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E-Article

Evidence for Trait-Based Dominance in Occupancy among Fossil Taxa and the Decoupling of Macroecological and Macroevolutionary Success

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abstract: Biological systems provide examples of differential success among taxa, from ecosystems with a few dominant species (ecological success) to clades that possess far more species than sister clades (macroevolutionary success). Macroecological success, the occupation by a species or clade of an unusually high number of areas, has received less attention. If macroecological success reflects heritable traits, then successful species should be related. Genera composed of species possessing those traits should occupy more areas than genera with comparable species richness that lack such traits. Alternatively, if macroecological success reflects autapomorphic traits, then generic occupancy should be a by-product of species richness among genera and occupancy of constituent species. We test this using Phanerozoic marine invertebrates. Although temporal patterns of species and generic occupancy are strongly correlated, inequality in generic occupancy typically is greater than expected. Genus-level patterns cannot be explained solely with species-level patterns. Within individual intervals, deviations between the observed and expected generic occupancy correlate with the number of lithological units (stratigraphic formations), particularly after controlling for geographic range and species richness. However, elevated generic occupancy is unrelated to or negatively associated with either generic geographic ranges or within-genus species richness. Our results suggest that shared traits among congeneric species encourage short-term macroecological success without generating short-term macroevolutionary success. A broad niche may confer high occupancy but does not necessarily promote speciation.

Keywords: occupancy, dominance, macroecology, speciation, fossil record.

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Introduction

Inequity abounds in biological systems at multiple scales of organization. At the community level, there typically are a few species with many individuals and many species with few individuals (Preston 1948; Magurran and Henderson 2003; McGill et al. 2007). At the clade level, there are a small number of species-rich clades and many species-poor ones (Alfaro et al. 2009). Occupancy—that is, the number of places inhabited by a taxon—might be an important link between ecological success and macroevolutionary success, yet it has gotten much less theoretical and empirical attention than have abundance and diversification. Species abundant in any one locality also tend to occupy many localities (Buzas et al. 1982; Brown 1984; Chao et al. 2005), suggesting that there is inequity in occupancy. Brown (1984; see also Wagner and Erwin 1995; Goldberg et al. 2011; Castiglione et al. 2017) posits that the macroecological success of being widespread should lead to macroevolutionary success, because species found in many places should be more prone to allopatric speciation. Conversely, Servedio and Kirkpatrick (1997) note that species with densely filled ranges could have lower probabilities of achieving peripheral isolation because of elevated gene flow offsetting the effects of selection and drift. Given the established relationship between abundance and occupancy, it is important to explore patterns of success and dominance in occupancy and how they relate to species richness.

Although occupancy is related to geographic range (Gaston 2003), the density of occurrences within a geographic range also is important to occupancy. The "Swiss cheese" model (Rapoport 1982; Hurlbert and White 2005, 2007) makes this distinction clear. Suppose we represent the distributions of two species as two slices of cheese with the same dimensions, but one slice is cheddar and the other is Swiss. The species represented by cheddar occupies more of its geographic

range (i.e., the area of the slice) than does the species represented by Swiss. Brown (1984; also Gaston and Spicer 2001; Slatyer et al. 2008) suggests that species with traits promoting broad niche breadths can occupy more habitats than species with similar geographic ranges but narrower niche breadths. This is equivalent to reducing the number and/or size of the holes in the Swiss cheese model. Mechanisms, such as dispersal ability, that affect geographic range (e.g., Jablonski 1987) are equivalent to changing the size of a slice of cheese. Thus, species can achieve the macroecological success of high occupancy through wide geographic ranges (large cheese slices) and/or denser inhabitation of those ranges (fewer holes per slice).

The predictions of these models are not restricted to individual species: phylogenetic autocorrelation (Raup and Gould 1974; Felsenstein 1985) predicts that, in general, closely related species will share traits because of common ancestry. We have no a priori reason to think that traits affecting occupancy should be exceptions to this rule; that is, there is no reason why only autapomorphies might promote high occupancy as opposed to synapomorphies. For example, dispersal capabilities often are similar among closely related species, and species with good dispersal ability often have high potential to occupy many areas (e.g., Jablonski 1987). As a corollary, occupancy patterns among genera should be more than just a by-product of variation in occupancy among species and variation in species richness among genera. Instead, because congeneric species should share traits affecting occupancy, generic occupancy should be an indirect "trait" of the genus, generated by traits shared by constituent species.

The fossil record is a useful system for distinguishing the predictions of models about what drives dominance in occupancy and how macroecological success corresponds with macroevolutionary success. Several studies use locality-level data to look at occupancy patterns among fossil taxa (Foote et al. 2007; Carotenuto et al. 2010; Liow 2013; Foote 2016), although their uses of the concept of occupancy differ somewhat. These locality data, in turn, provide us with information about (paleo)geographic ranges (Kiessling and Aberhan 2007; Miller et al. 2009; Wu and Miller 2014; Foote et al. 2016; Ritterbush and Foote 2017) and different basic sedimentary environments inhabited by fossil taxa (e.g., Heim and Peters 2011; Foote 2014). These consequently are important for assessing ideas about how dispersal ability and ecological flexibility affect occupancy.

In this article, we set out to assess three basic ideas. First, we ask whether occupancy patterns among fossil genera in different time intervals suggest that traits shared among closely related species affect occupancy or whether occupancy among genera is just a by-product of occupancy among species and variation in species richness among genera. Second, if species-level patterns of occupancy and richness within genera combined do not explain genus-level patterns in occupancy, then we assess whether deviations from expected genus-level occupancy correlated with estimates of environmental breadth and geographic range. Finally, we evaluate the contrasting predictions for association between macroevolutionary success (i.e., evolving many species) and macroecological success (i.e., occupying many communities). If high occupancy promotes speciation, or if common factors promote both occupancy and speciation, then we expect positive correlations between excess occupancy and species richness. Conversely, models in which success in one comes at the expense of success in the other predict negative associations.

Data and Methods

Fossil Occurrences and Associated Data

We analyzed trilobite, brachiopod, gastropod, bivalve, cephalopod, and echinoid species and genera from the Paleobiology Database (PaleoDB; https://paleobiodb.org/#/). These taxa include archetypal representatives of the Cambrian, Paleozoic, and Meso-Cenozoic faunas (sensu Sepkoski 1981) and represent a range of basic ecologic modes, including sessile benthic, mobile benthic, and nektonic taxa. These are also known (or thought) to represent a range of basic metabolisms (see Bambach et al. 2002), from very low (e.g., brachiopods and trilobites) to very high (e.g., mollusks). Thus, shared ecology or morphology are unlikely to explain any commonalities in basic occupancy patterns among these six taxa.

We downloaded the occurrence data on September 29, 2013. We vetted species records extensively prior to our analyses. Because we wished to assess whether species-level occupancy patterns alone explain genus-level occupancy patterns, we used only records in which a species is identified rather than only a genus. That is, we used records for only, say, *Bellerophon vasculites* or *Turritella subangulata* but not for *Bellerophon* sp. or *Turritella* sp. We used the latest generic assignments for species for which there are taxonomic data in the PaleoDB. In addition to this, we also checked extensively for misspellings. Finally, we converted all species names to gender-neutral versions. Thus, our analyses consider *Trochonema umbilicata, T. umbilicatum*, and *T. umbilicatus* to be the same species within a genus, even if there are no entered taxonomic opinions to those effects.

We treat subgenera as genera in our analyses. In part, we simply follow the protocols of earlier diversity studies (e.g., Sepkoski 1997). We also do so because researchers use genera and subgenera inconsistently in published articles and thus in PaleoDB entries. Although taxonomic fields fix these ranks to the latest opinion in many genera and subgenera, they do not yet do so for all cases. Thus, *Leptaena* (*Septomena*) *juvenilis*, *L. juvenilis*, and *Septomena juvenilis* all are occurrences for *S. juvenilis*.

We use presence or absence in a PaleoDB collection as our unit of occurrence (see, e.g., Alroy et al. 2001) and thus as our

basic unit of occupancy. Note that this is essentially the numerator for measures of occupancy in other paleobiological studies (e.g., Carotenuto et al. 2010; Liow 2013; Hannisdal et al. 2017), which divide sites occupied by the total possible sites occupied for an interval. However, variation in how researchers delimit fossil localities and sample areas with fossils means that raw occurrence numbers might misrepresent occupancy. For example, whereas some studies simply record the fossils found in a rock unit in a general area, other studies provide bed-by-bed lists of fossils over many meters of the same rock section. Such binge sampling can result in a species known only from a restricted area having numerous records if it appears in multiple rock layers in a well-studied section (see, e.g., Raup 1972). Therefore, we lumped together all collections within 5 km of each other (even those from different rock units). This effectively creates a grid of 5-km cells for each time interval and makes our unit of occupancy comparable to studies using grids rather than sites (Foote 2016). We get similar results using a smaller 1-km radius (supplementary information, available online). We stress that grid approaches are not a complete antidote for the more general issue of fossiliferous localities being nonrandomly distributed geographically (e.g., Plotnick 2017), but they do address one of the more obvious aspects of nonrandom sampling.

The six taxonomic groups we analyze include 84,677 species from 14,222 genera (table S1; tables S1–S29 are available online). The raw data include 369,637 records from 65,821 localities. After lumping together collections within 5 km of each other, there are 164,135 records from 18,152 localities to analyze. We partitioned those data into 50 time units of approximately 10 million years each, spanning the Cambrian through the Late Cenozoic (see Alroy et al. 2008; note that these are modified to reflect the timescale in Gradstein et al. 2012). Counting each combination of taxon and time independently (i.e., each species or genus that occurs in multiple bins is tallied for each bin), there were 31,058 total genus-bin combinations and 98,059 species-bin combinations.

Our data come from 6,315 studies and/or published data sets (supplementary references, available online). Twenty studies contributed more than 1,400 records each (King 1931; Reed 1944; Gardner 1947; Besairie and Collignon 1972; Cooper and Grant 1977; Toulmin 1977; Woodring 1982; Sohl and Koch 1983, 1984, 1987; Gitton et al. 1986; Manivit et al. 1990; Aberhan 1992; Tozer 1994; Jablonski and Raup 1995; Fürsich 1999, 2006; Rode and Lieberman 2004; Holland and Patzkowsky 2007; Hendy et al. 2008). We provide all of the references in the online supplementary information.

We tallied generic occupancy using the minimum and maximum possible counts. The minimum possible allows one genus occurrence per locality, regardless of how many constituent species appear there. The maximum possible simply sums the occurrences of constituent species. Thus, a genus with three species occupying one locality occupies the locality three times given the maximum criterion but only once given the minimum criterion. Minimum counts offer a safeguard against oversplitting of genera, which often manifests itself in specimens from well-sampled sites being split into multiple species, owing to differences that likely represent intraspecific variation (e.g., Batten 1966; Labandeira and Hughes 1994; Alroy 2002). The relational taxonomic fields in the PaleoDB do synonymize many species following alpha taxonomic studies. However, many relevant taxonomic opinions have not been entered. Moreover, many taxa have not undergone species-level alpha taxonomic revisions in recent decades. Thus, the problem could be rampant. Conversely, legitimate congeneric species found at the same localities might indicate that a genus occupies a greater number of niches and/or is more flexible in its environmental requirements than are genera that lack co-occurring congeneric species. If both minimum and maximum occupancy patterns point to the same conclusions, then our results are robust to these potential difficulties.

Our data (tables S2, S3; fig. S1; figs. S1–S29 are available online) replicate the results of prior studies showing that generic occupancy correlates positively with rock units occupied, geographic range, and species richness (e.g., Liow 2007; Foote et al. 2016). Therefore, we contrast deviations from expected generic occupancy (see below) with rock units occupied, geographic span occupied, and species richness. We use formations for rock units, after standardizing PaleoDB records of formation names in the following ways. We treat rock units that differ by inclusion of rock types (e.g., Burgess Shale and Burgess) as the same formation. In cases where the rock units do not yet have formal formation names, we informally name the unit based on the local stage and continental plate on which the rock unit occurs. A very different problem is that some rock units are ranked as formations by some researchers and as members by others. Rules of stratigraphic nomenclature do allow a rock unit to be a member of two formations or a formation in one place but a member in another place. However, for the cases we researched, different rankings represent a change in opinion about the rank of the rock unit, akin to the issue of whether specimens represent a subspecies or species. Thus, for such rock units, we used the rank from the latest reference contributing occurrence data to the PaleoDB. This rank was applied to all collections that included that rock unit. Similarly, we used the latest formation-member combination (including a rank as formation) for all members assigned to multiple formations.

We used paleocoordinates provided by the PaleobDB for each locality to test the effects of geographic ranges. We used maximum span, which provides a good proxy for the geographic area encompassed by a species (Wu and Miller 2014).

Finally, species richness per genus requires only the species records we used to measure dominance. However, we

expect average species richness to be higher in well-sampled intervals than in poorly sampled intervals, simply because increased sampling provides a greater chance for finding rare species within genera. Therefore, instead of using raw species-per-genus counts, we use average species-per-genus counts after sampling standardization (see below).

Measuring Dominance in Occupancy among Genera

We measured dominance in occupancy among genera using the Gini index (Gini 1912; Ceriani and Verme 2012). This index is best known as a measure of income inequality in economic studies (Bradlow and Fader 2001; Chin and Culotta 2014; Underwood 2014); however, ecologists have used it as a dominance metric in community ecology studies (Damgaard and Weiner 2000; Wittebolle et al. 2009). Gini contrasts two different cumulative frequency curves (i.e., Lorenz curves): (1) an empirical curve with taxa and (2) a theoretical curve giving the maximum possible equality among taxa. Note that the Lorenz curves sum observed and theoretical frequencies from rarest to most common. Gini then summarizes the area separating the two curves as

$$G = \left(\frac{S+1}{S} - \frac{2 \times \sum_{j=1}^{S} \sum_{i=1}^{j} f_i}{S \times N} \right),$$

where S is the total number of taxa, N is the total number of occurrences, and f_i is the frequency of the ith taxa. If all taxa have the same number of occurrences (e.g., $n_1 = n_2 = \cdots = n_S$), then the second term goes to $(S + 1)/S$ and Gini $= 0.0$. Gini approaches 1.0 as inequality increases. However, for any particular data set, the maximum possible G depends both on S and the number of localities or colections, C. Suppose we have $N = 350$, $S = 100$, and $C = 100$. Because $n_{\max} = 100$, the most inequitable distribution of occurrences is two genera with $n = 100$, one with $n = 53$, and 97 with $n = 1$. Thus, $G_{\max} = 0.696$, not 1.0. Unless N is evenly divisible by S, there also is a limit on the minimum G. At $N = 350$ and $S = 100$, the most equitable distribution of occurrences has 50 genera with $n = 3$ and 50 genera with $n = 4$. (Note that C is not relevant here because the minimum number of collections must be equal to or greater than the average number of collections.) Thus, $G_{\min} = 0.071$. Our permutation tests described below will generate different minimum and maximum Gini when using minimum generic occupancy (i.e., one locality per genus) because the number of co-occurring congeneric species will differ from one run to the next. We therefore rescaled the metric to

$$G' = \frac{G_{\text{obs}} - G_{\min}}{G_{\max} - G_{\min}}.$$

Now, $G' = 0.0$ means the minimum possible dominance, and $G' = 1.0$ means the maximum possible dominance.

For each interval, we have an occupancy distribution for observed genera (fig. 1*A*). Our null hypothesis is that genus-occupancy distributions reflect only the occupancy distribution among the constituent species of those genera (fig. 1*B*, showing occurrences and occupancy for 1,730 Late Ordovician species) and the distribution of species richnesses within those genera (fig. 1*C*). We constructed expectations for the null hypothesis by giving each genus with X species the localities of X species drawn at random (without replacement) from the species-occupancy distribution (fig. 1*B*; see also fig. S2). We repeated this permutation test 1,000 times to estimate the expected genus-occupancy distribution under the null hypothesis (fig. 1*D*). Note that our example in figure 1*D* tallies minimum generic occupancy. In each run, we also calculated G' from the cumulative frequency curve from permuted generic-occupancy distribution (fig. 1*E*), calculating both the median G' (based on the medium blue curve) and the range of simulated G's (the blue-gray cloud around that line). For comparison, we illustrate the empirical cumulative frequency curve from figure 1*A* in red. In this case, because the empirical cumulative frequency curve is more convex than the simulated cumulative frequency curves, the empirical G' (and thus inequality) is greater than the expected G'. We assessed the significance based on the proportion of permutation runs that equal or exceed the empirical G'; in this case, none do (fig. 1*F*), so we assigned $P < .001$ here.

We also analyzed the six higher taxa individually. Although all six taxa generally show high sampling levels (Foote and Sepkoski 1999), the relative sampling within each taxon varies over time (Connolly and Miller 2001). What might be more relevant to our study is that it might be easier to separate closely related species within genera, such as trilobites and echinoids, than it is to distinguish equally closely related species in the other taxa, due to differences in overall morphological complexity (Schopf et al. 1975; Smith 1994). The different higher taxa tend to favor different basic environments, which in turn vary in their relative representation within and over time intervals (see, e.g., Jablonski et al. 1983; Sepkoski and Miller 1985; Sepkoski 1991; Miller 1997; Holland and Zaffos 2011). Finally, turnover rates within groups such as brachiopods and (especially) trilobites are much higher than among groups such as gastropods and bivalves (Sepkoski 1981), which in turn makes it easier for gastropods and bivalves to persist over entire intervals. All of these factors could affect the expected occupancy among species and genera with N species without shared traits elevating expected occupancy. Thus, replicating general patterns within these taxa suggests that these factors are not the primary drivers of those patterns.

Paleontologists have sampled fossils from North America and Europe more thoroughly than fossils from other areas (Sheehan 1977; Signor 1985). Thus, genera known from North America or Europe might be more prone to having high

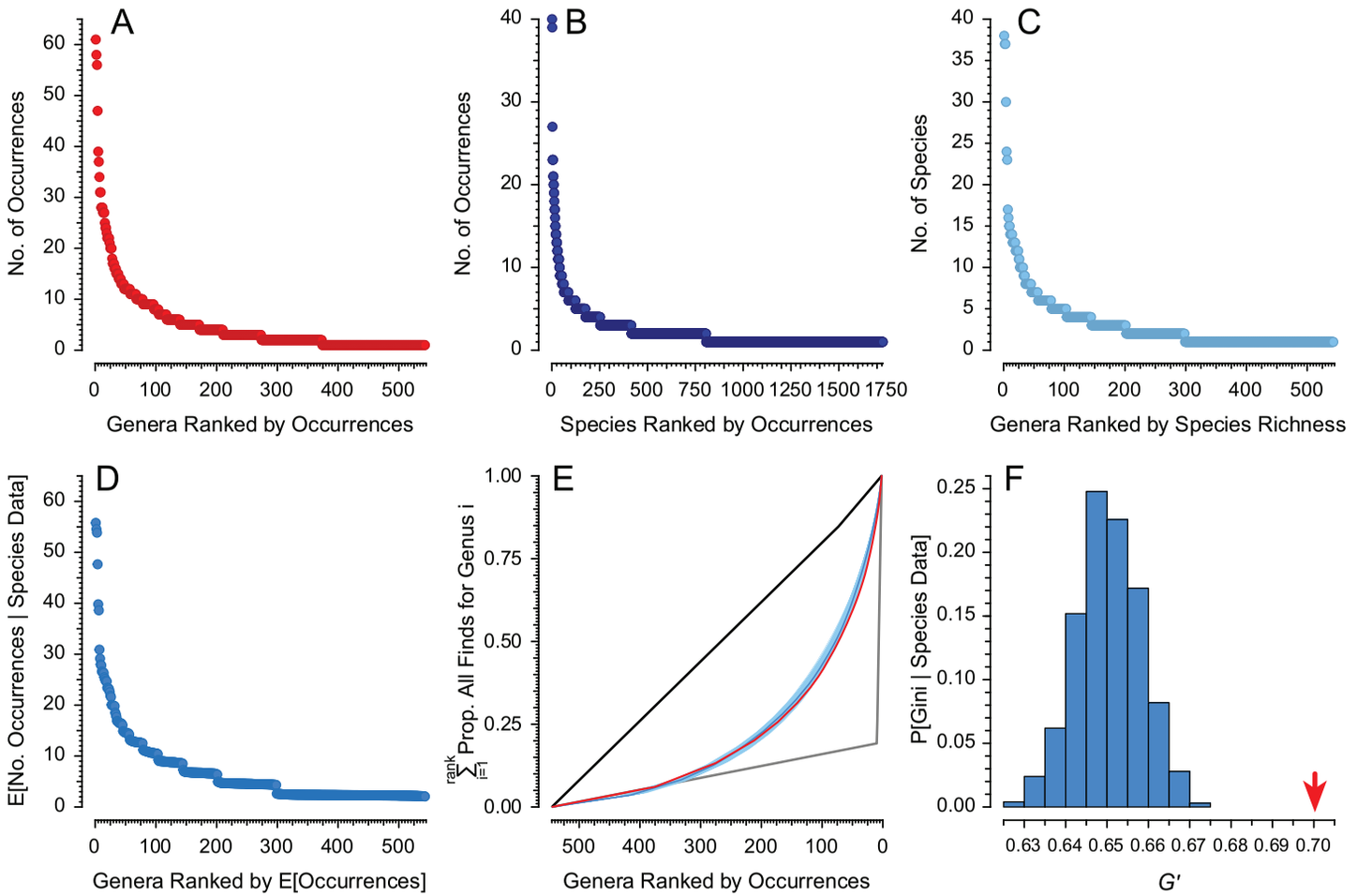

Figure 1: Testing whether inequality in occupancy among Late Ordovician genera exceeds expectations. *A*, Rank-order occurrence and occupancy distribution for 543 bivalve, gastropod, cephalopod, brachiopod, trilobite, and echinoid genera in the Late Ordovician (458–448 million years ago). *B*, Rank-order occurrence and occupancy distribution for species belonging to those genera. *C*, Rank-order species richness for those same genera. *D*, Expected rank-order occurrence and occupancy distribution for 543 genera with species-richness distribution given in *C* and occupancies among those species given in *B*. This is based on 1,000 permutations in which each genus randomly draws (without replacement) the localities for *N* species from *B*, with *N* determined by the genus's position on *C*. This represents the expectations of the null hypothesis that generic occupancy in *A* is a product purely of species occupancy in *B* and species-richness patterns among genera in *C*. *E*, Cumulative frequency (Lorenz) curves for observed generic occupancy (red) and the permutation test (medium blue). The blue-gray borders around the medium-blue curved line give the range of cumulative frequency curves generated in the 1,000 permutations. The black line is the Lorenz curve from the most equal possible occupancy distribution of 4,622 total occurrences among 543 genera. The gray lines show the most unequal possible occupancy distribution given the data (i.e., 543 genera with 4,005 occurrences from 295 localities). As the area under the arcs separating the black maximum equality line and the cumulative frequency curves increases, Gini (G') increases. This area is standardized to the maximum possible (given by the gray lines) to yield G'. Because the arc for the empirical curve (red) is stronger than those for the expected curve (blue), observed G' (and thus inequality in generic occupancy) is greater than expected under the null hypothesis. *F*, Histogram showing the range of G' produced under the permutation test. None of the 1,000 permutations generates inequality as great as observed, yielding a *P* value of <.001.

sampled occupancy than genera restricted to rocks in other parts of the world. To control for this effect, we repeated our analyses for the European and North American records only.

Finally, variation in bin durations or turnover within those bins could affect results. Therefore, we also ran the permutations for the pooled data set, but using only midlife genera that were sampled before and after each interval. Unless they are polyphyletic, midlife genera necessarily exist throughout each interval. Differences among these cannot be attributed to different life spans and thus are unaffected by turnover within the bin.

Assessing Correlates of Excess or Deficient Occupancy

The permutation tests described above also determine expected occupancies for genera with one, two, three, or more species and thus the excess or deficient occupancy for each genus. This is given by the difference between the red dots and the blue line in figure 2 and for the genera in the figure 1 example. We then used Kendall's rank correlation tests to assess the associations between excess generic occupancy and our three test variables. Kendall's correlation is better suited to dealing with ties in ranks (which are ubiquitous in our data) than are other nonparametric correlation metrics such as Spearman's (Sokal and Rohlf 1981).

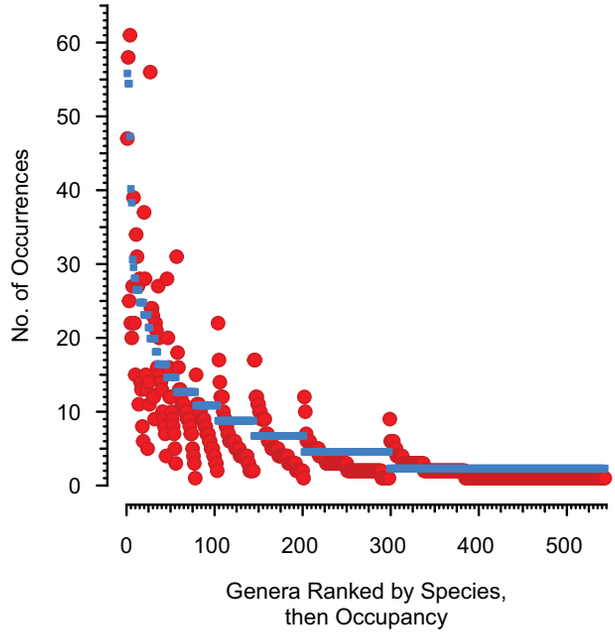

Figure 2: Estimating excess and deficient occupancy for individual genera from the Late Ordovician (458–448 million years ago). Red dots correspond to those in figure 1*A*, but they are ordered first by species richness and then by occupancy and occurrences. Individual groups of genera with the same number of species therefore create distinct occupancy distribution curves. The medium-blue line represents the average occupancy for a genus with X species, based on permutation tests outlined in the text and in figure 1. Thus, the red curve corresponding to each blue line gives the occupancy distribution for genera with N species. The difference between each red dot and the blue line gives the excess (or deficient) occupancy of that genus.

Kendall's correlation metric also is amenable to partial correlations, which are useful here because occupied rock units, maximum geographic span, and subsampled species richness all show significant correlations with each other (fig. S1*B*; table S3). Thus, a causal relationship between excess occupancy and any of our three extrinsic variables might induce correlations between excess occupancy and the other two variables. For example, suppose that extended geographic range causes excess occupancy. High-occupancy genera with extended geographic ranges should occur in many formations, simply because formations are geographically constrained units of sediments. This, in turn, would create a correlation between excess occupancy and numerous occupied rock units. Partial correlations should indicate that excess or deficient generic occupancy does not correlate with occupying more rock units than expected given geographic ranges. We used the R package ppcor (Kim and Yi 2006) to assess the unique effects of each variable after accounting for the general association between each of the variables.[1]

We restricted both the standard and partial Kendall's correlation tests to genera with more than two occurrences within a time interval. Otherwise, singletons would create very strong positive associations in all tests: genera with one species known from one locality necessarily have minimum rock units occupied and geographic span; such genera also have minimum species richness. To assess the possible effects of different taxa and different sampling regimes, we repeated the tests on the six individual higher taxa separately for North American and European data. In these cases, we examined only intervals with more than 10 genera known from more than localities.

Variation in sampling intensity among intervals will affect observed species richness within genera. Therefore, we estimated average species richness per genus after sampling standardization. We employed shareholder quorum subsampling (SQS; Alroy 2010; Chao and Jost 2012), which uses coverage statistics (Good 1953; Chao et al. 2015) to approximate comparable levels of sampling among intervals. Thus, genera are species rich only if they have many frequently subsampled species. We used SQS based on the minimum species-level coverage ($U = 0.438$) to estimate the average subsampled species richness for each genus based on 1,000 SQS replications (fig. 3).

Examining partial correlations between average subsampled species richness and either formations occupied or max-

1. R code developed for these analyses is given in the supplemental material. Code that appears in *The American Naturalist* is provided as a convenience to the readers. It has not necessarily been tested as part of the peer review.

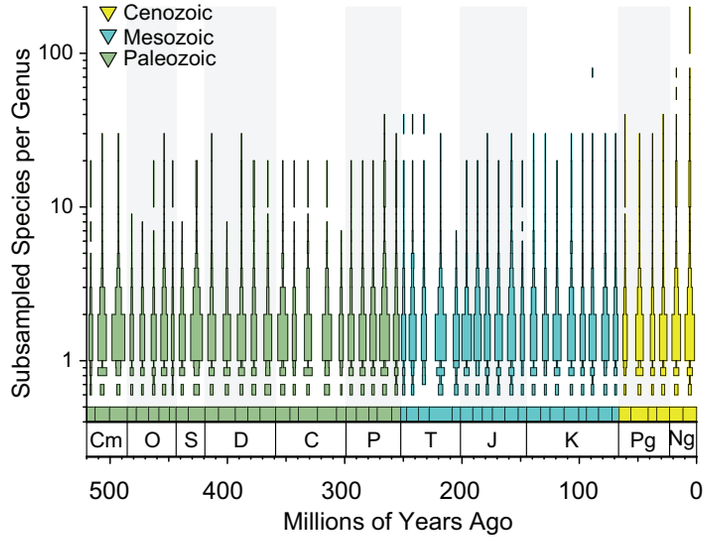

Figure 3: Distributions of average subsampled species richnesses for each genus in every interval after 1,000 shareholder quorum subsampling (SQS) runs. SQS analyses are based on the minimum Good's coverage for species ($U = 0.438$). Spindles within each bin are scaled so that the most common average subsampled species is the widest bar, and thus they are not scaled to each other.

imum geographic span might appear to be double dipping, given that deviations from expected generic occupancy are relative to expected occupancy given the number of species in a genus. However, the important question here is whether a two-species genus with deviations from expected occupancy also occurs in more formations and/or over a broader geographic range than do other two-species genera. Removing the effect of species richness on occupied formations and/or geographic span might further emphasize important correlations. Conversely, if there is a positive or negative association between species richness and occupancy (i.e., macroevolutionary and macroecological success), then it might become more apparent when we remove the effect of formations occupied or geographic span.

Controlling for "Wastebasket" Species

It has long been noted that some taxa become default classifications for groups of similar-looking species. Although paleontologists have been more concerned with this at the genus level (e.g., Plotnick and Wagner 2006), examples also exist at the species level (e.g., Hoel 2005; Antoine 2012). Such species will artificially create apparent excess generic occupancy by simply attributing the occurrences of several species to one species and thus cause the genus to have greater occupancy than expected given reported species richness. Although a genus might have one "wastebasket" species, it is very improbable that it will have two. Therefore, we examined the association between the second most common species in a genus and excess generic occupancy. This necessarily is restricted to genera with more than two species. We again used Kendall's rank correlation test. If excess generic occupancy is driven by "wastebasket" species artificially inflating generic occupancy, we should see no association between excess generic occupancy and occupancy of the second most common species. However, if excess occupancy is driven by traits shared by congeneric species, we expect that the second most common species will have high occupancy too.

Results

Occupancy Inequity among Genera

Inequality in occupancy among species and that among genera correlate strongly with each other regardless of whether generic occupancy represents all unique localities (minimum) or all occurrences of constituent species (maximum; figs. S3–S5). Nevertheless, inequality in generic occupancy is greater than expected given our null model in all 50 intervals given either minimum or maximum generic occupancy. Furthermore, generic inequality is greater than expected in 47 of 48 intervals given minimum occupancy among only midlife genera (i.e., those also known in earlier and later intervals; fig. 4; table S4). Moreover, the differences typically are significant at $P \leq .05$ for all intervals given maximum occupancy, 43 intervals given minimum occupancy, and 46 intervals given midlife genera only.

These results are largely replicated in subsets of the data. Within the six major taxonomic groups, 181 of 225 intervals with collections of more than 50 show excess generic dominance given minimum generic occupancy, with 110 of those cases being significant at $P \leq .05$ (fig. 5; table S5). Given

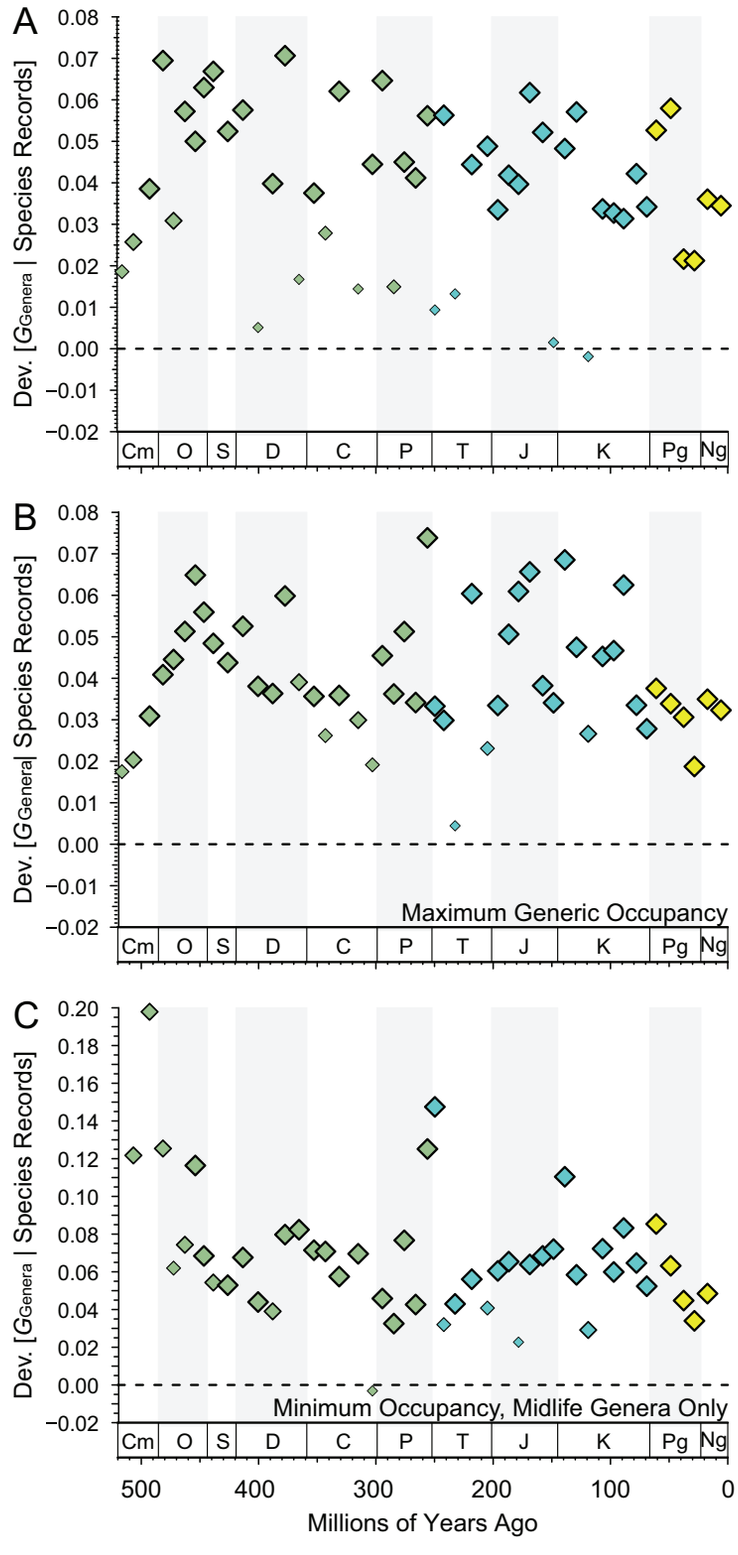

Figure 4: Deviations between observed Gini for genus-level occupancy patterns and expected Gini for genus-level occupancy patterns given the distributions of species-level occupancy patterns and species-richness patterns within genera. Positive deviations indicated greater occupancy dominance than expected. Significance is based on the proportion of permutations where permuted Gini equaled or exceeded observed Gini. *A*, Minimum generic occupancy (correlation with time: $\tau = -0.117$, $P = .250$). *B*, Maximum generic occupancy ($\tau = -0.082$, $P = .398$). *C*, Minimum occupancy among midlife genera only ($\tau = -0.180$, $P = .082$). Colors are as in figure 3. See also table S2.

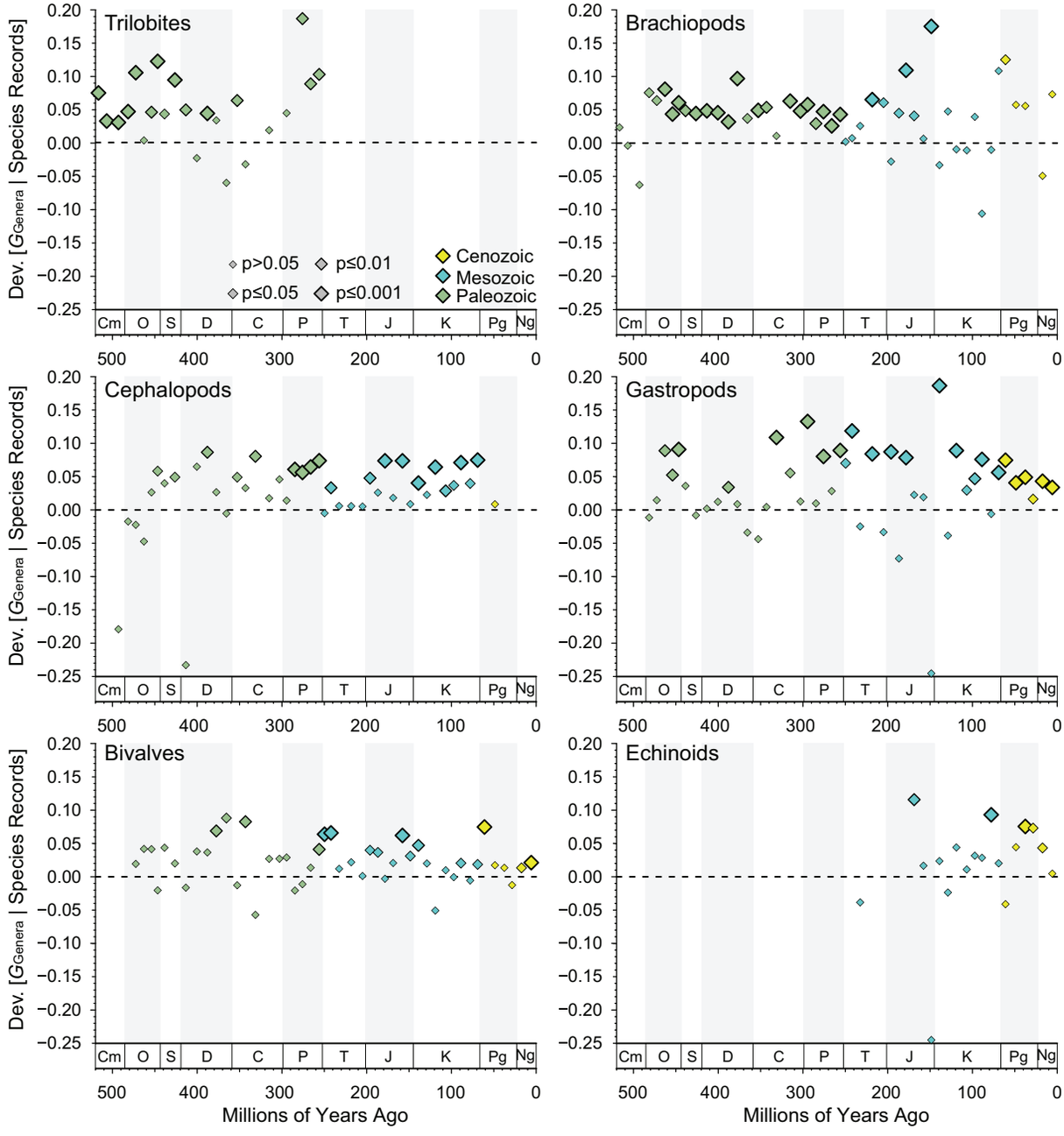

Figure 5: Deviations between observed and expected Gini within each of the six higher taxa analyzed, given minimum generic occupancy. Colors are as in figure 3.

maximum occupancy, 194 intervals show excess generic dominance, with 111 of those cases significant at $P \leq .05$ (fig. S6). When we look at only midlife genera, 126 of 190 intervals show excess generic dominance, with 48 of those cases being significant at $P \leq .05$ (fig. S7).

Within Europe and North America, 77 of 100 intervals (33 of 50 in Europe and 44 of 50 in North America) show excess generic dominance given minimum occupancy, with 58 of those cases (27 in Europe and 31 in North America) being significant at $P \leq .05$ (fig. 6; table S6). Given maximum generic occupancy, 92 of 100 intervals (44 of 50 in Europe and 48 of 50 in North America) show excess generic dominance, with 62 of those cases (28 in Europe and 34 in North America) significant at $P \leq .05$ (table S6). Minimum occupancy among only midlife genera shows excess generic dominance in 70 of 93 intervals (36 of 47 in Europe and 34 of

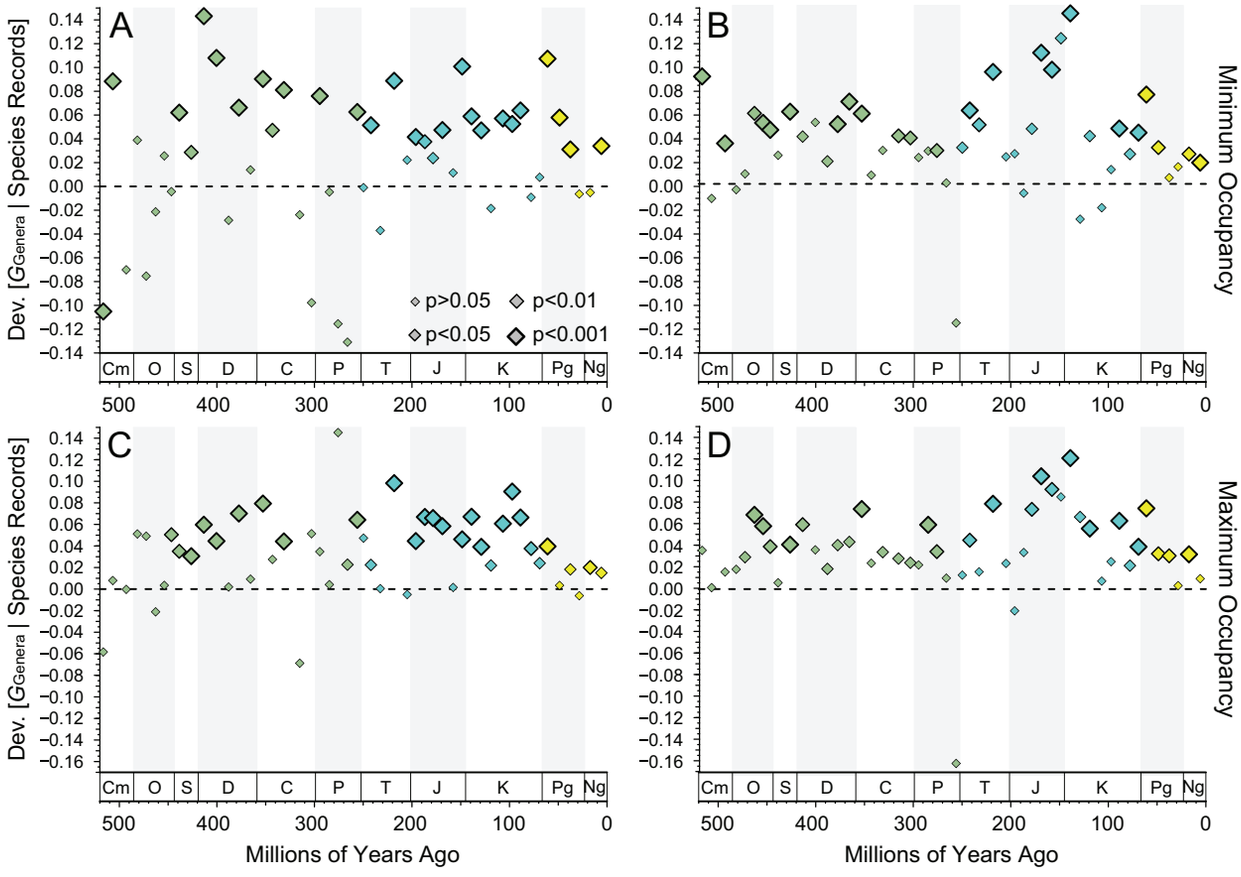

Figure 6: Deviations between observed and expected Gini using only European (*A*, *C*) and North American (*B*, *D*) given minimum (*A*, *B*) and maximum (*C*, *D*) generic occupancy. Colors are as in figure 2.

46 in North America), with 40 of those cases (25 in Europe, 15 in North America) significant at $P \leq .05$ (table S6).

Elevated Occupancy among Second Species

Among genera with more than two species and using minimum occupancy, deviations from expected generic occupancy correlate positively with the occupancy of the second most common species in 49 of the 50 intervals examined (fig. 7; table S7). The correlations are significant at $P \leq .05$ in 45 of the 50 intervals and at $P \leq .001$ in 35 of the 50 intervals. Using maximum occupancy, then the associations are positive and significant at $P \leq 10^{-7}$ in all intervals (table S7). Using minimum occupancy among midlife genera, associations are positive in 45 of 48 intervals, with associations significant at $P \leq .05$ in 47 intervals and $P \leq .001$ in 45 intervals (table S7).

Correlates of Excess or Deficient Occupancy among Genera

Excess generic occupancy correlates strongly with rock units occupied (tables 1, S8, S11, S14). Although minimum generic occupancy shows positive associations for only 29 of 50 intervals, 12 of those are significant at $P \leq .05$, whereas only 5 of the 21 negative associations are significant at $P \leq .05$ (fig. 8; table S8). Given either maximum generic occupancy (fig. S8; table S11) or minimum occupancy among only midlife genera (fig. S9; table S14), nearly all intervals show positive associations, with the preponderance significant at $P \leq .05$. Under all three metrics, controlling for the effects of both maximum geographic span and average subsampled species richness results in nearly all intervals having positive associations, with most significant at $P \leq .05$.

Excess occupancy shows similar associations with both maximum geographic span and average subsampled species richness (tables 1, S9, S10, S12, S13, S15, S16). Positive associations are common given either maximum occupancy or midlife occupancy, whereas negative associations predominate given minimum occupancy. Controlling for rock units occupied greatly decreases positive associations, except for the association between excess occupancy for midlife genera and average subsampled species richness. In contrast, controlling for average subsampled species richness or geographic

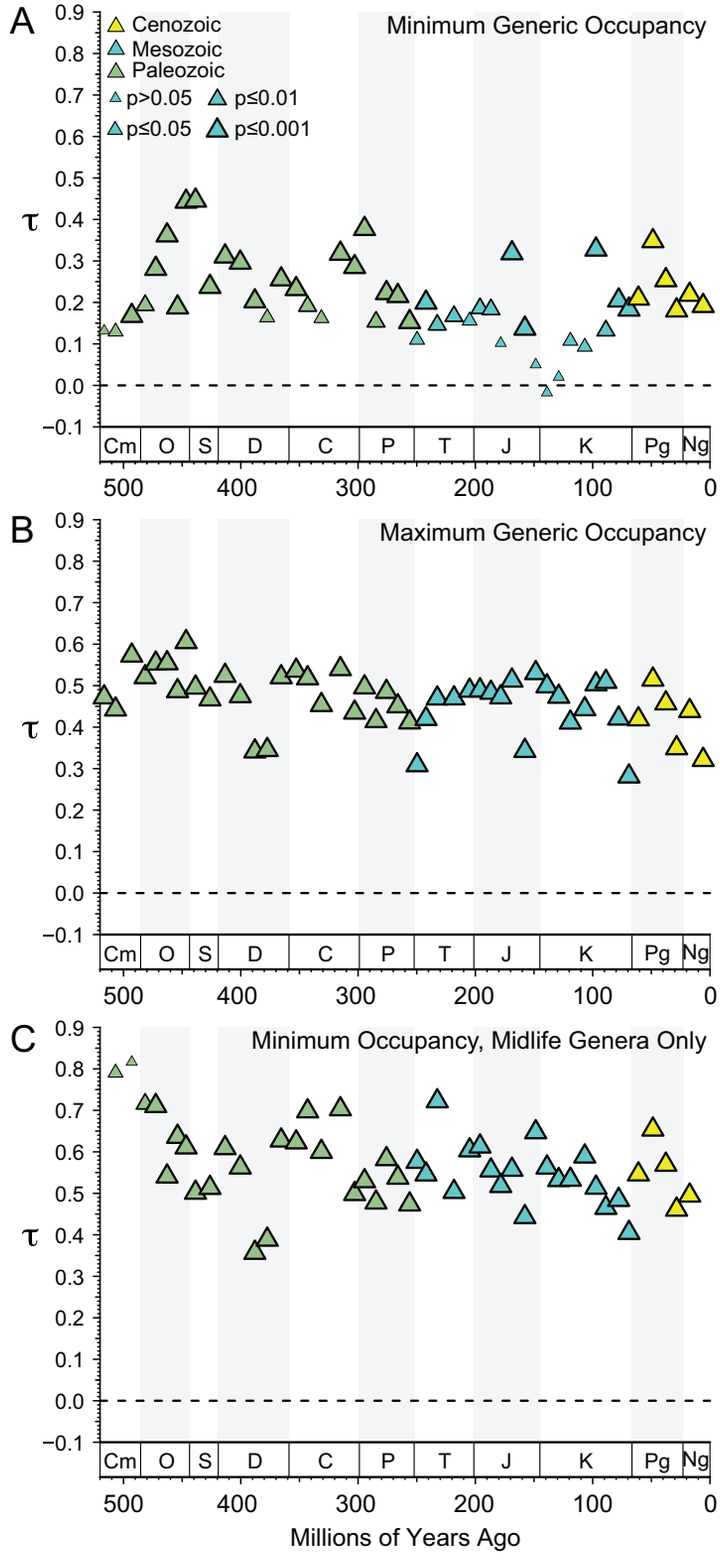

Figure 7: Kendall's correlation between excess or deficient generic occupancy and the occupancy of the second most common species in a genus. Analysis necessarily limited to genera with more than two species. *A*, Minimum generic occupancy. *B*, Maximum generic occupancy. *C*, Minimum occupancy among midlife genera only. See also table S7.

Table 1: Summaries of positive associations between excess generic occupancy for all genera given minimum and maximum measures of occupancy as well as minimum occupancy among midlife genera (those known both before and after an interval)

	Positive association	Positive $P \leq .05$	Negative $P \leq .05$	Positive given rocks	Positive $P \leq .05$	Negative $P \leq .05$	Positive given S_{SQS}	Positive $P \leq .05$	Negative $P \leq .05$
Excess generic occupancy versus rock units:									
Minimum	29	12	5	45	26	1	50	44	1
Maximum	49	42	0	50	47	0	50	50	0
Midlife only	48	42	0	48	45	0	48	43	0
Excess generic occupancy versus span:									
Minimum	2	0	32	1	0	43	21	5	14
Maximum	33	15	5	1	0	0	36	12	0
Midlife only	38	20	1	5	0	19	38	19	1
Excess generic occupancy versus S_{SQS}:									
Minimum	1	0	45	0	0	48	2	1	48
Maximum	29	6	10	1	0	40	24	7	9
Midlife only	24	1	4	23	1	3	24	2	4

Note: Numbers give numbers of intervals of 50 for minimum and maximum occupancy and of 48 midlife genera. Associations are measured using Kendall's correlation. Rock units give numbers of formations; span gives maximum geographic span; S_{SQS} = average subsampled species richness (S) given shareholder quorum subsampling (SQS). See tables S8–S16.

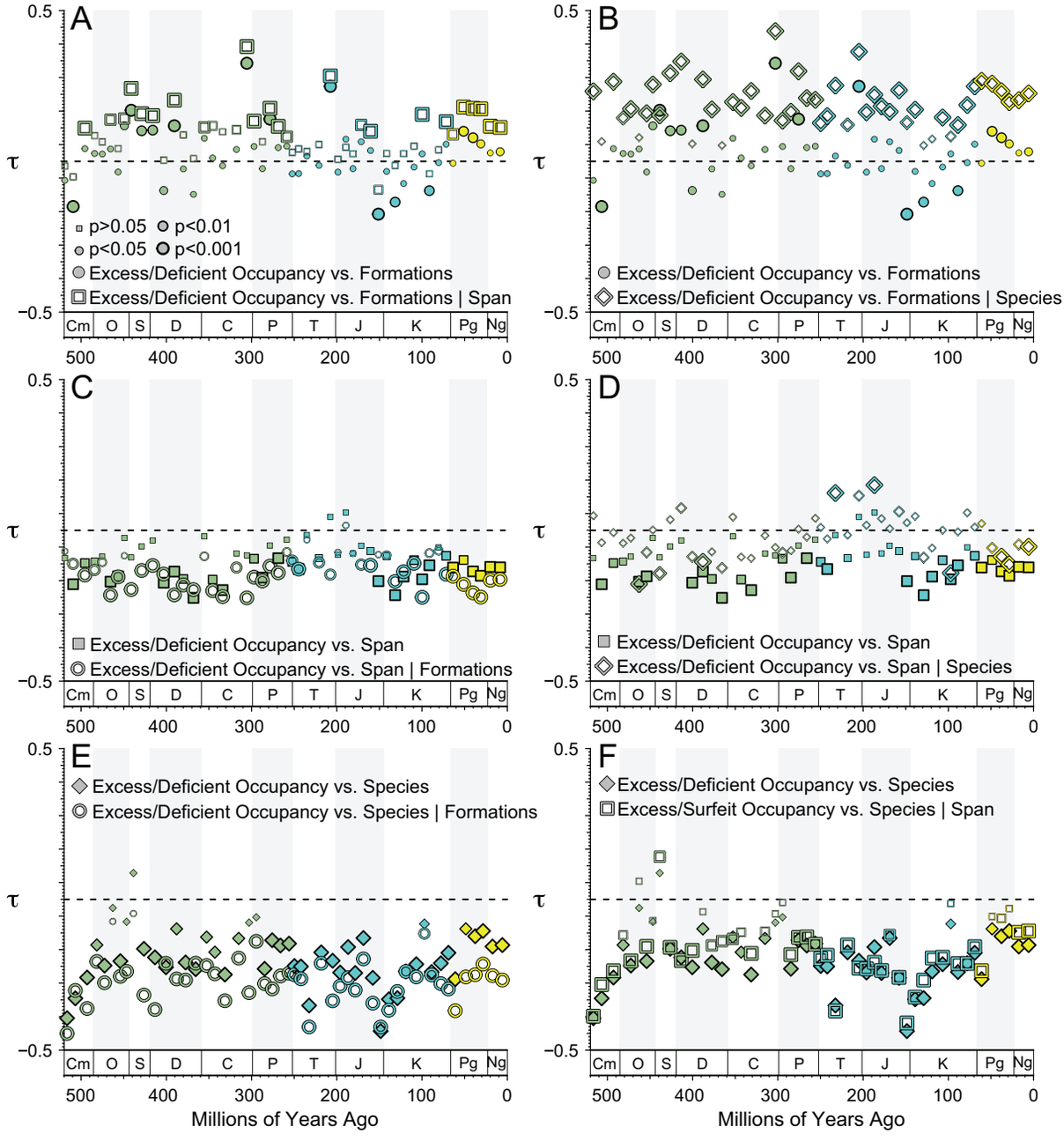

Figure 8: Kendall's correlations and partial correlations for deviations from expected (i.e., excess or deficient) occupancy given minimum generic occupancy. The correlation coefficient is shown by τ. Increased τ for partial correlation means that, say, the association between excess occupancy and formations occupied improves once we take into account the expected correlation between occupied formations and maximum geographic span. All comparisons are restricted to genera with more than two occurrences in a given interval. *A*, *B*, Formations, controlling for maximum geographic span (*A*) and average subsampled species richness (*B*). *C*, *D*, Maximum geographic span, controlling for formations (*C*) and average subsampled species richness (*D*). *E*, *F*, Average subsampled richness, controlling for formations (*E*) and maximum geographic span (*F*). See tables S8–S10; see also figures S8, S9.

span has little effect on associations for geographic span or average subsampled species richness.

Each of the three types of analyses was run on each individual clade (figs. S10–S27; tables S17–S25). The results are consistent with the patterns found when all clades are analyzed together. In particular, brachiopods consistently show strong positive associations between deviations from expected generic occupancy and rock units occupied (tables 1, S10).

There are some exceptions. For example, trilobites, which tend to be short-lived, do not show the pattern when using only the midlife genera. However, because the overall results for the individual clades generally recapitulate the results for all taxa, and because discussing the results of the analyses on individual clades is beyond the scope of this article, we do not attempt to dissect individual deviations in great detail.

Within either Europe or North America, the same general correlations are repeated (figs. S28, S29; tables S27–S29). Excess occupancy correlates positively with occupied rock units, particularly after controlling for the effects of geographic range and average subsampled species richness. Similarly, weak positive or negative associations between excess occupancy and either maximum geographic span or average subsampled species richness tend to become stronger negative associations after controlling for occupied rock units.

Discussion

Trait-Based Macroecological Success

Our results demonstrate that occupancy patterns among genera cannot be explained solely by occupancy patterns among species. This conclusion cuts across time intervals, taxonomic groups, and biogeographic units. In particular, unusually high occupancy correlates with genera occupying more rock units than expected given geographic span or species richness. Thus, we have evidence that some genera are truly macroecologically dominant in the sense that they occupy more areas than would be expected by chance.

Macroecologically successful genera seemingly have more high-occupancy species than expected, rather than a single highly successful species (fig. 7). Moreover, there is a strong positive correlation between the number of formations in which a genus occurs and how much more common that genus is than expected given its species richness (fig. 8). Although there is not a 1 : 1 correspondence between environment and formation, differences in lithology reflecting differences in sedimentary environments are a primary reason why stratigraphers separate contemporaneous and geographically adjacent rock units into separate formations. Thus, the simplest explanation for this association is that genera with excess occupancy include species that can inhabit a wider variety of environments than can those with expected or deficient occupancy. Genera occupying more environments than average would have relatively few Swiss cheese holes in their distributions and a high probability that the strata yielding their species are separated into multiple formations because of differences in lithology. Indeed, a common explanation for why the two species co-occur in some formations but not in others is differences in environmental tolerances (see, e.g., Holland 2003). Because congeneric species should share numerous traits, this corroborates Brown's (1984) suggestion that species traits shared among close relatives contribute to greater niche breadth, greater environmental tolerance, or greater ability to engineer niches and allows them to occupy a greater range of environmental types within their geographic ranges (see also Gaston and Spicer 2001; Slatyer et al. 2008). Unfortunately, less than one-third of the localities used in this study include environmental interpretations more exact than indeterminate carbonate or siliclastic environments. However, our results and the interpretation of those results predict that macroecologically dominant genera will show greater disparity in occupied environments than is typical.

Although our results are consistent with trait-based macroecological success, identifying which traits contribute to macroecological success will be difficult. In some cases, the trait or traits responsible might be among those diagnosing a genus. However, in many cases, unfossilizable traits in soft tissue or physiology inherited from a common ancestor will be important. Identifying particular ecological models responsible for macroecological success also is problematic, and it is possible that no one particular model predominates. For example, an intuitively appealing model is one in which traits favoring niche construction (Laland et al. 1999; Erwin 2008) explain differences in generic occupancy. Gastropods and cephalopods both would be good candidates for niche-construction models, as they both possess mobility, fairly high metabolisms, and biochemistries buffered against local seawater chemistry (Bambach et al. 2002). However, both show correlations between occupied rock units and excess occupancy only after controlling for species richness. Conversely, brachiopods are sedentary, low-metabolism organisms and thus poor candidates for niche construction models. Nevertheless, they fit the overall model quite well. There also are no clear temporal trends (e.g., fig. 4), even though the dominant taxa and types of ecosystems vary substantially over the Phanerozoic. The wide variety of basic life histories (e.g., sedentary vs. mobile, nektonic vs. benthic, etc.) generating the same basic pattern further confounds any attempt to infer some universal tactic for macroecological dominance.

With regard to the above stated, traits that allow marine organisms to inhabit a variety of different sedimentary environments might be key. This would explain why their fossils occur in sediments generating greater numbers of rock units over some geographic spans than is typical for genera with similar geographic spans. Examining this would best be done using independent contrasts where we can look at apparently independent derivations of macroecological dominance on a phylogeny.

The Apparent Decoupling of Macroecological and Macroevolutionary Success

An equally important conclusion is that our results imply that macroevolutionary success and macroecological success of-

ten are decoupled and are even at odds with one another. The negative associations between species richness and deviations from expected generic occupancy reflect species-rich genera often having numerous restricted species. Although our estimate of expected generic occupancy is based on species richness, lower-than-expected occupancy for high-richness genera should not be an artifact of that. One reason is that just having two high-occupancy species accounts for much of the pattern (fig. 7), and species-rich genera have a higher probability of having two high-occupancy species just by chance. Another reason is that we generally expect even species-rich genera to have few occurrences. Only 10 of the 50 intervals have a median species occupancy of two; in all others, it is one (fig. S4*B*). However, species-rich genera seem prone to including those rare species.

The scale at which we lump together collections might somehow affect the patterns we document. However, if we repeat these analyses by lumping together collections within 1 km, then we achieve essentially the same results and reach the same conclusions.

Our minimum occupancy criterion (i.e., one locality per genus) offers a control for oversplitting species within genera. A different taxonomic problem is the possibility of "wastebasket" genera. These could drive this pattern if researchers nonrandomly lump together rare contemporaneous species into polyphyletic genera. However, it seems to be more typical for such genera to be distributed widely over time (Plotnick and Wagner 2006). Moreover, it seems that such genera are most apt to be used for genus-only identifications rather than for specimens identified at the species level (Wagner et al. 2007). Because our study uses only occurrences identified with specific identifications, this cannot be a factor.

Yet another possibility is that inconsistencies in sampling in the fossil record might drive this pattern. However, the global results are replicated within each of the major taxonomic groups, despite the fact that those groups represent a range of sampling rates (Foote and Sepkoski 1999). These taxa also exhibit a wide range of skeletal complexity (Schopf et al. 1975) and show a range of propensities for homoplasy (Wagner 2012). Thus, it is not likely that our results separate complex genera with easily distinguished species from simple genera with easily conflated species within, say, only gastropods. Moreover, differences in the effects of homoplasy cannot explain the association between deviations from expected generic occupancy and rock units occupied. Finally, we also find these basic patterns within North America or Europe alone. This indicates that nonrandom sampling of easily accessible and/or long-studied rocks (Sheehan 1977) is not driving the pattern; we are not getting densely sampled European genera separating out from poorly sampled Australian ones in the European-only (or North American-only) results.

Our two primary results, that is, that genera occupying more sites than expected occur in high numbers of rock units within their geographic ranges and that there is a negative association between species richness and deviations from expected generic occupancy, raise an important question: Does short-term macroecological success come at the expense of short-term macroevolutionary success, or vice versa? The Swiss cheese model offers an explanation for this apparent dichotomy (Rapoport 1982; Hurlbert and White 2005, 2007). We usually think of allopatric speciation as happening on the outer rim of species ranges. However, under a Swiss cheese model, the air bubbles within species ranges represent additional peripheries that might allow allopatric speciation. Moreover, the factors encouraging holes might encourage isolation, which in turn makes it easier for selection and drift to fix new morphotypes (Sanderson 1989; Servedio and Kirkpatrick 1997). Analogous scenarios have been invoked to explain elevated speciation associated with restricted geographic ranges and sexual selection in orchids (Hodges and Arnold 1995). This is also consistent with Foote et al.'s (2016) finding that broad geographic ranges for genera correlate with among-species geographic dispersion.

Conversely, cheddar cheese distributions would work against allopatric speciation models. Dense occupation of a range would effectively decrease the overall periphery of a geographic range. Greater adjacency between populations would encourage gene flow, which would demand stronger reinforcing selection for incipient species to remain independent (Servedio and Kirkpatrick 1997). Moreover, the niche breadth that would favor dense occupation of geographic ranges could reduce the intensity of reinforcing selection and thus make it easier for gene flow to prevent complete speciation (Servedio and Noor 2003; Hoskin et al. 2005).

The apparent disassociation between unexpectedly high genus-level occupancy and average subsampled species richness contradicts Brown's (1984) suggestion that traits encouraging high occupancy should also encourage speciation. However, Brown's model might still apply if we are contrasting closely related species (e.g., Wagner and Erwin 1995; Goldberg et al. 2011) and if we focus on geographic span. If two species have similar occupation densities within those ranges, then the one with the greater geographic range will have more periphery. Moreover, geographic range size should affect evolutionary potential over longer terms than the bins analyzed here. Many paleontological studies show negative correlations between extinction risk and geographic range size (e.g., Anstey 1986; Jablonski 1986, 1987; Miller 1997; Aberhan and Baumiller 2003; Jablonski and Hunt 2006; Kiessling and Aberhan 2007; Liow 2007; Foote et al. 2008; Harnik 2011; Heim and Peters 2011; Hopkins 2011; Foote and Miller 2013). Thus, broad geographic distribution with low occupancy might foster both high speciation within one interval and survival into the next interval. This would represent a difference between macroevolutionary success (i.e., numerous progeny and/or prolonged survival) and unusual

macroecological success (i.e., high occupancy, given geographic ranges, and species richness). In other words, our results suggest that within-interval macroecological success is decoupled from macroevolutionary success in the short-term and possibly over the long term.

Future Directions

Although Linnaean taxonomy often is a good substitute for phylogeny (Soul and Friedman 2015), one obvious next step is to examine occupancy patterns in a phylogenetic context. Two studies (Wagner 2000; Carotenuto et al. 2010) indicate that occurrences and occupancy do show strong phylogenetic signal, which corroborates our interpretation of high occupancy being trait based. However, these results have implications for phylogenetic studies themselves. Researchers have begun using fossilized birth-death (FBD) analyses (e.g., Heath et al. 2014) for analyses of fossil taxa (e.g., Cau 2017; Wright 2017), in which sampling intensity affects both the likelihood and prior probabilities of phylogenies (e.g., Huelsenbeck and Rannala 1997; Foote et al. 1999; Wagner 2000). As noted above, occupancy is nearly identical to paleobiological concepts of sampling intensity (Liow 2013). Thus, FBD models should allow for occupancy and sampling rates to be randomly distributed across phylogeny. An even more general implication of our results is that macroecological theory should play a role in paleobiologists' attempts to model sampling from the fossil record.

Our results also have implications for conservation biology. Anthropogenic homogenization of environments could be hurting the evolutionary potential of species-rich clades with many locally specialized species. Moreover, our Swiss cheese + peripheral isolation model requires that some holes in ranges ultimately include habitable regions. This is much less apt to be the case in the modern world than in the past (e.g., Lyons et al. 2016).

Conclusions

Inequality in occupancy patterns among marine fossil genera cannot be explained solely by inequalities in species occupancy patterns and species richness among genera. Moreover, elevated occupancy among genera correlates with the number of stratigraphic formations in which constituent species occur but not with the maximum geographic span encompassed by those species or the number of species in the genus. This suggests that macroecological success (high occupancy) and macroevolutionary success (numerous species) are decoupled during marine evolution. In other words, macroecological success might be a trade-off for macroevolutionary success when the traits that permit members of a genus to occupy many environments (and thus ubiquity in the fossil record) also reduce the potential of those members to leave additional daughter taxa.

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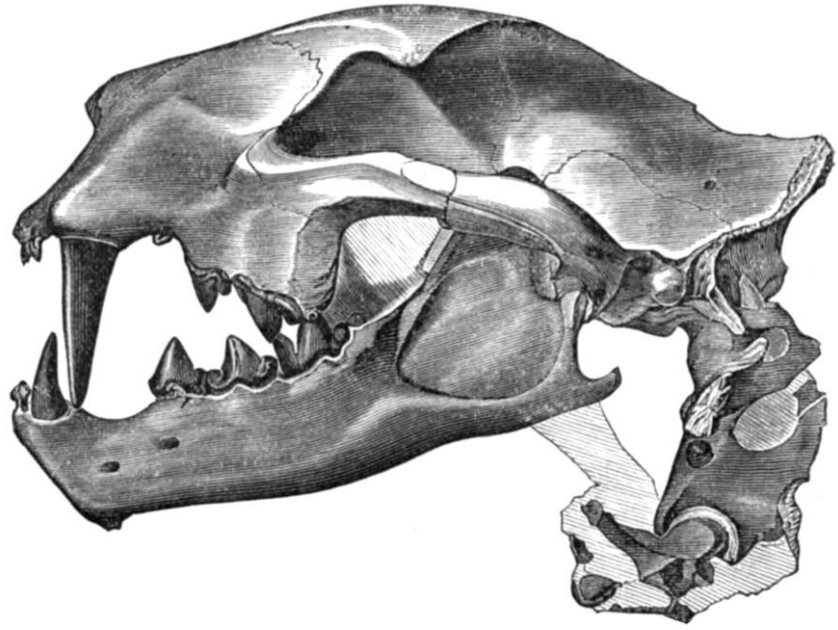

"In *Nimravus* the superior canine begins to have the enlarged size of the sabre-tooths, but its form is peculiar in the *N. gomphodus*, being spike-shaped rather than sabre-shaped." From "On the Extinct Cats of America" by E. D. Cope (*The American Naturalist*, 1880, 14:833–858).