



## Contrasting patterns and connections of rock and biotic diversity in the marine and non-marine fossil records of North America

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### ABSTRACT

Macrostratigraphy uses packages of continuous sedimentation that are bound by hiatuses of non-deposition, erosion, or alternations between environments/lithologies to characterize spatiotemporal patterns of sedimentation. Previous work has linked the macrostratigraphy of marine shelf environments to many different macroevolutionary patterns in the marine animal fossil record. Here we use an improved macrostratigraphic database for North America, combined with fossil occurrence data in the Paleobiology Database, to show that macroevolutionary and macrostratigraphic patterns are correlated more strongly in marine environments than in non-marine environments. We also test the hypothesis that the temporal distribution of lithological diversity (measured as evenness, similar to ecological evenness based on the number of lithostratigraphic units with a given lithologic type within each time interval) has a relationship to genus-level taxonomic diversity in both the marine and non-marine realms. Uneven sampling of lithologies and their corresponding depositional environments can bias our perception of taxonomic diversity by causing taxa from poorly sampled environments to be underrepresented in the fossil record. Our results show a negative correlation between lithologic evenness and marine vertebrate generic richness – less even sampling of lithologies corresponds to a higher observed taxonomic richness, and no correlation with lithologic evenness and non-marine diversity measures. This suggests a difference in the relationship between biologic and sedimentary processes at work in the marine and non-marine realms, and possibly differences in the magnitude of the bias imposed by the rock record on the underlying biologic patterns.

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### 1. Introduction

A growing body of research has repeatedly demonstrated correlated dynamics of marine metazoan evolution and sedimentary deposition on geologic timescales (e.g., Raup, 1976; Sepkoski, 1976; Peters and Foote, 2001; Smith, 2001; Smith et al., 2001; Peters, 2005, 2008a, 2008b; McGowan and Smith, 2008). Recent investigations strongly suggest that, rather than simply being a sampling artifact caused by a heterogeneous rock record, the strong correlation between biotic and sedimentary patterns is “real” and the result of direct responses to a single influencing factor (the “common-cause” hypothesis; Peters, 2008a; Hannisdal and Peters, 2011; Peters and Heim, 2011). For example, changes in sea-level would change the area of epicontinental seas, which directly determines area available for both biotic habitats and sediment accommodation in similar ways (Newell, 1952; Simberloff, 1974; Crampton et al., 2011).

Links between the rock and fossil records are strengthened when organisms are stenotopic, having narrow affinities for particular environments, as reflected by their preferred sedimentary environments.

For example, Peters (2008a) demonstrated that some of the largest scale patterns of marine biodiversity over the Phanerozoic (e.g., rise and fall of “evolutionary faunae” Sepkoski, 1981) could be directly related to differences between the temporal and spatial distributions of carbonate and siliciclastic lithofacies. Specifically, the evolutionary dynamics of stenotopic organisms, particularly those with narrow affinities for specific sedimentary environments, track the dynamics of those environments themselves.

A link between habitat heterogeneity and taxonomic diversity is another way in which the geologic processes might directly influence living organisms to yield correlated patterns in the rock and fossil records. Habitat heterogeneity over geographic space is a strong determinant of taxonomic richness within modern non-marine settings (e.g., Kerr and Packer, 1997; Guégan et al., 1998; Jetz and Rahbeck, 2002; Báldi, 2008) and marine communities (Heck and Wetstone, 1977; Levin et al., 2001; Ellingsen, 2002; Matias et al., 2010) at various geographic scales (see Rosenzweig, 1995; Tews et al., 2004 for reviews). Specifically, heterogeneity has been shown to have a stronger influence on regional taxonomic richness (e.g., beta-diversity) than does habitable geographic area in non-marine nature preserves (Báldi, 2008), primary productivity in birds (Jetz and Rahbeck, 2002) and mammals (Kerr and Packer, 1997), and distance between benthic sample sites (Ellingsen, 2002).

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Similarly, variation of depositional environment is correlated positively with sampled taxonomic richness in the fossil record (Rosenzweig, 1995; Wall et al., 2009, 2011; Crampton et al., 2011), but this relationship raises the possibility that our understanding of fossil taxonomic richness will be distorted when environments are not proportionally represented in the rock record. There are several reasons why dominance of a small number of environments in the sedimentary record could influence sampled taxonomic richness when taxa have narrow environmental affinities. In the simplest case, if some environments are entirely absent from the sedimentary record, taxa restricted to those environments will be absent from the fossil record, as with the taphonomic megabiases of the Cenomanian/Turonian event (Smith et al., 2001). Even if all environments are sampled, sampled taxonomic richness can be distorted if fossil presence in the rock record is uneven. However, the potential for this distortion is predicated on taxa being restricted to one or a few environments. Certainly, if all taxa inhabited, in life, all sampled depositional environments, then the distribution of those environments will have no direct effect on sampled taxonomic richness.

Empirical studies do confirm stenotopy in modern benthic marine communities where diversity at several geographic scales is strongly related to sediment grain-size, and specifically to heterogeneity of grain-size (e.g., Etter and Grassle, 1992; Ellingsen, 2002; Ellingsen and Gray, 2002). Many benthic marine organisms are deposit feeders and process sediment to acquire food, and the narrow range of sediment grain-sizes they can process limits their environmental distributions (e.g., Etter and Grassle, 1992). The link between non-marine organisms and sediments or depositional environments is less clear. Most metazoan taxa preserved in non-marine deposits (e.g., vertebrates) are more vagile than benthic marine invertebrates (many of which are sessile), and depend less on the sediment for food or shelter. We might therefore expect a weaker relationship between environmental heterogeneity (as measured by sedimentary characteristics) and non-marine taxonomic richness. Of course, there are clear relationships between non-marine habitat heterogeneity and taxonomic richness. But the parameters that characterize these non-marine habitat heterogeneity (e.g., temperature, vegetation, precipitation) are not likely to be directly reflected by broad lithologic categories in the rock record. Therefore, comparing and contrasting patterns of environmental heterogeneity and taxonomic richness in marine and non-marine settings might better resolve the interactions between the rock record and the fossil record.

Here, we leverage the Paleobiology Database (PALEODB; <http://paleobd.org>) and the Macrostrat Database (MACROSTRAT; <http://macrostrat.org>) to explore the relationship between environmental heterogeneity and

sampled taxonomic richness in both the marine and non-marine rock and fossil records of North America. These databases facilitate comparison of marine and non-marine realms because they store equivalent data for each. We restrict our study to the Late Cretaceous–Pliocene of North America because MACROSTRAT is particularly and comparably complete for this region and time interval with respect to both marine and non-marine rocks. 91.56% of PALEODB collections are matched to MACROSTRAT lithologic units of this interval.

## 2. Materials and methods

### 2.1. Lithologic and macrostratigraphic data

MACROSTRAT contains information regarding lithology and depositional environment for rock units, as well as their temporal and spatial extents. Data used in this study originated from the stratigraphic columns of widely used correlation charts of the United States and Canada (see Fig. 1) (Childs, 1985; Salvadore, 1985; Gabrielse and Brookfield, 1988; Stott, 1991; Trettin, 1991). MACROSTRAT data comprise gap-bound packages, which are genetically related sets of sedimentary units bounded above and below by temporal gaps, typically on the order of 1–3 Myr in duration (Peters, 2006b, 2008b). These gaps represent areas of non-deposition, erosion, or alternate-realm depositions, such as marine incursions into a non-marine package and vice versa (Peters, 2006b, 2008b). MACROSTRAT allows quantitative comparisons of lithology, depositional environment, and other rock-based information in the marine and non-marine sedimentary records because it contains similar data (e.g. dates, lithology, depositional environment, etc.) from both realms.

In this study, we used dominant and subordinate lithology information from MACROSTRAT as a proxy for depositional environment because comparable data are available in that form for the marine and non-marine realms. The categorization of a unit's dominant and subordinate lithologies is qualitative, but was taken from the original correlation charts and represents the major lithologies that are visible in outcrop or core and recognizable by field geologists. Dominant lithologies make up the majority of the unit and subordinate lithologies are successively smaller components. Furthermore, a single unit can have multiple dominant lithologies. For example, the estuarine deposits of the Paleogene Sagavanirktok Formation in northern Alaska have dominant lithologies of siltstone and shale with subordinate lithologies of sandstone, coal and conglomerates. MACROSTRAT currently contains 54 possible sedimentary lithologies. For each time interval, we determined total numbers of gap-bound packages, lithologic units contained in those packages, and lithology types that make up those

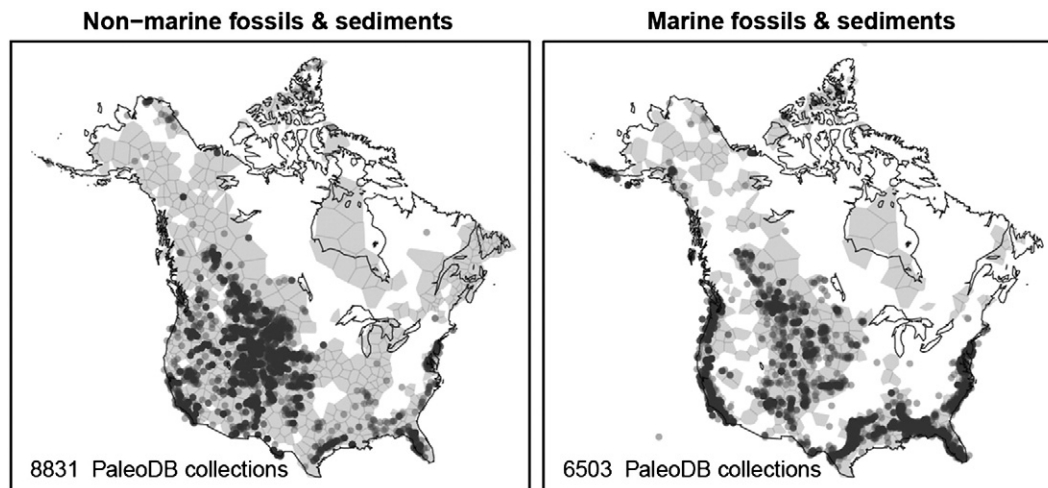


Fig. 1. Paleobiology and Macrostrat Databases. Paleobiology Database collections (circles) and polygons around Macrostrat columns (shaded) for the marine and non-marine of North America.

units using MACROSTRAT. We determined these data separately for marine and non-marine environments.

## 2.2. Measuring lithologic heterogeneity

We measured environmental variation as the proportional representation of each lithology within a time interval. Evenness ranges from 0.0 to 1.0, where 1.0 is completely even with all lithologies contributing an equal proportion of lithologic units to the total number of units in the time period, and lower values indicating that one or a few lithologies dominate. An evenness value of zero indicates that there is only one lithology represented within the interval. Note that the evenness of lithologies preserved in the available rock record is a composite measure of the true distribution of ancient depositional environments, modified by the relative preservation and sampling of those environments. For example, if an interval were dominated by one or a few lithologies, this could reflect either the dominance of one or a few depositional environments in the ancient geosphere or the preferential preservation of those environments in the available rock record.

We applied an evenness metric that is commonly used by ecologists to describe the relative abundances of species within a community, the probability of interspecific encounter (PIE; Hurlbert, 1971). We chose PIE because it is an intuitive measure of evenness and not biased by sample size (Olszewski, 2004). Thus, we calculated lithologic evenness within one time interval as:

$$\text{PIE} = \left( \frac{N}{N-1} \right) \left( 1 - \sum_{i=1}^S \left( \frac{N_i}{N} \right)^2 \right)$$

where, within that time interval,  $S$  is the total number of lithology types,  $N_i$  is the number of lithologic units of the  $i$ -th lithology type, and  $N$  is the total number of lithologic units of all types. We considered both dominant and subordinate lithologies and in this calculation, subordinate lithologies were weighted as half a lithology type in the calculation of  $N_i$ .

## 2.3. Fossil occurrence data

The PALEODB contains user-entered information concerning published collections of fossil taxa (Fig. 1) along with integrated geologic, geographic, temporal, and other available information (Alroy et al., 2001), usually from published faunal lists. We determined total sampled-in-bin genus richness for vertebrates and all taxa within each interval from genus occurrences from the PALEODB. The PALEODB mirror at the University of Wisconsin-Madison was queried March 11, 2012 for Late Cretaceous–Pliocene in North America with all default PALEODB download form options except extant and informal taxa were allowed.

## 2.4. Timescale

We confined our analysis to the last 100 Ma, the Late Cretaceous (Cenomanian) to the Pliocene. We used a total of 21 time intervals, mostly geologic stages, ranging from 1.9 to 12.9 Myr each, with a median duration of 4.2 Myr (Table 1S). The time intervals used here reflect the time scale used by the geologists who originally compiled the lithologic data contained in MACROSTRAT. Although the use of unequal time intervals can induce artificial correlation between time-series (e.g., rock and fossil records), the ages of lithologic packages could not be resolved to any finer timescale, so this “natural” time scale minimizes artificial package extension by lumping packages into extended temporal bins.

## 2.5. Correlation between lithologic evenness and taxonomic richness

We calculated the correlation of total numbers of distinct lithologies and lithologic evenness with taxonomic richness per time interval using

Pearson's product-moment ( $r$ ) and Spearman's rank-order ( $\rho$ ) correlation coefficients. All correlation analyses were performed on time-series data of each of the above variables, using time-series that were temporally de-trended by taking the first-differences (e.g., Heim and Peters, 2011). Though generalized differences (McKinney, 1990) have been used in recent studies (i.e. Benson and Butler, 2011; Lloyd et al., 2012), first differences overcompensate for autocorrelation and will not cause false positives when there is no serial correlation. Therefore first differences are a more conservative method of de-trending the data than generalized differences. Correlations using generalized differences had minor and variable disparities from the first difference correlations, but not substantial enough to change our overall conclusions. For these reasons, we present only first difference correlations here. To show that time bin length does not influence our conclusions, partial correlations are presented (Table 2S).

## 3. Results

### 3.1. Macrostrat and diversity

Counts of sediment packages in the non-marine and marine realms show opposing long-term trajectories, including a large decrease in the marine and increase in the non-marine during the latest Cretaceous (Fig. 2A). The number of non-marine packages shows relatively little variability throughout the Paleogene. Total numbers of lithologic units within time intervals follow similar overall patterns to those of the total packages in both environments (Fig. 2B), but with much more interval-to-interval variation throughout the Paleogene than observed for packages (Fig. 2B). This difference reflects both variability in lithologies, stratigraphic practice, and research effort. A peak in the number of

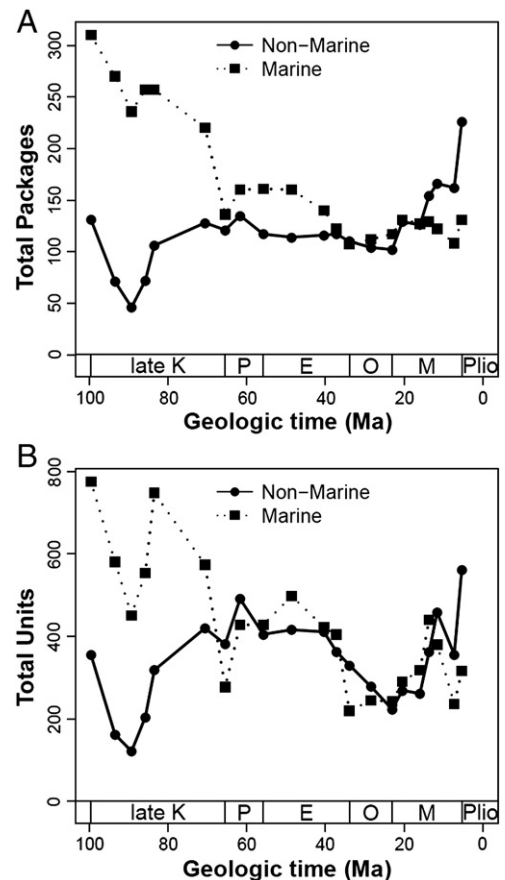


Fig. 2. Macrostratigraphic measures. A) Gap-bound packages, genetically related sets of sedimentary units, and B) individual lithologic units for the non-marine (solid line, circles) and the marine (dotted line, squares).

non-marine units is present (Fig. 2B) during the mid to late Paleocene (Selandian and Thanetian) that is mirrored in the number of packages (Fig. 2A). This peak in non-marine units is preceded in the prior interval by a substantial decrease in both marine packages and units (Fig. 2). The Miocene is a time of similar unit totals and patterns in the two realms (Fig. 2).

Non-marine vertebrate taxonomic richness closely tracks total non-marine richness (Fig. 3A). Though a similar pattern exists between marine total and vertebrate richness, the magnitude difference is much more severe (Fig. 3B). The close correspondence between vertebrate and total non-marine richness is due to the overwhelming proportion of total non-marine richness attributable to vertebrates (67% mean over the time interval), as compared to 4.9% in the marine. Non-marine richness shows a peak at the Paleocene/Eocene boundary. After an Eocene decline in richness, non-marine richness steadily (though not monotonically) increases towards the Recent (Fig. 3A). Marine total richness shows a peak during the latest Cretaceous (Fig. 3B), which is during a time of slow decline in vertebrate richness. During the Cenozoic, the marine shows equivalent peaks at the mid-Eocene, early Miocene, and Pliocene interspersed with equivalent minima during the mid-Oligocene and late Miocene, with no increase in the overall trend in total richness but a slight increase in vertebrate richness (Fig. 3B).

Though non-marine vertebrate richness is strongly correlated with total richness, we found no significant correlations between non-marine richness and any of the lithologic measures (Table 1). Statistically significant, though weak correlations exist between total marine packages and marine vertebrate and total richness, though total richness lacks significant rank-order correlation (Table 2). In the marine realm, total

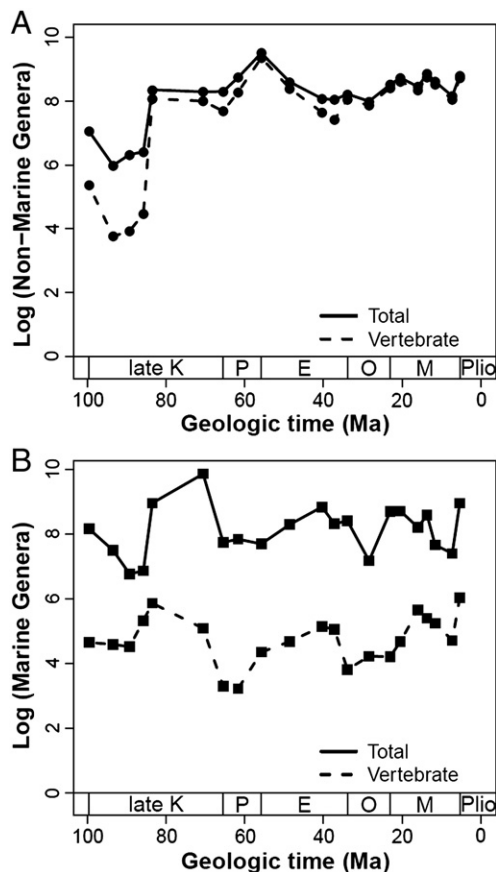


Fig. 3. Taxonomic richness. Total generic richness (solid line) and total vertebrate richness (dashed lines) for the natural log-transformed A) non-marine data (circles) and B) marine data (squares).

Table 1

Non-marine comparisons of total richness, vertebrate richness, total packages, and total units. First difference Pearson's product-moment correlation coefficient ( $r$ ) on top right and Spearman's rank-order correlation coefficient ( $\rho$ ) on bottom left of each section. Bold correlations  $p \leq 0.05$ ,  $p$ -values can be found in Table 3S.

	Total richness	Vertebrate richness	Total packages	Total units
Total richness		<b>0.9895</b>	0.2375	0.1761
Vertebrate richness	<b>0.9699</b>		0.1880	0.1338
Total packages	0.3266	0.3078		<b>0.9191</b>
Total units	0.2992	0.2571	<b>0.8435</b>	

Table 2

Marine comparisons of total richness, vertebrate richness, total packages, and total units. First difference Pearson's product-moment correlation coefficient ( $r$ ) on top right and Spearman's rank-order correlation coefficient ( $\rho$ ) on bottom left of each section. Bold correlations  $p \leq 0.05$ ,  $p$ -values can be found in Table 4S.

	Total richness	Vertebrate richness	Total packages	Total units
Total richness		0.2288	<b>0.4907</b>	0.4119
Vertebrate richness	0.2376		<b>0.5950</b>	<b>0.6311</b>
Total packages	0.2828	<b>0.5619</b>		<b>0.8557</b>
Total units	0.3609	<b>0.6391</b>	<b>0.8379</b>	

lithologic units, while not correlating significantly with total richness, do correlate with vertebrate richness (Table 2).

### 3.2. Heterogeneity measures and diversity

Lithologic evennesses in the non-marine and marine realms have similar long-term trajectories (Fig. 4). Lithologic evenness in both realms is relatively invariant throughout the Cenozoic, with no secular trends over the past 65 Myr. The only statistically significant relationship between lithologic heterogeneity and taxonomic richness is a weak negative correlation between marine vertebrate richness and the evenness of marine lithologies (Tables 3 and 4).

### 3.3. Non-marine and marine comparisons

The congruence of time-series of sedimentary packages suggests a relationship between sedimentation processes in the marine and non-marine realms of North America in the Cenozoic (Fig. 2). Specifically, the total number of non-marine packages trend is opposite that of total marine packages in the long term, though the two time-series are positively correlated in interval-to-interval changes (Table 5). Total non-marine diversity and vertebrate richness are

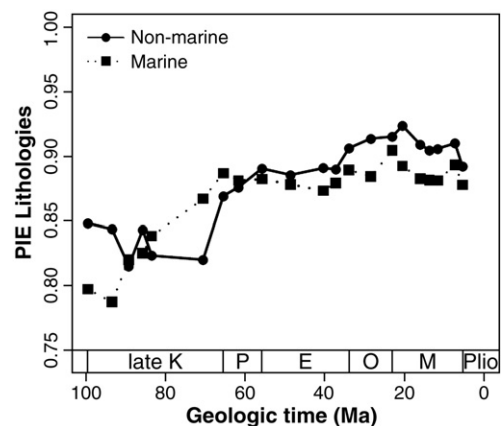


Fig. 4. Evenness metrics in the non-marine and marine. Evenness of lithologies in the non-marine (solid line) and marine (dotted line).

**Table 3**

Non-marine comparisons of lithological evenness (PIE), total and vertebrate richness. First difference Pearson's product-moment correlation coefficient ( $r$ ) on top right and Spearman's rank-order correlation coefficient ( $\rho$ ) on bottom left of each section. Bold correlations  $p \leq 0.05$ ,  $p$ -values can be found in Table 5S.

	PIE	Total richness	Vertebrate richness
PIE		0.0293	0.0100
Total richness	0.0331		<b>0.9895</b>
Vertebrate richness	−0.0211	<b>0.9699</b>	

**Table 4**

Marine comparisons of lithological evenness (PIE), total and vertebrate richness. First difference Pearson's product-moment correlation coefficient ( $r$ ) on top right and Spearman's rank-order correlation coefficient ( $\rho$ ) on bottom left of each section. Bold correlations  $p \leq 0.05$ ,  $p$ -values can be found in Table 6S.

	PIE	Total richness	Vertebrate richness
PIE		0.0324	− <b>0.5686</b>
Total richness	0.0737		0.2288
Vertebrate richness	− <b>0.5263</b>	0.2376	

also significantly, though weakly, correlated with total marine packages, while total non-marine packages correlates with total marine richness but not vertebrates (Table 5).

## 4. Discussion

### 4.1. Macrostratigraphy and diversity

We found marine sampled-in-bin richness to be significantly correlated with the total number of packages within intervals, as has been described previously (Peters, 2006a, 2006b; Heim and Peters, 2011; Peters and Heim, 2011). However, non-marine richness was not significantly correlated with total number of packages, suggesting little influence, if any, of this measure of the rock record on non-marine biologic diversity. Likely, the distinctly mobile vertebrates that make up a greater percentage of non-marine taxonomic richness may not be as strongly associated with their depositional environments as their marine invertebrate counterparts. Interestingly, our result differs from that of Butler and Barrett (2008) who found that many groups of Cretaceous herbivorous dinosaurs were associated with one or another "terrestrial", "coastal", or "marine" depositional environments, or found less often in them. However, differences in time, scale, and their associations between taxa and specific facies (which contrast with our focus on lithological evenness in general) may lead to this distinction.

Despite the weak first-difference correlations overall, there are particular spans of time where the two records appear to covary. For instance, both the total number of non-marine genera and total non-marine packages/units increase during the early Paleocene, though the non-marine genera then continue to increase through the Paleocene/Eocene boundary while the non-marine packages/

**Table 5**

Non-marine and marine comparisons. First difference Pearson's product-moment ( $r$ ) and Spearman's rank-order ( $\rho$ ) correlation coefficients for comparisons between marine (top) and non-marine (left) packages, total and vertebrate richness. Bold correlations  $p \leq 0.05$ ,  $p$ -values can be found in Table 7S.

Coefficients	Non-marine/ marine	Total packages	Total richness	Vertebrate richness
Pearson's product-moment correlation $r$	Total packages	<b>0.5284</b>	0.4232	0.3949
	Total richness	0.2283	0.1407	0.1884
	Vertebrate richness	0.2614	0.1781	0.1937
Spearman's rank-order correlation $\rho$	Total packages	<b>0.5533</b>	<b>0.5553</b>	0.3213
	Total richness	<b>0.4949</b>	0.3398	0.1759
	Vertebrate richness	<b>0.4957</b>	0.4090	0.2075

units remain constant (Figs. 2 and 3A). The Neogene marine total package and both richness measures have similar trends (Figs. 2B and 3B). It is therefore possible that the connection between the rock and fossil records may be complex, variable through time, and variable depending on time scale.

### 4.2. Heterogeneity measures and diversity

Lithologic heterogeneity was measured as evenness within each stage and compared to sampled-in-bin diversity of both the marine and non-marine realms. Marine richness may be driven by changes in dominance of particular environment types in the rock record. Expansion of available open niche space, and the creation of new niches as a consequence, would serve as real biological causes for such a richness trend. When a single type of environment becomes dominant, inhabitants of that environment are expected to persist regionally, whereas the loss of certain environments could cause the regional extinction of endemic inhabitants of those environments. This would more likely be the case in the marine, where stenotopic organisms have a much closer association with their immediate depositional environment, which is often determined by the original habitat.

Contrary to these ideas, only marine vertebrate richness was significantly correlated with lithologic evenness (Table 4). Recent work in marine tetrapods has shown a relationship between the amount of shallow marine shelf-area (based on sea-level change proxies) and the taxonomic richness in these groups. This relationship is lost in open ocean organisms, where sampling is a more likely cause of changes in richness (Benson and Butler, 2011). The shallow marine tetrapod relationship is congruent with our findings of a correlation between our lithological proxy for environment and marine vertebrate data.

The overall lack of correlation in other comparisons could be due to one or more of several factors. First, there may be a weak correspondence between the broad categories of lithology in MACROSTRAT and organism habitats. For example, it is possible that some lithologic categories subsume several distinct habitats, and that some habitats may fall into several lithologic categories. Second, even if lithologic categories faithfully indicate habitats, it is possible that our measure of lithologic evenness does not accurately describe environmental heterogeneity. In modern ecological studies, habitat heterogeneity is commonly measured using a combination of numerous parameters, e.g. vegetation gradients and vertical structure in rainforests (Williams et al., 2002) or plant species richness and biomass in sea grass (Heck and Wetstone, 1977), that are not available from MACROSTRAT. Third, the relationship between lithologic heterogeneity and taxonomic richness might not be linear, but may be a complex function dependent on the underlying ecological abundance distributions of the organisms within the sampled environments. Specifically, overrepresentation of dominant sedimentary environments increases the likelihood of sampling rare taxa in the living community of those environments, and reduces the probability of sampling rare taxa from underrepresented environments. Therefore, if the overrepresented environments were less taxonomically rich or had substantially more uneven ecological abundance distributions, then sampled taxonomic richness would be lower than if lithologies were represented evenly. This could be further tested by repeating these analyses on communities for which the abundance distributions are known. Fourth, spatial transport of skeletal material of organisms from their original habitats could reduce the correspondence between the fossil and rock records. For example, apparent richness within a homogeneous depositional environment might be distorted if it included an allochthonous assemblage, weakening a positive or strengthening a negative correlation with overall evenness. Such a cause for a lack of correlation would be more frequent in fluvial and deltaic deposits, for instance, but not restricted to them. Finally, this could represent a real pattern, and environmental heterogeneity might not be an important determinant of taxonomic richness over the temporal and spatial scales analyzed in this study.

When compared to highly mobile vertebrates, sessile invertebrates are hypothesized to be more likely affected by changes in their immediate environments, being constantly encompassed by the habitat in which they lived. Therefore the lack of correlation between total marine richness and marine lithologic evenness (Table 2) is surprising because the marine fossil record is largely composed of invertebrates (see Fig. 3B). The significant positive correlation between marine packages and marine vertebrate richness (Table 4) could be disproportionately influenced by a sampling bias, such as focused collections from marine vertebrate sites and concentrations of vertebrate fossils caused by sequence-stratigraphic cycles (Banerjee and Kidwell, 1991; Peters et al., 2009). The preferential collection of vertebrate fossils would increase richness without necessarily increasing the number of units or lithology types, while sequence-stratigraphic cycle concentrations due to decreased sedimentation would also limit the number of units/lithology types for that time period. Finally, marine vertebrates may simply be more closely related to their habitats than might be expected. Studies with larger temporal and spatial scales have made similar claims of environmental bias affecting richness curves in the marine realm (Raup, 1976; Peters and Foote, 2001; Smith, 2001; McGowan and Smith, 2008; Wall et al., 2009). More focused study on depositional environments and their associations with taxa, similar to that already accomplished at large geographical scale with herbivorous dinosaurs (Butler and Barrett, 2008), and increasing the amount of taphonomic data available in these databases will allow further study of this possible richness bias. As MACROSTRAT grows and improves, more specific environmental calculations may also be possible.

#### 4.3. Non-marine and marine comparisons

The marine and non-marine realms are often separated in large-scale analysis, commonly due to variations in data-collection and publication methods. Recent database analyses have allowed for comparable data from the marine and non-marine to be examined. Here we find a previously unexamined connection that exists between the non-marine and marine. Short-term variation in package totals correlate across the realms (Table 5). This will require further investigation, but is a very intriguing result from these two datasets.

Though one of the first of its kind, the study presented here shows the types of questions paleontologists can ask with the resources now available. Future studies could investigate other potential reasons for correlated patterns of sedimentary and biological change, and in particular those that might uniquely affect either marine or non-marine realms. In the future, large scale comparative analyses of the rock and fossil records will continue to shed light on the similarities and differences between the evolutionary development of life on land and in the ocean, and how large-scale changes have not only affected biotic processes, but the way these processes are recorded on the land and in the sea.

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#### Appendix A. Supplementary data

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.palaeo.2012.10.006>.

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