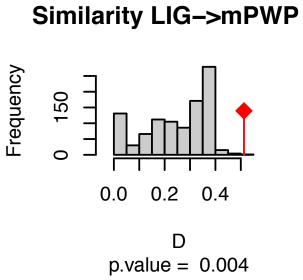
Lucina pensylvanica: **LIG—mPWP**





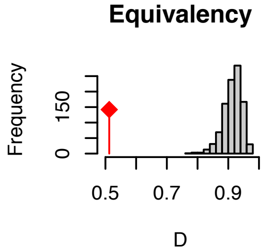


p.value = 0.67732



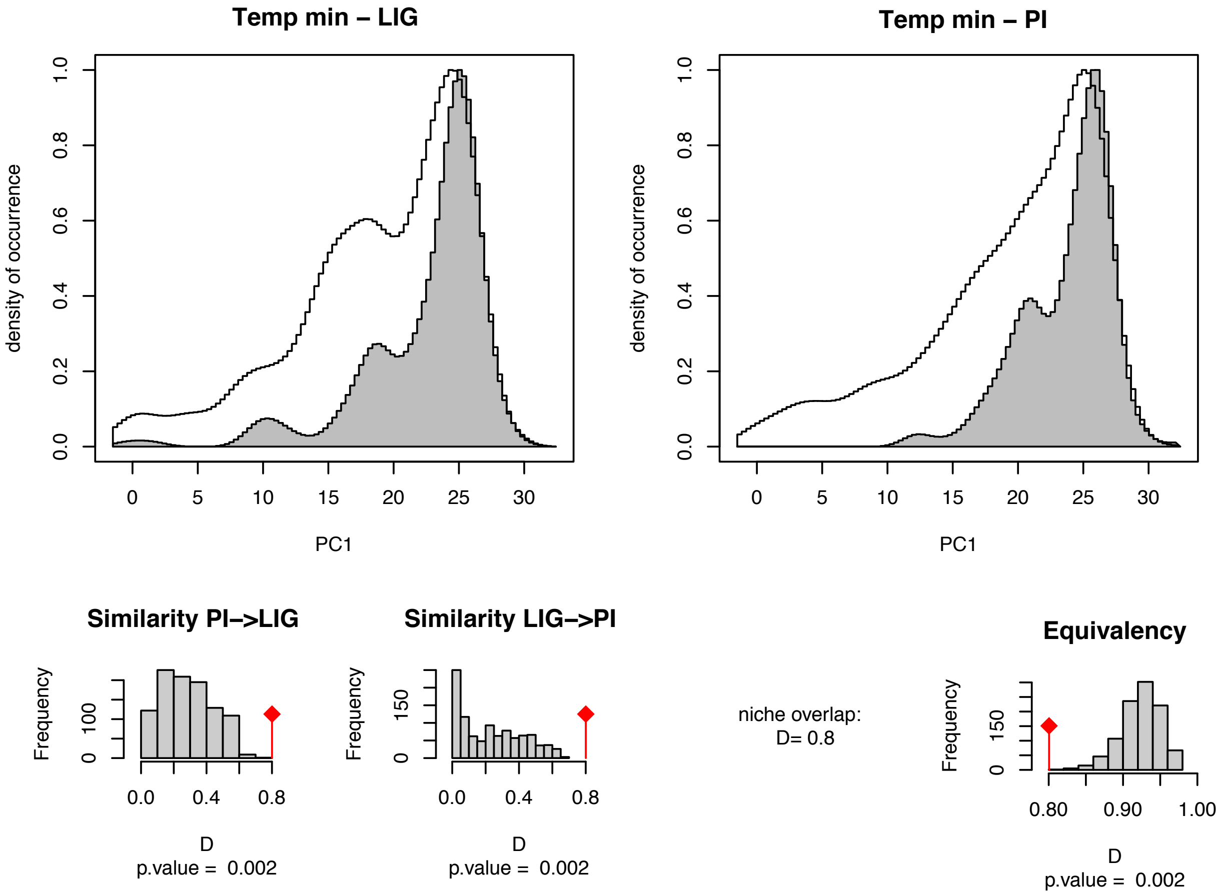
p.value = 0.004

niche overlap:
D= 0.512

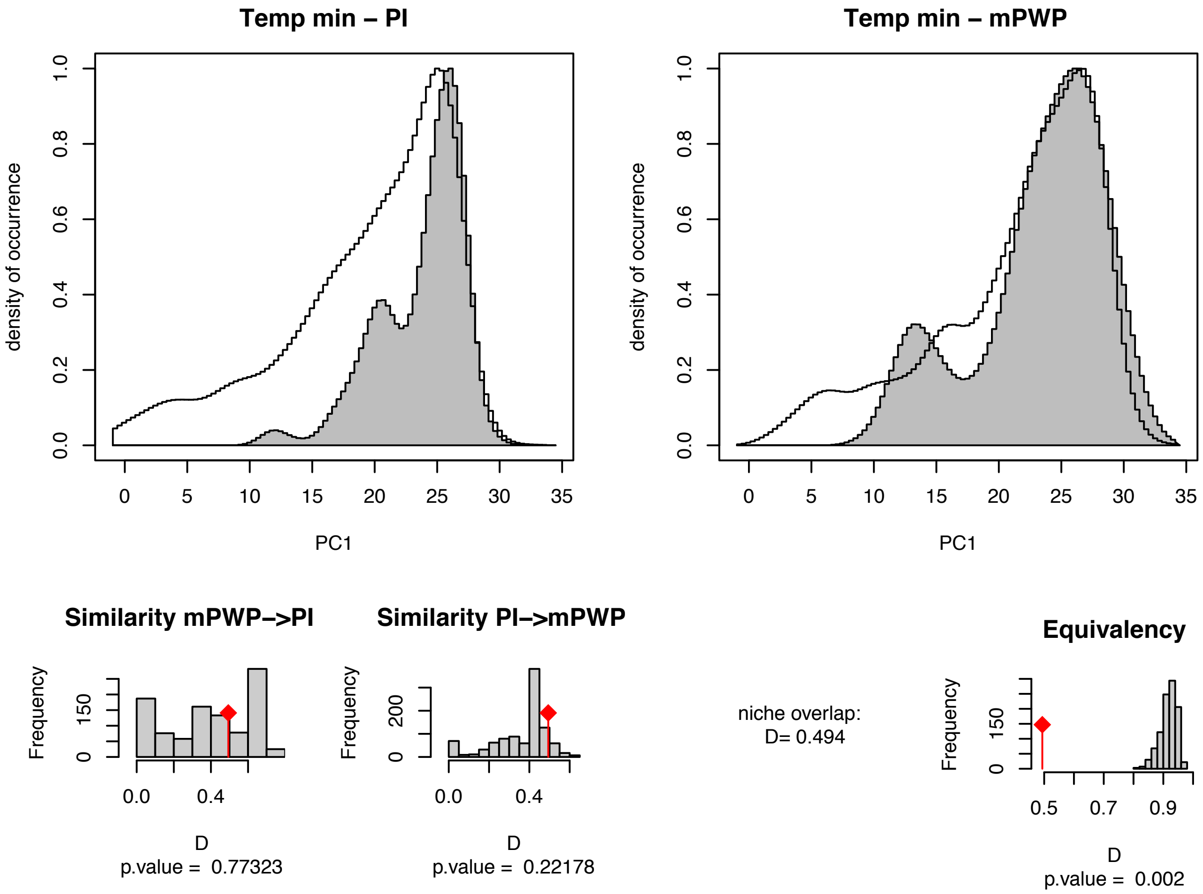


p.value = 0.002

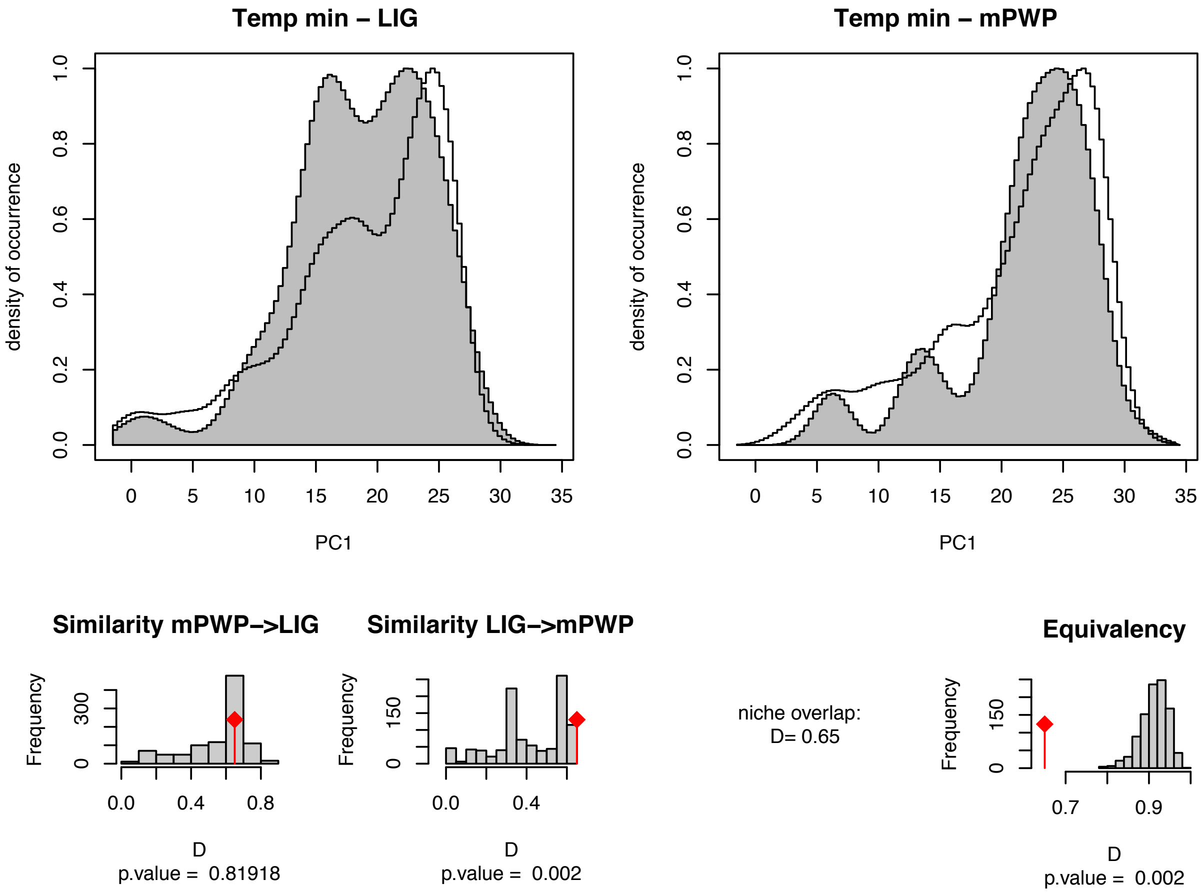
Lucina pensylvanica: **LIG—PI**



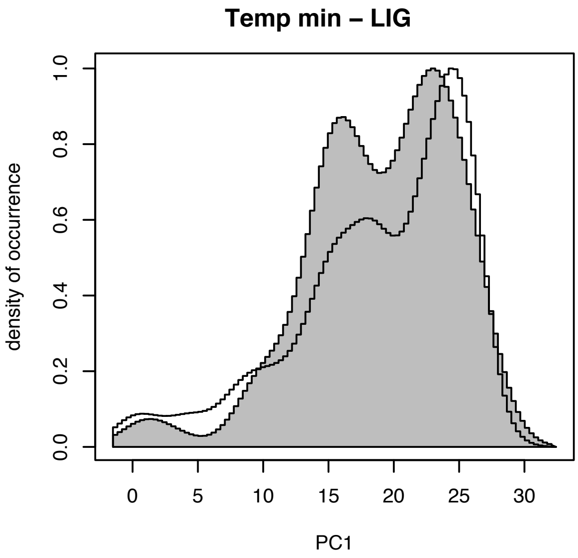
Lucina pensylvanica: **PI—mPWP**

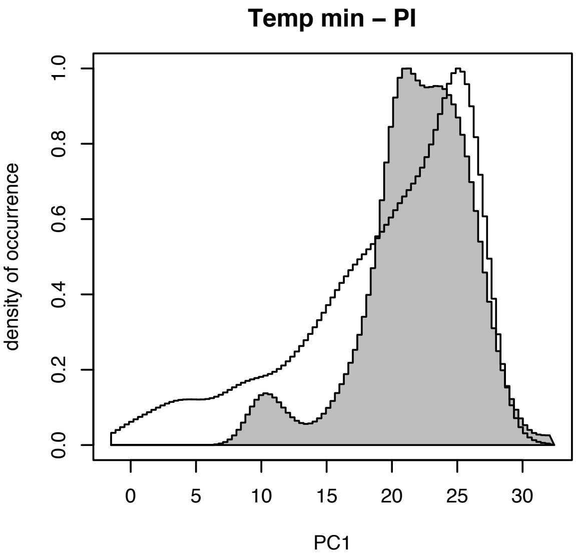


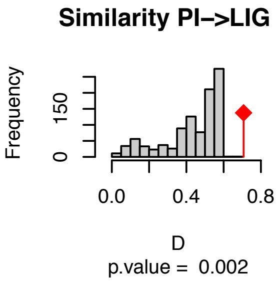
Mercenaria campechiensis: **LIG—mPWP**

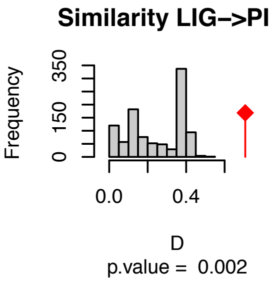


Mercenaria campechiensis: **LIG—PI**

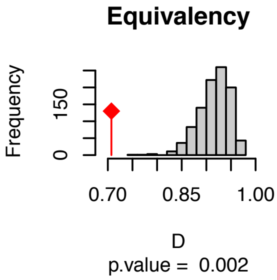




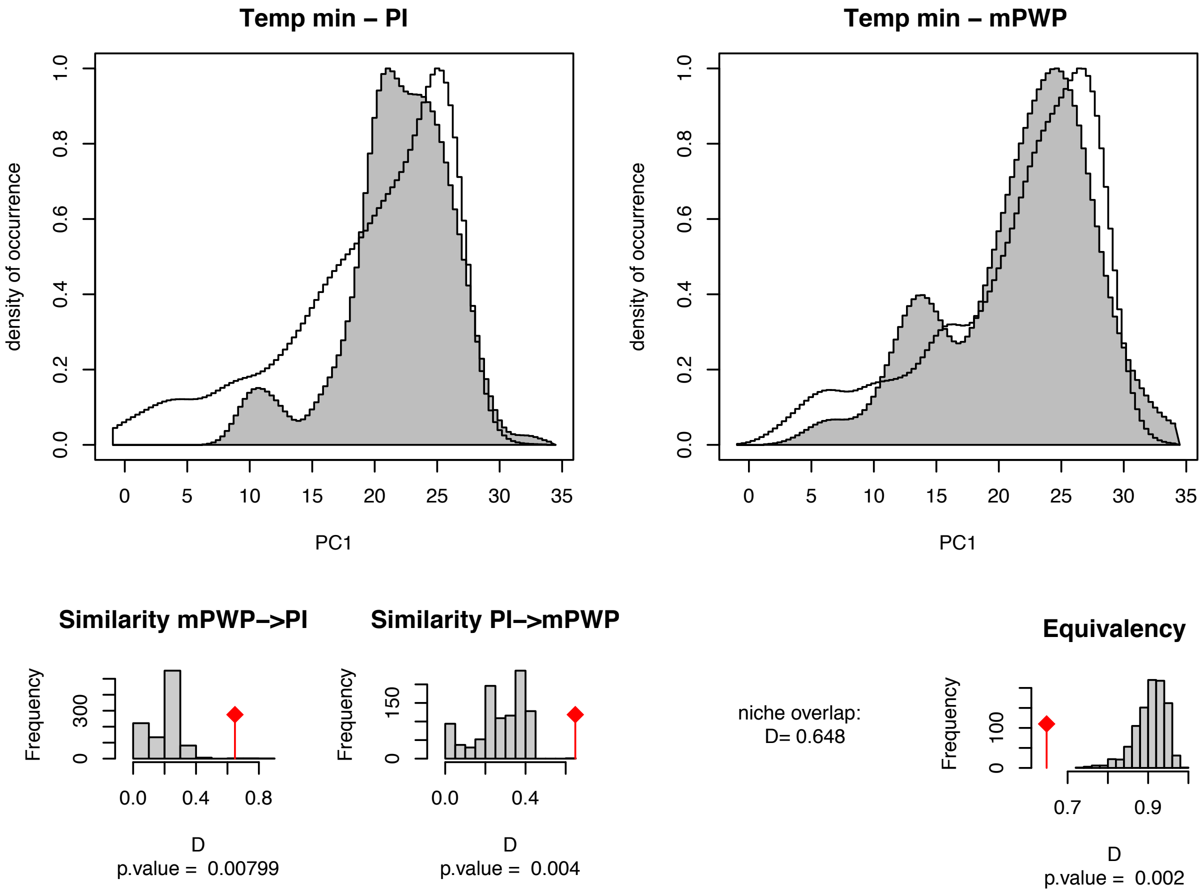




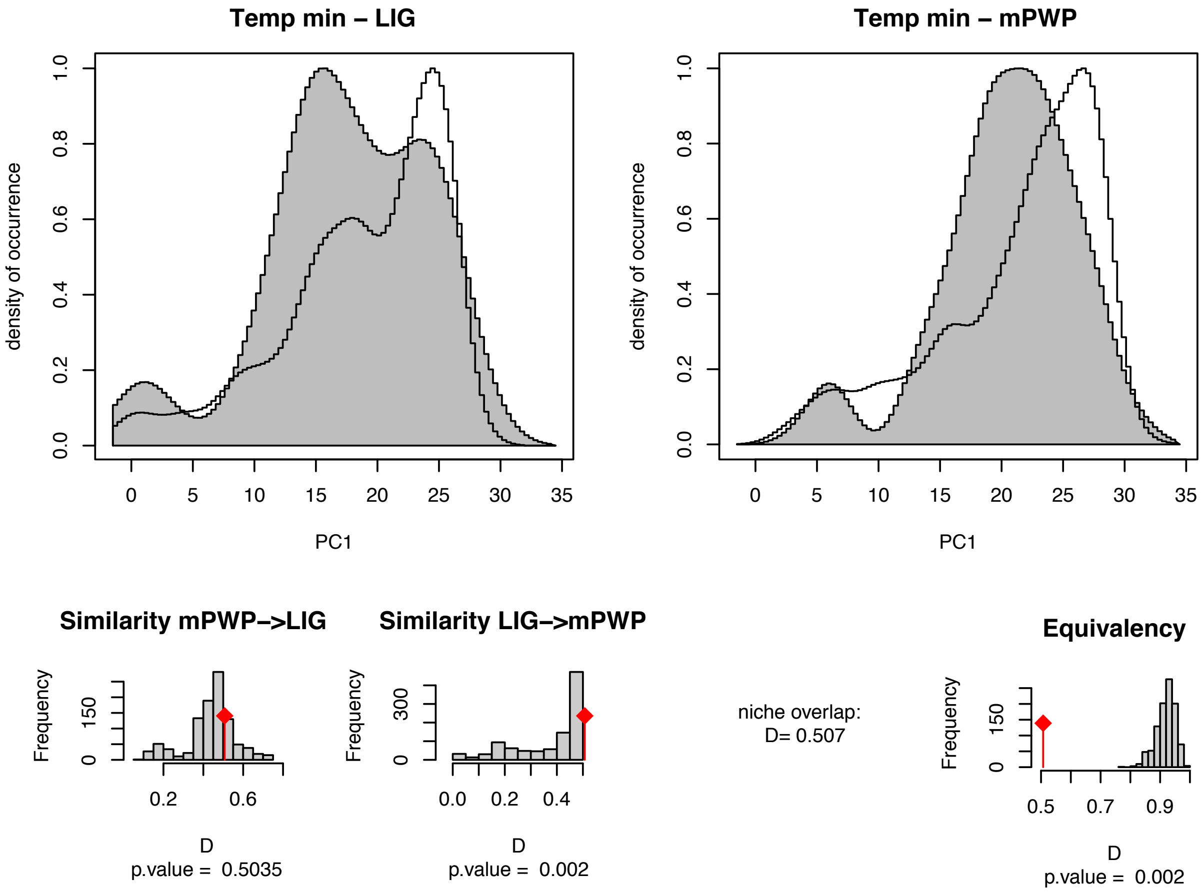
niche overlap:
D= 0.707



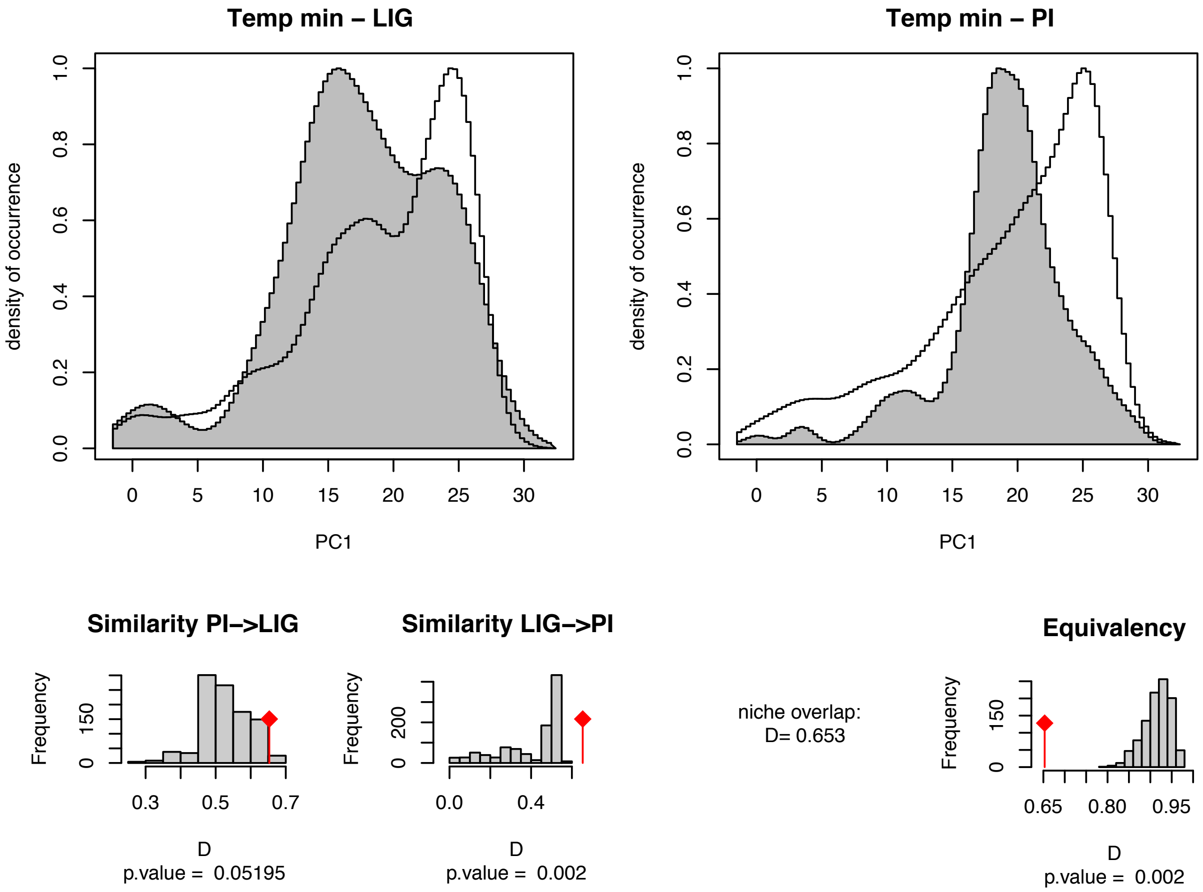
Mercenaria campechiensis: **PI—mPWP**



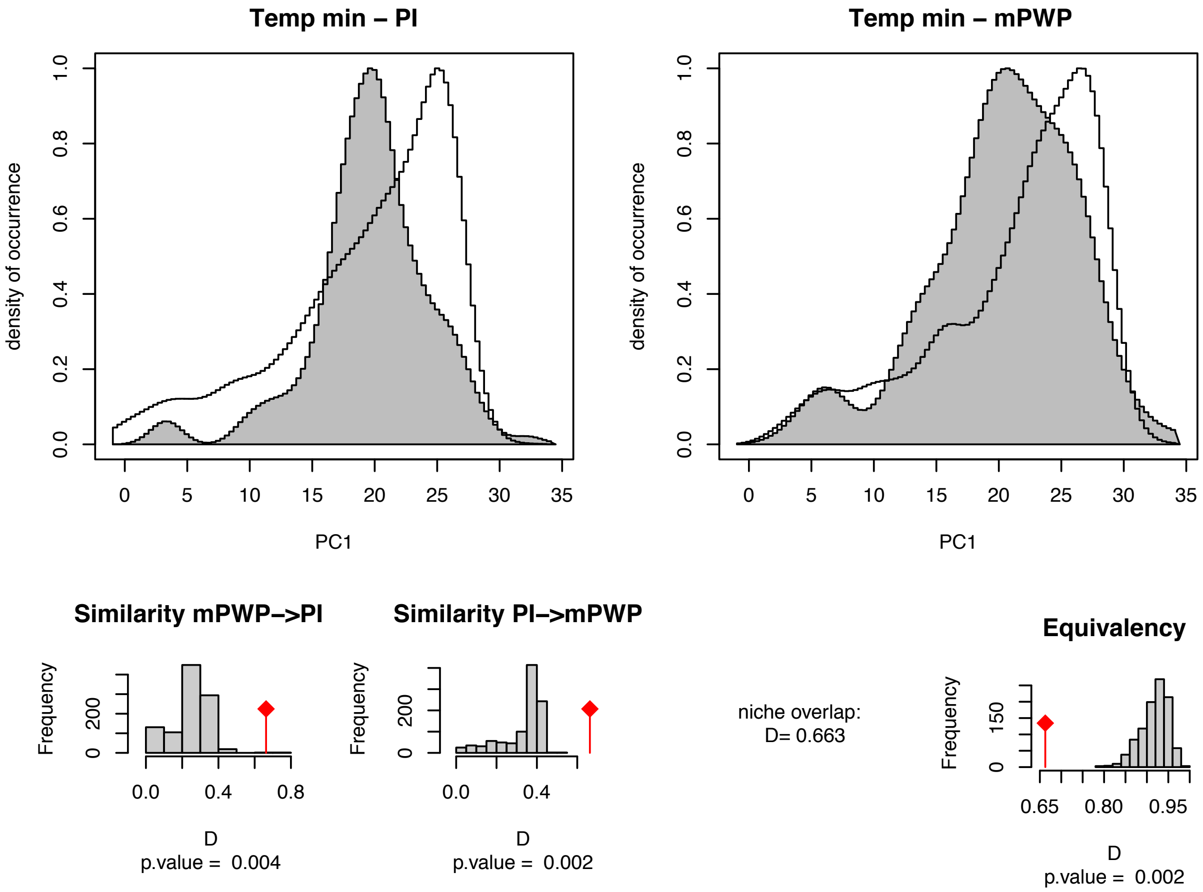
Neverita duplicata: **LIG—mPWP**



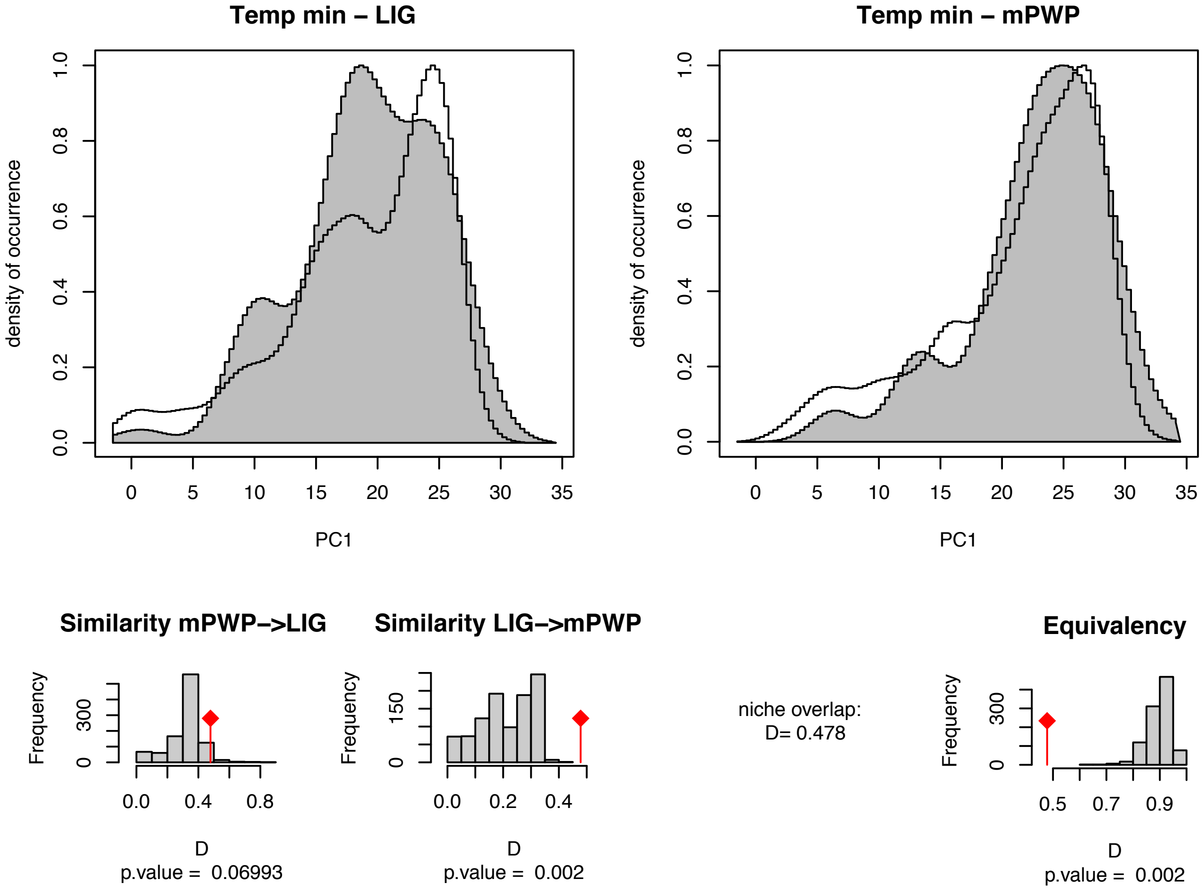
Neverita duplicata: **LIG—PI**



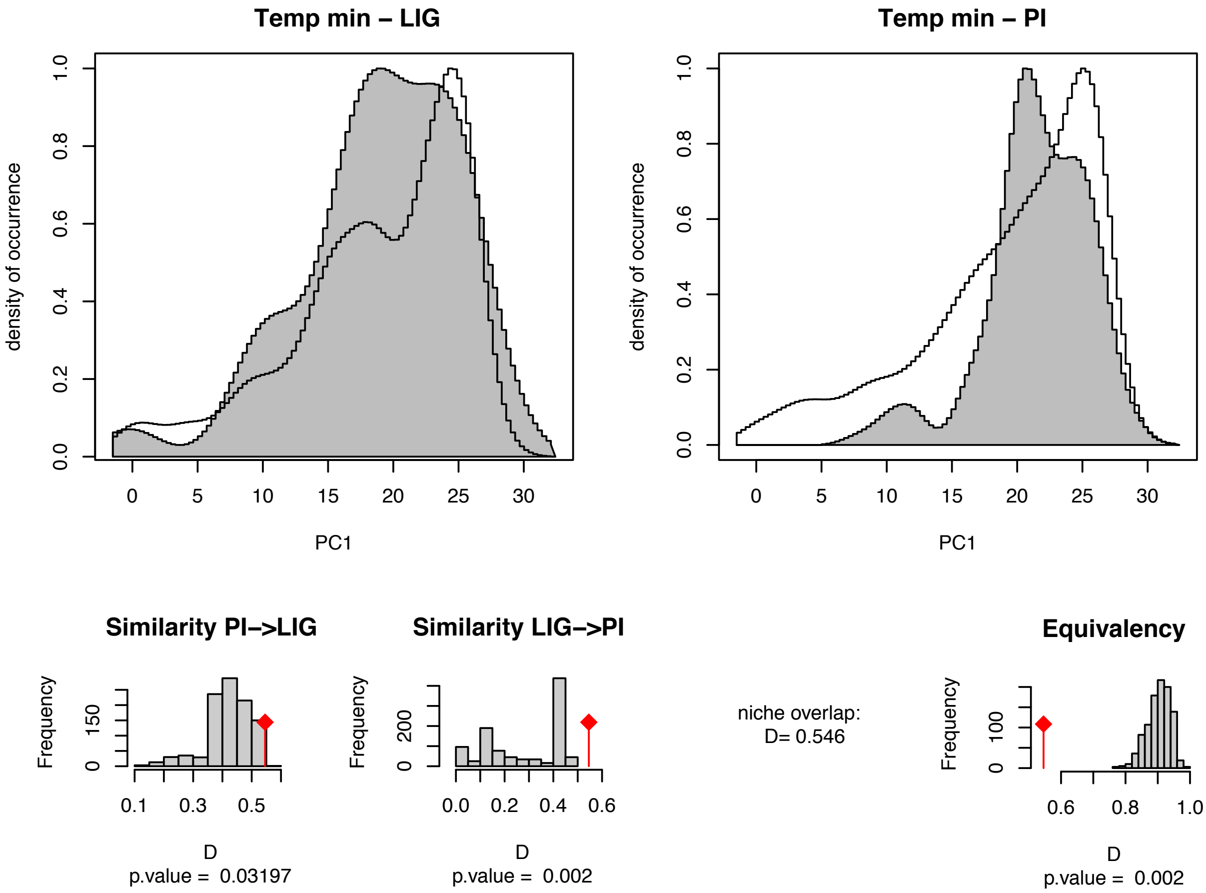
Neverita duplicata: PI—mPWP



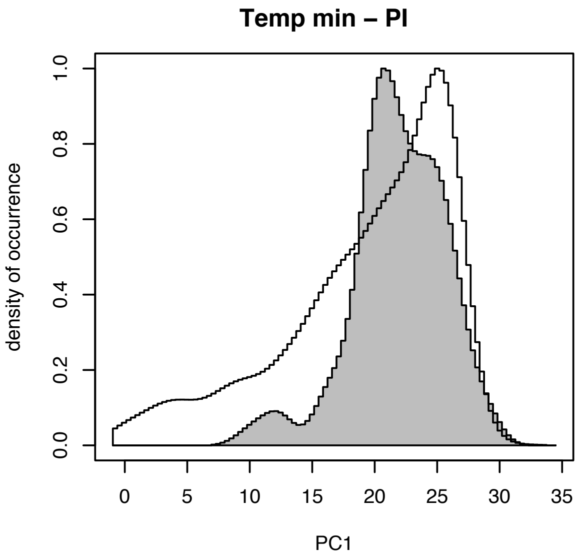
Oliva sayana: **LIG—mPWP**

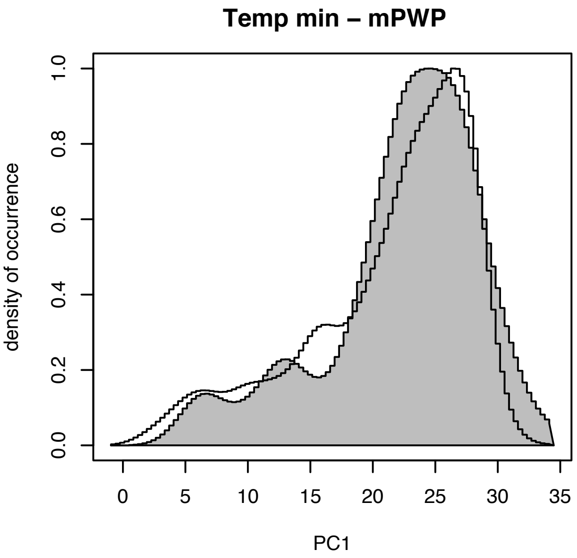


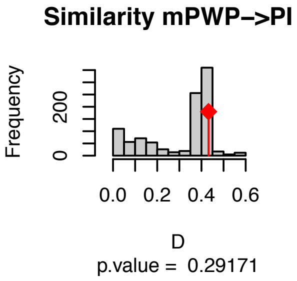
Oliva sayana: **LIG—PI**

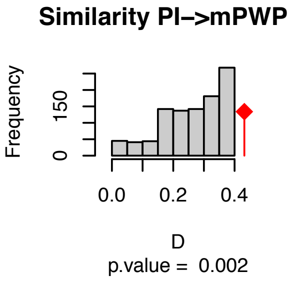


Oliva sayana: **PI—mPWP**

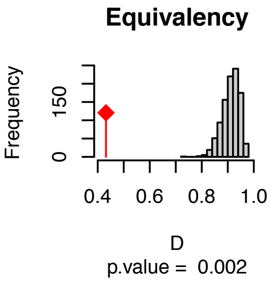




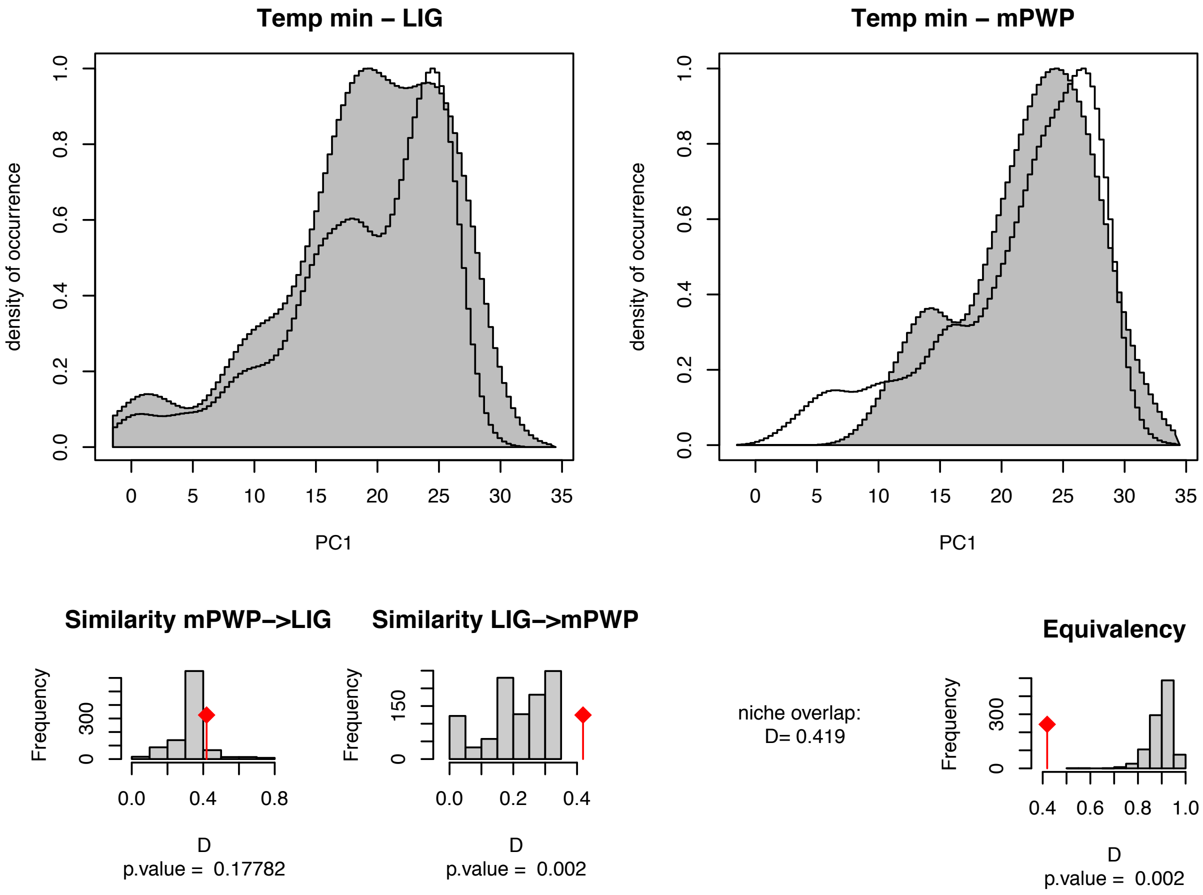




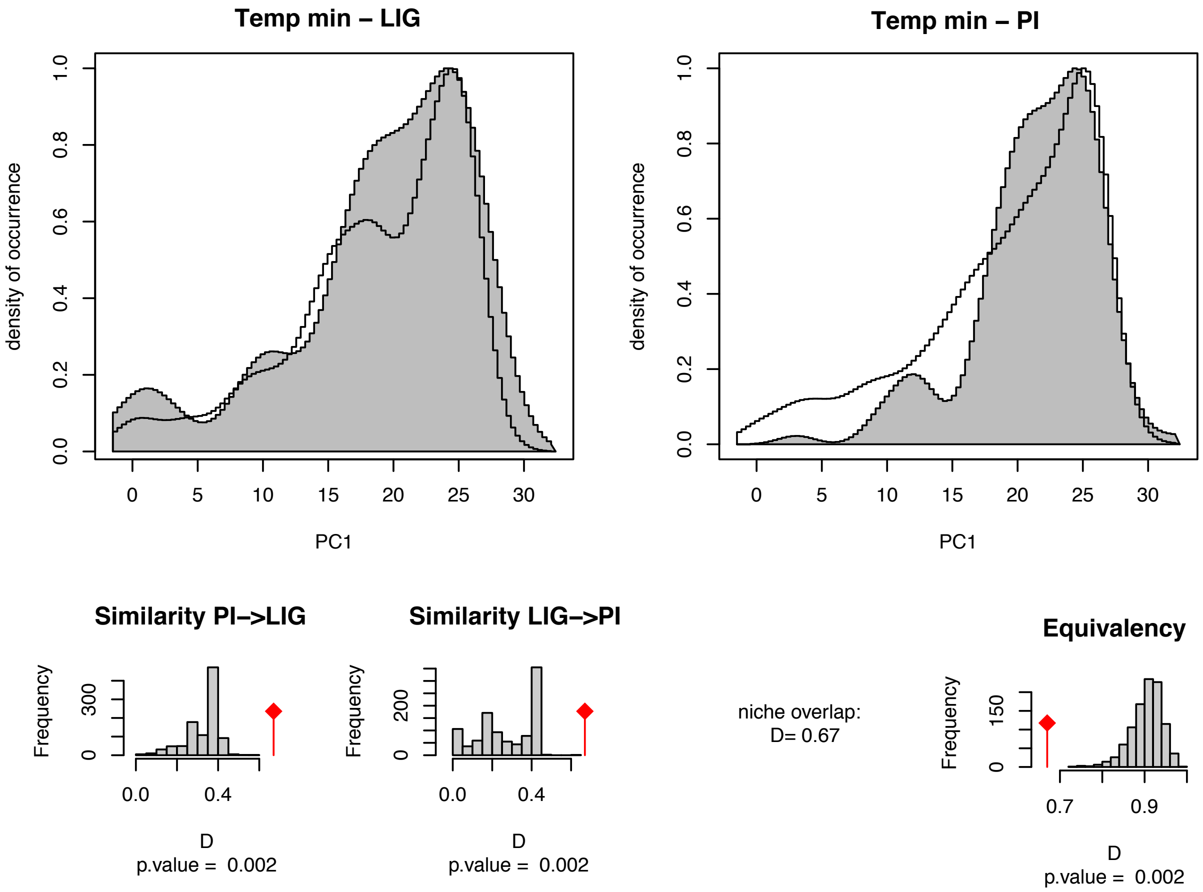
niche overlap:
D= 0.432



Terebra dislocata: **LIG—mPWP**



Terebra dislocata: **LIG—PI**



niche overlap:
D= 0.67

Terebra dislocata: **PI—mPWP**