Extreme rarity of competitive exclusion in modern and fossil marine benthic ecosystems

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ABSTRACT

Competitive interactions have been invoked as major drivers of ecological and evolutionary trends through time, but the strength and frequency of such interactions is notoriously difficult to evaluate. Here we use inferences from species co-occurrence patterns to determine the frequency of the extreme endmember of competition—competitive exclusion—in modern and fossil benthic marine invertebrate assemblages. Within environmentally and temporally well-constrained species pools, we examine the percentage of all species pairs that co-occur less often than expected by chance (segregated pairs) as a maximum measure of competitive exclusion. Segregated pairs are very rare, with most assemblages containing none, and the frequency of segregated pairs shows no trend throughout the Phanerozoic. Contrary to the competition-relatedness hypothesis, we find little evidence that segregated pairs are more common among closely related species except potentially for congeneric pairs in deeper water settings where physical disturbance is relatively low. Although taphonomy, post-mortem transport, and time-averaging could obscure original co-occurrence patterns, analyses suggest that these factors are unlikely to fully explain the low frequency of segregated pairs. Our findings support the hypothesis that predation and disturbance keep marine benthic communities below carrying capacity and thus reduce the potential for competitive interactions to dictate community composition in shallow waters.

INTRODUCTION

Marine ecosystems have become more taxonomically and ecologically diverse throughout the Phanerozoic (Bambach et al., 2007; Alroy et al., 2008), and several lines of evidence suggest that this diversification may have been facilitated or driven by increasingly complex ecological interactions (Wagner et al., 2006; Huntley and Kowalewski, 2007; Nürnberg and Aberhan, 2015). The rich fossil record of drill holes, scars, and other traces in a variety of invertebrates provides some evidence that predation and parasitism have become more common through time (Huntley and Kowalewski, 2007; Klompmaker and Boxshall, 2015), but quantifying evidence of competition has been more difficult. With the exception of overgrowth relationships in encrusting taxa (Taylor, 2016), direct evidence of interspecific competition is extremely rare. Hence, the role of competition in marine ecosystems through time remains poorly understood. Although competition is a cornerstone of evolutionary theory (Darwin, 1859) and has been invoked to explain some major clade replacements (Stanley and Newman, 1980; Sepkoski et al., 2000; Liow et al., 2015), others have argued that competition is not a major evolutionary force in marine ecosystems (Benton, 1996; Stanley, 2008; Myers and Lieberman, 2011).

It is difficult to quantify the strength of competitive interactions among modern marine species and impossible to do so for most fossil species, but it may be possible to recognize competitive exclusion, the extreme endmember of competition in which two species with identical niches cannot locally coexist (Hardin, 1960). Here we employ a recently developed analytical approach (Lyons et al., 2016, and references therein) to evaluate the frequency of competitive exclusion in fossil and modern benthic marine invertebrate assemblages. We examine co-occurrence patterns within local species pools to determine whether species pairs co-occur less often than expected by chance (segregated or negative pairs) (Sfenthourakis et al., 2006). We assess (1) the commonness of competitive exclusion, as measured by the percentage of segregated species pairs of all pairs within assemblages, in modern and fossil marine assemblages through time; (2) whether segregated pairs occur more often among closely related taxa, as predicted by the competition-relatedness hypothesis (Cahill et al., 2008) originally proposed by Charles Darwin (Darwin, 1859); and (3) whether the frequency and taxonomic distribution of segregated pairs is affected by water depth, a rough proxy for disturbance frequency and strength.

METHODS

Data on fossil benthic marine invertebrate assemblages were downloaded from the Paleobiology Database (https://paleobiodb.org/; Appendices DR1–DR2 and Fig. DR1A in the GSA Data Repository[1]). We assembled databases of modern benthic assemblages from two sources: EurOBIS (European Node of the international Ocean Biogeographic Information System, https://www.eurobis.eu; Appendix DR3, Europe) and EMAPS (https://iobis.org; Appendix DR4, North America) (Fig. DR1B). A probabilistic model (R package cooccur 1.3; Griffith et al., 2016) was used to identify truly random, aggregated, and segregated species pairs from datasets of the presence/absence of species within samples. We defined species pools as datasets in which (1) all collections come from within 0.2° longitude × 0.2° latitude, to maximize sample size while minimizing turnover along geographic, bathymetric, and substrate gradients; (2) at least ten species and ten samples are included to ensure an adequate number of pairs per species pool (Lavender et al., 2016); and (3) all samples in a species pool have the same estimated age to minimize temporal turnover. We performed additional analyses to test the sensitivity of our results (Appendix DR1). Ideally the competition-relatedness hypothesis should be evaluated in the context of a known phylogenetic history (Violle et al., 2011), but phylogenies are unavailable for the vast majority of fossil and modern taxa. As a proxy for phylogenetic distance, we evaluated the percentage of segregated pairs of all pairs at six levels of taxonomic distance: (1) congenerics; (2) species in the same family but different genera; (3) same order but different families; (4) same class but different orders; (5) same phylum but different classes; and (6) species pairs from different phyla. Furthermore, we assessed the degree of segregation per water depth interval per taxonomic distance for modern data. This approach detects competitive exclusion among congeners for a classic example of competition, the Galapagos finches (Fig. DR2).

RESULTS

Among the 301 Paleobiology Database datasets that met our criteria, the median percentage of segregated species pairs among all pairs in a species pool is nearly always 0% for all taxonomic distances (Fig. 1A; Figs. DR3–DR6). Similar results are seen when the datasets are grouped by era, suggesting that there is no trend throughout the Phanerozoic (Fig. DR7). This median percentage is also 0% for all taxonomic distances for the 307 modern datasets (Fig. 1B) and similar results hold for nearly all subsets and groupings of these data (Figs. DR8–DR12). Results are also consistent when limiting analyses to shelly mollusks, a group that is very common in modern and fossil databases (Table DR1; Figs. 1C and 1D). Modern datasets from 40 m to 60 m deep within the same substrate and energy regime show elevated levels of segregation among congenerics, consistent with the hypothesis that competitive interactions are more apparent in lower-disturbance settings (Fig. 2; Figs. DR10–DR12). However, the median percentage of segregated pairs across all taxonomic distances is not statistically different from that of the 0–20 m depth grouping (Wilcoxon signed-rank test, W = 350, p = 0.55).

In the modern datasets, the rare segregated congeneric species pairs occur primarily among polychaete annelids, amphipod arthropods, and mollusks (Table DR2, Appendix DR5). Strong competition among congeneric and confamilial polychaetes has been documented (Woodin and Jackson, 1979; Wilson, 1991), and has been hypothesized among species of gammaridean amphipods (Van Riel et al., 2007), which make up most of the segregated amphipod pairs. Deep-water segregated congeneric pairs include annelids, amphipods, and ophiuroids (Appendix DR6). For the fossil data, three segregated congeneric and confamilial pairs are recorded (Table DR2, Appendix DR5).

DISCUSSION

A number of processes may distort the apparent frequency of segregated species pairs in the fossil record. These include time-averaging (Kowalewski et al., 1998; Tomašových and Kidwell, 2009), post-mortem transport (Olszewski and West, 2007), and differences in preservation potential among members of the species pool (Parsons-Hubbard et al., 2008; Klompmaker et al., 2017) (Table DR1). Time-averaging and post-mortem transport could reduce the frequency of segregated pairs by homogenizing spatiotemporal structure and obscuring transient or spatially limited cases of exclusion. On the other hand, grouping collections into species pools based on relatively coarse temporal and environmental units could increase the apparent frequency of segregated pairs through the inclusion of species that never coexisted in time or in the same microhabitat. Lastly, the poor preservation potential of groups such as polychaetes and amphipods that account for a large proportion of segregated pairs in modern datasets could reduce the frequency of segregated pairs in fossil datasets. However, analysis of fossil data at the finest stratigraphic scale possible (individual beds) yields identical results (Fig. DR5), as does analysis of Cambrian Lagerstätten that include taxa with a low preservation potential and are less time-averaged than most shelly fossil assemblages (Fig. DR6). Furthermore, if time-averaging obscures our results, we might expect to see (1) a decrease in the percentage of segregated pairs through time as the depth and intensity of bioturbation has increased (Thayer, 1979), and (2) higher percentages of aggregated pairs in the fossil record relative to today. However, the percentage of segregated pairs is consistently low throughout the Phanerozoic (Fig. DR7) and aggregated pairs are no more common in fossil datasets than in modern datasets (Fig. DR13).

The extreme rarity of segregated species pairs in modern and fossil datasets does not rule out the possibility of some strong competitive
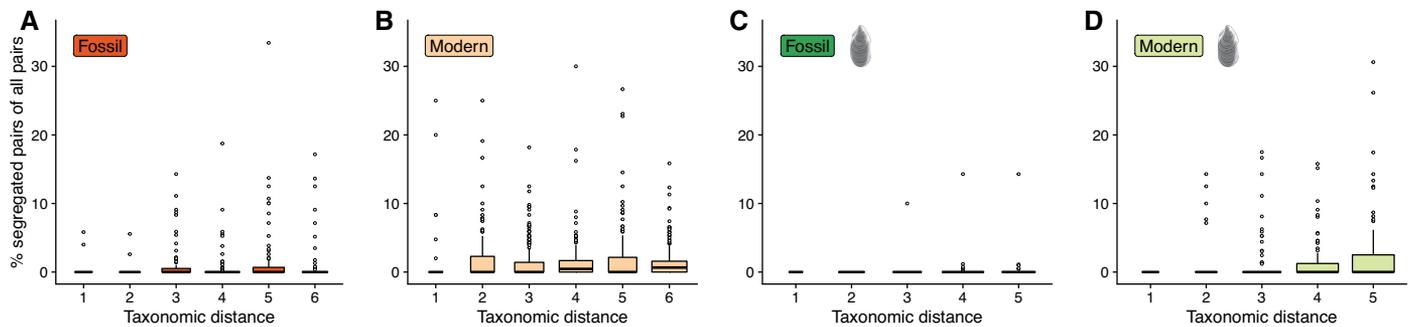

Figure 1. Boxplots of the percentage of segregated species pairs of all pairs versus taxonomic distance. Boxplots show a box bounded by the 25th and 75th percentiles with the median within, whiskers for the 1st and 4th quartiles, and outliers as dots; width proportional to sample size within each plot. A: All fossil data, sample sizes per taxonomic distance: 27–104. B: All modern data, sample sizes: 47–287. C: Fossil Mollusca, sample sizes: 4–36. C: Modern Mollusca, sample sizes: 15–92. Minimum number of pairs per data point (= species pool) is 10 for A and B and 5 for C and D to increase sample size per taxonomic distance.
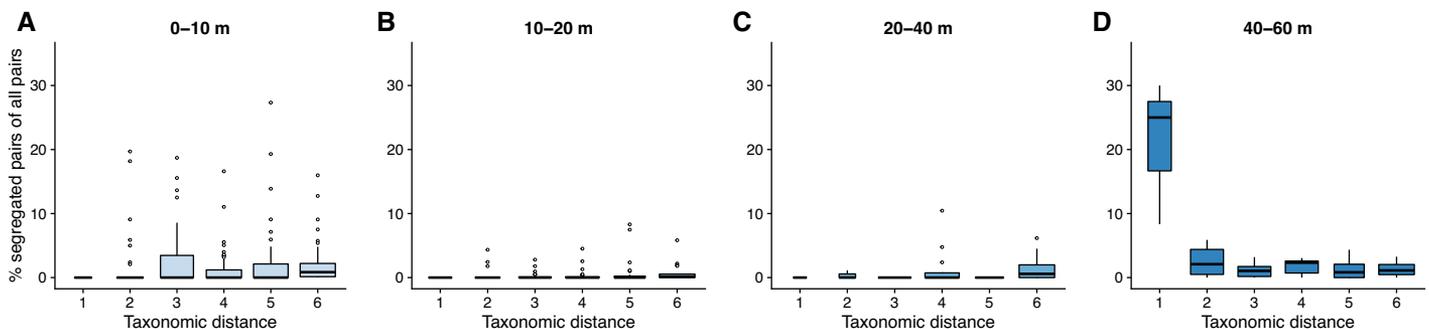

Figure 2. Boxplots of the percentage of segregated species pairs of all pairs versus taxonomic distance for depth intervals with sufficient data from the EurOBIS database (www.eurobis.eu). A: sample size: 14–57. B: sample size: 13–30. C: sample size: 2–14. D: sample size: 3–7.

interactions; some segregation between taxa might also be attributed to one species settling first and subsequently consuming larvae of other species, even those that are competitively superior (Sale's lottery hypothesis; Sale, 1977). Ecological character displacement, in which one or more morphological characters such as body size or shape diverge so that closely related species do not occupy identical niches (Grant and Grant, 2006), provides another potential mechanism for closely related species to coexist. However, character displacement appears rare: most convincing examples occur in non-marine taxa today (Stuart and Losos, 2013) and only some examples have been claimed for the marine fossil record (Hermoyian et al., 2002; Tyler and Leighton, 2011). Coexistence of three or more competing species is possible through the presence of competitive networks rather than hierarchies (Laird and Schamp, 2006), although most marine invertebrates appear to be ecological opportunists, not specialists (Stanley, 2007). Such competitive networks may be present in modern coral reefs (Buss and Jackson, 1979), but reefs constitute only ~10% of the analyzed datasets. Consequently, the most parsimonious interpretation is that competitive interactions leading to exclusion are rare and have been through time. This finding supports the view that competition is not a dominant process in structuring shallow soft-substrate benthic marine ecosystems (Johnson, 1964; Stanley, 2008).

Predation and disturbances provide possible explanations for the extreme rarity of competitive exclusion in marine benthic ecosystems because they may keep local communities from reaching their theoretical carrying capacities and becoming ecologically saturated, thereby reducing the intensity of interspecific competition. The shallow soft-substrate benthic habitats analyzed herein experience generally higher predation intensities than rocky intertidal zones (Stanley, 2008), but predation reduces the strength of competitive interactions even in these relatively harsh, low-predator communities (Paine, 1974). Predation has likely had a pervasive impact on benthic ecosystems throughout the Phanerozoic (Signor and Brett, 1984; Vermeij, 1987; Baum and Worm, 2009), and both the taxonomic proportion of predators (Bambach, 2002) and the frequency of predatory traces (drill holes and repair scars) (Huntley and Kowalewski, 2007) have increased through time. However, the fact that segregated pairs are rare in both Paleozoic and modern datasets (Fig. 1; Fig. DR7) implies either that predation levels were already sufficiently high to keep most populations below carrying capacity in the Paleozoic or that predation is not the primary explanation for the rarity of competitive exclusion. Disturbance by storms causes damage to shallow marine benthic communities by inflicting mass mortality, especially to epifaunal taxa (Posey et al., 1996) that are abundant in our datasets. Recovery of benthic

communities from storms may take hundreds of days (Dernie et al., 2003). As much as 10% of the ocean floor may be impacted by recurrent physical disturbances (Harris, 2014), and the vast majority of our modern and fossil datasets come from these shallow, disturbance-prone settings. How this regime has fluctuated throughout the Phanerozoic depends on the extent of continental shelves and epeiric seas and on storm activity (Ito et al., 2001). Disturbance due to bioturbation (Thayer, 1979) may also reduce competition.

Both disturbances and durophagous predation are thought to decrease with depth (Harper and Peck, 2016). Thus, competitive exclusion between organisms may be more readily visible at greater depth if disturbance and predation are important factors in limiting exclusion at shallow depths. Increased levels of segregation are indeed seen for congenerics (Fig. 2; Figs. DR9–DR11), although this result is tentative because these pairs originate from one region (the English Channel) and the number of datasets available for deep waters is limited. Nevertheless, this result is consistent with the competition-relatedness hypothesis and suggest that disturbance and predation may dampen competitive exclusion.

Long-term increases in global taxon richness and abundance (Kidwell and Brenchley, 1994; Stanley, 2007; Alroy et al., 2008; Harmon and Harrison, 2015; Holland and Sclafani, 2015) suggest that either global carrying capacity has risen throughout the Phanerozoic in response to factors such as key innovations and ecosystem engineers (Erwin, 2008; Marshall and Quental, 2016; Allmon and Martin, 2014) or that marine invertebrates have been below their capacities. A lack of saturation could also apply to local and/or regional capacities because invasions usually lead to an increase in diversity (Patzkowsky and Holland, 2007; Harmon and Harrison, 2015; Stigall et al., 2017). The rarity of competitive exclusion documented herein is consistent with the hypothesis that most shallow-water benthic local communities have been below their theoretical carrying capacities throughout the Phanerozoic.

CONCLUSIONS

Our analyses serve as a first step in quantifying the intensity of competition through time. We find that competitive exclusion, as expressed by the percentage of segregated species pairs of all pairs, is rare in ancient and modern marine benthic ecosystems based on >600 datasets. Moreover, segregated species pairs do not occur more frequently for pairs that are more closely related, lending little support for the competition-relatedness hypothesis except perhaps for congenerics in less disturbed settings. The low frequency of competitive exclusion herein is consistent with the hypothesis that most marine benthic communities have been below their theoretical carrying capacities throughout the Phanerozoic, which may be explained by predation and disturbances.

REFERENCES CITED
Allmon, W.D., and Martin, R.E., 2014, Seafood through time revisited: The Phanerozoic increase in marine trophic resources and its macroevolutionary consequences: Paleobiology, v. 40, p. 256–287, https://doi.org/10.1666/13065.
Alroy, J., et al., 2008, Phanerozoic trends in the global diversity of marine invertebrates: Science, v. 321, p. 97–100, https://doi.org/10.1126/science.1156963.
Bambach, R.K., 2002, Supporting predators: Changes in the global ecosystem inferred from changes in predator diversity: Paleontological Society Papers, v. 8, p. 319–352, 10.1017/S1089332600001145.
Bambach, R.K., Bush, A.M., and Erwin, D.H., 2007, Autecology and the filling of ecospace: Key metazoan radiations: Palaeontology, v. 50, p. 1–22, https://doi.org/10.1111/j.1475-4983.2006.00611.x.
Baum, J.K., and Worm, B., 2009, Cascading top-down effects of changing oceanic predator abundances: Journal of Animal Ecology, v. 78, p. 699–714, https://doi.org/10.1111/j.1365-2656.2009.01531.x.
Benton, M.J., 1996, On the non-prevalence of competitive replacement in the evolution of tetrapods, in Jablonski, D., et al., eds., Evolutionary Paleobiology: Chicago, University of Chicago Press, p. 185–210.
Buss, L.W., and Jackson, J.B.C., 1979, Competitive networks: Nontransitive competitive relationships in cryptic coral reef environments: American Naturalist, v. 113, p. 223–234, https://doi.org/10.1086/283381.
Cahill, J.F., Kembel, S.W., Lamb, E.G., and Keddy, P.A., 2008, Does phylogenetic relatedness influence the strength of competition among vascular plants?: Perspectives in Plant Ecology, Evolution and Systematics, v. 10, p. 41–50, https://doi.org/10.1016/j.ppees.2007.10.001.
Darwin, C., 1859, On the Origin of Species: London, John Murray.
Dernie, K.M., Kaiser, M.J., and Warwick, R.M., 2003, Recovery rates of benthic communities following physical disturbance: Journal of Animal Ecology, v. 72, p. 1043–1056, https://doi.org/10.1046/j.1365-2656.2003.00775.x.
Erwin, D., 2008, Macroevolution of ecosystem engineering, niche construction and diversity: Trends in Ecology & Evolution, v. 23, p. 304–310, https://doi.org/10.1016/j.tree.2008.01.013.
Grant, P.R., and Grant, B.R., 2006, Evolution of character displacement in Darwin's finches: Science, v. 313, p. 224–226, https://doi.org/10.1126/science.1128374.
Griffith, D.M., Veech, J.A., and Marsh, C.J., 2016, cooccur: probabilistic species co-occurrence analysis in R: Journal of Statistical Software, v. 69, p. 1–17, https://doi.org/10.18637/jss.v069.c02.
Hardin, G., 1960, The competitive exclusion principle: Science, v. 131, p. 1292–1297, https://doi.org/10.1126/science.131.3409.1292.
Harmon, L.J., and Harrison, S., 2015, Species diversity is dynamic and unbounded at local and continental scales: American Naturalist, v. 185, p. 584–593, https://doi.org/10.1086/680859.

Harper, E.M., and Peck, L.S., 2016, Latitudinal and depth gradients in marine predation pressure: Gradients in marine predation pressure: Global Ecology and Biogeography, v. 25, p. 670–678, https://doi.org/10.1111/geb.12444.

Harris, P.T., 2014, Shelf and deep-sea sedimentary environments and physical benthic disturbance regimes: A review and synthesis: Marine Geology, v. 353, p. 169–184, https://doi.org/10.1016/j.margeo.2014.03.023.

Hermoyian, C.S., Leighton, L.R., and Kaplan, P., 2002, Testing the role of competition in fossil communities using limiting similarity: Geology, v. 30, p. 15–18, https://doi.org/10.1130/0091-7613(2002)030<0015:TTROCI>2.0.CO;2.

Holland, S.M., and Sclafani, J.A., 2015, Phanerozoic diversity and neutral theory: Paleobiology, v. 41, p. 369–376, https://doi.org/10.1017/pab.2015.10.

Huntley, J.W., and Kowalewski, M., 2007, Strong coupling of predation intensity and diversity in the Phanerozoic fossil record: Proceedings of the National Academy of Sciences of the United States of America, v. 104, p. 15006–15010, https://doi.org/10.1073/pnas.0704960104.

Ito, M., Ishigaki, A., Nishikawa, T., and Saito, T., 2001, Temporal variation in the wavelength of hummocky cross-stratification: Implications for storm intensity through Mesozoic and Cenozoic: Geology, v. 29, p. 87, https://doi.org/10.1130/0091-7613(2001)029<0087:TVITWO>2.0.CO;2.

Johnson, R.G., 1964, The community approach to paleoecology, *in* Imbrie, J., and Newell, N., eds., Approaches to Paleoecology: New York, John Wiley & Sons, p. 107–134.

Kidwell, S.M., and Brenchley, P.J., 1994, Patterns in bioclastic accumulation through the Phanerozoic: Changes in input or in destruction?: Geology, v. 22, p. 1139–1143, https://doi.org/10.1130/0091-7613(1994)022<1139:PIBATT>2.3.CO;2.

Klompmaker, A.A., and Boxshall, G.A., 2015, Fossil crustaceans as parasites and hosts: Advances in Parasitology, v. 90, p. 233–289, https://doi.org/10.1016/bs.apar.2015.06.001.

Klompmaker, A.A., Portell, R.W., and Frick, M.G., 2017, Comparative experimental taphonomy of eight marine arthropods indicates distinct differences in preservation potential: Palaeontology, v. 60, p. 773–794, https://doi.org/10.1111/pala.12314.

Kowalewski, M., Goodfriend, G.A., and Flessa, K.W., 1998, High-resolution estimates of temporal mixing within shell beds: The evils and virtues of time-averaging: Paleobiology, v. 24, p. 287–304, https://doi.org/10.1666/0094-8373(1998)024[0287:HEOTMW]2.3.CO;2.

Laird, R.A., and Schamp, B.S., 2006, Competitive intransitivity promotes species coexistence: American Naturalist, v. 168, p. 182–193, https://doi.org/10.1086/506259.

Lavender, T.M., Schamp, B.S., and Lamb, E.G., 2016, The influence of matrix size on statistical properties of co-occurrence and limiting similarity null models: PLoS One, v. 11, e0151146, https://doi.org/10.1371/journal.pone.0151146.

Liow, L.H., Reitan, T., and Harnik, P.G., 2015, Ecological interactions on macroevolutionary time scales: Clams and brachiopods are more than ships that pass in the night: Ecology Letters, v. 18, p. 1030–1039, https://doi.org/10.1111/ele.12485.

Lyons, K.S., et al., 2016, Holocene shifts in the assembly of plant and animal communities implicate human impacts: Nature, v. 529, p. 80–83, https://doi.org/10.1038/nature16447.

Marshall, C.R., and Quental, T.B., 2016, The uncertain role of diversity dependence in species diversification and the need to incorporate time-varying carrying capacities: Philosophical Transactions of the Royal Society of London: Series B, Biological Sciences, v. 371, 20150217, https://doi.org/10.1098/rstb.2015.0217.

Myers, C.E., and Lieberman, B.S., 2011, Sharks that pass in the night: Using Geographical Information Systems to investigate competition in the Cretaceous Western Interior Seaway: Proceedings of the Royal Society: B, Biological Sciences, v. 278, p. 681–689, https://doi.org/10.1098/rspb.2010.1617.

Nürnberg, S., and Aberhan, M., 2015, Interdependence of specialization and biodiversity in Phanerozoic marine invertebrates: Nature Communications, v. 6, 6602, https://doi.org/10.1038/ncomms7602.

Olszewski, T.D., and West, R.R., 2007, Influence of transportation and time-averaging in fossil assemblages from the Pennsylvanian of Oklahoma: Lethaia, v. 30, p. 315–329, https://doi.org/10.1111/j.1502-3931.1997.tb00475.x.

Paine, R.T., 1974, Intertidal community structure: Oecologia, v. 15, p. 93–120, https://doi.org/10.1007/BF00345739.

Parsons-Hubbard, K.M., Powell, E.N., Raymond, A., Walker, S.E., Brett, C., Ashton-Alcox, K., Shepard, R.N., Krause, R., and Deline, B., 2008, The taphonomic signature of a brine seep and the potential for Burgess Shale style preservation: Journal of Shellfish Research, v. 27, p. 227–239, https://doi.org/10.2983/0730-8000(2008)27[227:TTSOAB]2.0.CO;2.

Patzkowsky, M.E., and Holland, S.M., 2007, Diversity partitioning of a Late Ordovician marine biotic invasion: Controls on diversity in regional ecosystems: Paleobiology, v. 33, p. 295–309, https://doi.org/10.1666/06078.1.

Posey, M., Lindberg, W., Alphin, T., and Vose, F., 1996, Influence of storm disturbance on an offshore benthic community: Bulletin of Marine Science, v. 59, p. 523–529.

Sale, P.F., 1977, Maintenance of high diversity in coral reef fish communities: American Naturalist, v. 111, p. 337–359, https://doi.org/10.1086/283164.

Sepkoski, J.J., McKinney, F.K., and Lidgard, S., 2000, Competitive displacement among post-Paleozoic cyclostome and cheilostome bryozoans: Paleobiology, v. 26, p. 7–18, https://doi.org/10.1666/0094-8373(2000)026<0007:CDAPPC>2.0.CO;2.

Sfenthourakis, S., Tzanatos, E., and Giokas, S., 2006, Species co-occurrence: The case of congeneric species and a causal approach to patterns of species association: Global Ecology and Biogeography, v. 15, p. 39–49, https://doi.org/10.1111/j.1466-822X.2005.00192.x.

Signor, P.W., and Brett, C.E., 1984, The mid-Paleozoic precursor to the Mesozoic marine revolution: Paleobiology, v. 10, p. 229–245, doi: 10.1017/S0094837300008174.

Stanley, S.M., 2007, An analysis of the history of marine animal diversity: Paleobiology, v. 33, p. 1–55, https://doi.org/10.1666/06020.1.

Stanley, S.M., 2008, Predation defeats competition on the seafloor: Paleobiology, v. 34, p. 1–21, https://doi.org/10.1666/07026.1.

Stanley, S.M., and Newman, W.A., 1980, Competitive exclusion in evolutionary time: The case of the acorn barnacles: Paleobiology, v. 6, p. 173–183, https://doi.org/10.1017/S0094837300025732.

Stigall, A.L., Bauer, J.E., Lam, A.R., and Wright, D.F., 2017, Biotic immigration events, speciation, and the accumulation of biodiversity in the fossil record: Global and Planetary Change, v. 148, p. 242–257, https://doi.org/10.1016/j.gloplacha.2016.12.008.

Stuart, Y.E., and Losos, J.B., 2013, Ecological character displacement: Glass half full or half empty?: Trends in Ecology & Evolution, v. 28, p. 402–408, https://doi.org/10.1016/j.tree.2013.02.014.

Taylor, P.D., 2016, Competition between encrusters on marine hard substrates and its fossil record: Palaeontology, v. 59, p. 481–497, https://doi.org/10.1111/pala.12239.

Thayer, C.W., 1979, Biological bulldozers and the evolution of marine benthic communities: Science, v. 203, p. 458–461, https://doi.org/10.1126/science.203.4379.458.

Tomašových, A., and Kidwell, S.M., 2009, Fidelity of variation in species composition and diversity partitioning by death assemblages: Time-averaging transfers diversity from beta to alpha levels: Paleobiology, v. 35, p. 94–118, https://doi.org/10.1666/08024.1.

Tyler, C.L., and Leighton, L.R., 2011, Detecting competition in the fossil record: Support for character displacement among Ordovician brachiopods: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 307, p. 205–217, https://doi.org/10.1016/j.palaeo.2011.05.020.

Van Riel, M.C., Healy, E.P., Van der Velde, G., and Bij de Vaate, A., 2007, Interference competition among native and invader amphipods: Acta Oecologica, v. 31, p. 282–289, https://doi.org/10.1016/j.actao.2006.12.006.

Vermeij, G.J., 1987, Evolution and Escalation: An Ecological History of Life: Princeton, New Jersey, Princeton University Press.

Violle, C., Nemergut, D.R., Pu, Z., and Jiang, L., 2011, Phylogenetic limiting similarity and competitive exclusion: Phylogenetic relatedness and competition: Ecology Letters, v. 14, p. 782–787, https://doi.org/10.1111/j.1461-0248.2011.01644.x.

Wagner, P.J., Kosnik, M.A., and Lidgard, S., 2006, Abundance distributions imply elevated complexity of post-Paleozoic marine ecosystems: Science, v. 314, p. 1289–1292, https://doi.org/10.1126/science.1133795.

Wilson, W.H., 1991, Competition and predation in marine soft-sediment communities: Annual Review of Ecology and Systematics, v. 21, p. 221–241, https://doi.org/10.1146/annurev.es.21.110190.001253.

Woodin, S.A., and Jackson, J.B.C., 1979, Interphyletic competition among marine benthos: American Zoologist, v. 19, p. 1029–1043, https://doi.org/10.1093/icb/19.4.1029.