



General models of ecological diversification. I. Conceptual synthesis

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Abstract.—Evolutionary paleoecologists have proposed many explanations for Phanerozoic trends in ecospace utilization, including escalation, seafood through time, filling of an empty ecospace, and tiering, among others. These hypotheses can be generalized into four models of functional diversification within a life-habit ecospace framework (functional-trait space). The models also incorporate concepts in community assembly, functional diversity, evolutionary diversification, and morphological disparity. The redundancy model produces an ecospace composed of clusters of functionally similar taxa. The partitioning model produces an ecospace that is progressively subdivided by taxa along life-habit gradients. The expansion model produces an ecospace that becomes progressively enlarged by the accumulation of taxa with novel life habits. These models can be caused by a wide range of ecological and evolutionary processes, but they are all caused by particular “driven” mechanisms. A fourth, neutral model also exists, in which ecospace is filled at random by life habits: this model can serve as a passive null model. Each model produces distinct dynamics for functional diversity/disparity statistics when simulated by stochastic simulations of ecospace diversification. In this first of two companion articles, I summarize the theoretical bases of these models, describe their expected statistical dynamics, and discuss their relevance to important paleoecological trends and theories. Although most synoptic interpretations of Phanerozoic ecological history invoke one or more of the driven models, I argue that this conclusion is premature until tests are conducted that provide better statistical support for them over simpler passive models.

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Accepted: 5 January 2016

Introduction

The history of life is marked by innumerable ecological trends for paleontologists to interpret. Diversity—both globally (Sepkoski 1981; Alroy et al. 2008) and within individual assemblages (Bambach 1977; Powell and Kowalewski 2002; Bush and Bambach 2004)—has increased during the Phanerozoic, and these changes—in addition to disturbances small and large (Miller 1998; Bambach et al. 2004)—have likely forced important changes to the ecological structure (ecospace) of these biotas through time (Bambach 1983; Bambach et al. 2007; Bush et al. 2007a; Novack-Gottshall 2007b; Bush and Bambach 2011). Many of the ecological trends are so persistent and independently affect so many clades that it is difficult to argue they are not caused by fundamental ecological tendencies. For example, increases in tiering (Ausich and Bottjer 1982; Bottjer and Ausich 1986) and predation (Vermeij 1987; Aberhan et al. 2006; Huntley

and Kowalewski 2007; Bush and Bambach 2011) are so well documented that it seems obvious that ecospace has become a more enriched, more specialized, and ultimately more competitive landscape for organisms to coexist.

Yet documentation of a trend is insufficient to draw conclusions on the processes causing it (Stanley 1973b, Gould 1988; McKinney 1990; McShea 1994). This lesson was well learned after the Marine Biological Laboratory (MBL) collaborations (Raup et al. 1973; Raup and Gould 1974; Schopf et al. 1975; Gould et al. 1977; Schopf 1979), in which the use of simple stochastic models provided informative—and often counterintuitive—benchmarks to better interpret evolutionary rates, clade dynamics, diversity trends, and morphological evolution. Macroevolutionary studies have embraced this critical framework, and now routinely employ such null models, while allowing for consideration of a wide range of potential artifacts and process-driven models

(e.g., Foote 1991; Wagner 2000; Hunt 2006; Hannisdal 2007; Bapst 2013; Korn et al. 2013; Wagner and Marcot 2013; Alroy 2014; Wagner and Estabrook 2014; Hunt et al. 2015). The use of such stochastic models in evolutionary paleoecology is comparatively rare. The best known remains Valentine's "tesserae model" (1980; Walker and Valentine 1984), a simulation used to demonstrate that ecological diversification (i.e., that associated with the origin of major clades) was easier to achieve during intervals of empty ecospace.

Arguably, the main obstacle for their broader implementation is the lack of consensus on how modern ecological communities are structured (cf. Maurer 1999; Weiher and Keddy 1999; Hubbell 2001; Chase and Leibold 2003; Clark et al. 2007; Rosindell et al. 2012). Where such ecological models are used (e.g., Clark and McLachlan 2003), their model assumptions and data have often been of a resolution or context not amenable to the data of deep-time paleontology (Bennington et al. 2009). Recent developments in ecology, however, have helped bridge these differences. The discipline of functional ecology (Keddy 1992b; Díaz and Cabido 2001; Petchey and Gaston 2002; McGill et al. 2006) has confirmed that organismal functional traits (i.e., those organismal characteristics that allow organisms to interact with their biotic and abiotic environment), manifested across multiple taxa and individuals, are as important to understanding community processes (or perhaps more so) as are phylogenetic relationships (taxonomic identity), morphology, abundance, and other characteristics of taxa individually. This discipline has also developed an impressive inventory of functional diversity (disparity) statistics (e.g., Villéger et al. 2008; Mouchet et al. 2010)—having goals identical with those of the study of morphological disparity—and hypotheses suited to testing with these statistics. Given the lengthy paleontological history of such functional inferences (Savazzi 1999; Plotnick and Baumiller 2000) and our discipline's comfort with disparity concepts (Foote 1996; Wills 2001), such a confluence offers much potential for mutual insight between ecologists and paleoecologists (e.g., Villéger et al. 2011; Berke et al. 2014).

The processes (and models) addressed by functional ecologists are fundamentally similar to those studied by all community ecologists, of course, and are often conceptualized as models of community assembly rules that incorporate processes such as habitat filters (Podani 2009; Kraft et al. 2015), competitive exclusion (Fargione et al. 2003; Schwillk and Ackerly 2005; Mouillot et al. 2007), or neutral settlement from regional pools (Hubbell 2005; Rosindell et al. 2012). Most of these studies evaluate hypothesized models with one or a few functional diversity metrics and often only test whether observed data are statistically different from those expected under the proposed model, typically based on a simple permutation test. This approach is reasonable, but it ignores that all functional diversity/disparity metrics contribute information on functional (ecospace) structure (Ciampaglio et al. 2001; Mouchet et al. 2010), and thus there is value in retaining all suitable metrics when possible. However, this multivariate approach requires new techniques to conduct model selection when one wishes to compare multiple models simultaneously.

In this first of two companion articles, I summarize four general models of community assembly (neutral, redundancy, partitioning, and expansion) that collectively characterize the main mechanisms inferred in structuring ecospace, whether at the scale of ecological communities or shaping entire biotas throughout evolutionary timescales. Although they have been introduced elsewhere (Novack-Gottshall 2006; Bush and Novack-Gottshall 2012), here I synthesize their bases in ecological and evolutionary theory and describe their expected statistical dynamics. These models have the useful property that they can be distinguished by their relationships between species richness and these functional diversity/ecological disparity statistics. I also discuss their relevance to long-standing paleoecological trends and theories and conclude that although most trends in Phanerozoic ecology are consistent with one or more of the driven models, the necessary statistical tests required to substantiate these claims have not been conducted. In the follow-up article,

I demonstrate how the models can be implemented as stochastic simulations, evaluate their performance under a range of ecospace frameworks (functional-trait spaces), introduce a novel method of multimodel inference that allocates relative support across multiple multidimensional models, and apply these methods to well-preserved assemblages from the Late Ordovician (type Cincinnati).

Four Models of Ecological Diversification

Four general models of ecological structure can result whenever the number of species increases within biotas. The statistical dynamics of these models are summarized in Table 1 and represented visually in Figure 1; which is based on simulations discussed in the companion article (Novack-Gottshall 2016). Table 2 lists common multivariate ecological disparity/functional diversity statistics mentioned in the text, but other statistics ought to display dynamics similar to those summarized below. Resulting structural patterns (topologies) generated by these models can be produced by multiple mechanisms operating at different scales, including short-term ecological processes accompanying community assembly and longer-term processes involving evolution, speciation, and sorting. Because of these generalities, I describe a range of ecological and evolutionary mechanisms consistent with each model and relate each model to existing hypotheses in the community assembly, functional diversity, evolutionary diversification, and morphological disparity literature. I also discuss their relevance to long-standing perspectives on synoptic paleoecological trends across the scale of the Phanerozoic. For convenience, I describe the models in terms of species-level community assembly, but they could as easily be described in terms of large-scale evolutionary diversification. Descriptions of model dynamics summarized here are based on mathematical expectations but confirmed by the behavior of simulations in the companion article (Novack-Gottshall 2016). For consistency, the term “rule” refers to the prescribed manner in which species are added to an assemblage (i.e., the assembly rule), and

“model” refers to the resulting dynamics and topology (i.e., the dynamic statistical properties) resulting from the action of each rule.

Redundancy Model

Model Dynamics.—The model of redundancy (Table 1) occurs when successive species in a community occupy life habits that are identical to those previously occurring in that community. In a weakened form of the rule, successive life habits will be similar but not identical to preexisting ones. The general structural topology (Fig. 1B) is one of clusters of functionally identical, or similar, species (Bush and Novack-Gottshall 2012). This model generally will yield the lowest values for disparity and functional diversity statistics of the four models. Life-habit richness (H) will remain at constant low values as species are added or increase slowly, depending on the strength of the rule’s enactment. Because of significant life-habit overlap among species, statistics that measure disparity/dispersion (such as total variance [V] and functional dispersion [$FDis$]) and spacing between species (such as functional evenness [$FEve$]) will decrease asymptotically as a function of increasing species richness. Because overall occupation of community ecospace is not enlarged by the addition of successive species, statistics sensitive to outliers such as maximum range [M] and functional richness [$FRic$] will remain low and constant or increase slightly, depending on how often the rule is followed (i.e., model strength). Statistics sensitive to internal structure (i.e., clumpiness or inhomogeneity) will vary, depending on what structural component they measure. For example, functional divergence ($FDiv$) will increase, whereas mean functional distance between species (D) will decrease asymptotically.

Mechanisms.—Classical ecological theory claims that competitive exclusion prevents true life-habit redundancy among species within local communities over long timescales (Gause 1934; Fargione et al. 2003; Loreau 2004; Purves and Turnbull 2010). The recognition of substantial degrees of redundancy within living communities (Hubbell 2005; Mouillot et al. 2014) is usually attributed to conditions

TABLE 1. Summary of the four models of ecological diversification. Model dynamics are based on simulations of community assembly, in which species' life habits (functional traits) were assigned according to the model rules. However, the models are generalizable to any scale or process in which taxonomic richness increases. Listed mechanisms are non-exclusive, and include representative hypotheses spanning ecological and evolutionary processes. Models are sorted according to typical ranking of ecological disparity/functional diversity statistics (i.e., the expansion model generally has greatest values, whereas redundancy has the smallest). Strict ("str.") and relaxed ("rel.") refer to alternative implementations of the partitioning model. Statistics listed are those frequently used in the morphological disparity and functional diversity literature, although the general dynamics ought to occur for other statistics. See Table 2 for description and abbreviations of each statistic. Dynamics are reported as a function of increasing species richness (S); most dynamics reach asymptotic values at sample sizes of 50–200 species. When model rules are enacted in weakened form, dynamics will be intermediate between those of the neutral model and the relevant model.

Model	Rule	Potential causal mechanisms	Dynamics			
			Richness (H)	Disparity/dispersion ($FDis$, V , $FRic$, M)	Internal structure ($FDiv$, D)	Spacing ($FEve$)
Expansion	Successive species occupy life habits divergent from those already inhabited.	Divergence, character displacement, adaptive radiation, ecological opportunity, ecological release, key innovation, habitat colonization, increased nutrient availability, (in part: ecosystem engineering, escalation, Red Queen, seafood through time)	$\approx S$	\uparrow (fastest)	$\downarrow FDiv$	Constant
Neutral	Successive species accumulate without regard to existing life habits.	Stochasticity, random colonization from species pool	$\approx S$	\uparrow (fast)	$\downarrow Fdiv$ D constant	Constant
Partitioning	Successive species occupy life habits intermediate to those already inhabited.	Niche partitioning, specialization, coevolution, ecological fitting	rel: $\leq S$ str: $< S$	\uparrow (slow) $FRic$, M , \downarrow (slow) $FDis$, V	\downarrow	\downarrow
Redundancy	Successive species occupy life habits already inhabited.	Keystone species, intermediate disturbance, competition—colonization trade-off, emergent neutrality, habitat filtering, niche conservatism, adaptive peaks, systems stability	Constant and low	$\downarrow FDis/V$, low $FRic$, constant M	$\uparrow FDiv$, $\downarrow D$	\downarrow

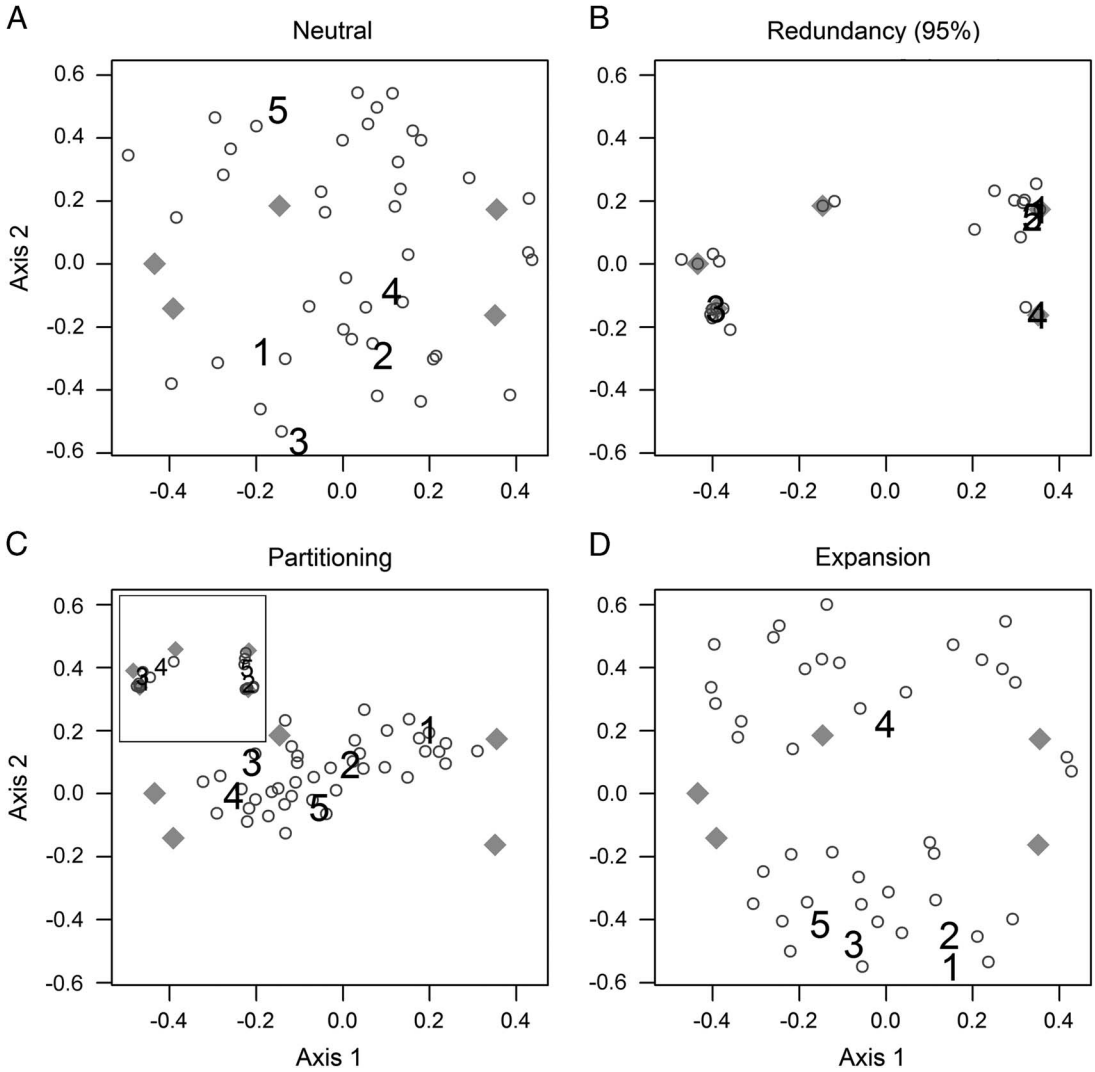


FIGURE 1. Typical examples of simulated 50-species assemblages produced by the four model rules. Assemblages are plotted on a common nonmetric multidimensional-scaling ordination space of functional traits to allow comparative evaluation of model behavior. Five gray diamonds represent common “seed” species whose life habits were assigned stochastically using an 18-character (functional-trait space) ecospace framework (modified from Novack-Gottshall 2007b), imposing a realistic constraint that each life habit could have at most two character states within a given character. Numbers illustrate the addition of five species to each assemblage (after seed species), with the remaining 40 species as hollow circles. All model rules, except redundancy, were enacted at 100%-rule following for each simulation; redundancy rules were weakened such that all successive species have habits 95% similar to preexisting ones; at 100% enactment, later life habits are limited to the “seed” species. A, In the neutral model, functional traits of all species are chosen independently at random, and the entire ecospace becomes inhabited through passive processes. B, In the redundancy model, new species have life habits similar to preexisting ones, producing an ecospace with distinct clusters. C, In the partitioning model, new species inhabit life habits intermediate to preexisting ones. This model can be enacted in a relaxed form (larger image), in which new species progressively fill in empty regions of the space originally defined by the seed species, and a strict form (inset), in which new species are restricted to gradients between preexisting species (typically leaving the center empty). D, In the expansion model, new species progressively inhabit novel life habits, producing an ecospace that expands its breadth over the simulation, while leaving the original region uninhabited.

that disrupt such competitive interactions. Well-known disruptive milieus include keystone species (Paine 1966, 1969; Terborgh 2015),

intermediate-scale environmental disturbances (Connell 1978), and predation (Stanley 2008). Spatial structure, demographic stochasticity,

TABLE 2. Description of statistics referred to in text and Table 1, listed according to the structural component that each statistic measures. These statistics are frequently used in the morphological disparity (Van Valen 1974; Foote 1993; Ciampaglio et al. 2001; Wills 2001) and functional diversity literature (Mason et al. 2005; Anderson et al. 2006; Villéger et al. 2008; Laliberté and Legendre 2010; Mouchet et al. 2010; Moullot et al. 2013), and further details on each statistic can be found in these references.

Statistic	Definition	References
Richness:		
<i>H</i> : Life-habit richness	Number of functionally unique trait combinations.	Ciampaglio et al. 2001; Novack-Gottshall 2007
Disparity/dispersion		
<i>M</i> : Maximum distance	Maximum pairwise distance between species in functional-trait space.	Ciampaglio et al. 2001; Wills 2001
<i>V</i> : Total variance	Sum of variances for each functional trait across species.	Van Valen 1974; Foote 1993; Ciampaglio et al. 2001
<i>FRic</i> : Functional richness	Minimal convex-hull volume in principal coordinates analysis (PCoA) trait-space ordination.	Villéger et al. 2008
<i>FD_{dis}</i> : Functional dispersion	Total deviance of species from the circle with radius equal to mean distance from PCoA trait-space centroid.	Anderson et al. 2006; Laliberté and Legendre 2010
Internal structure		
<i>D</i> : Mean distance	Average pairwise distance between species in functional-trait space.	Ciampaglio et al. 2001; Wills 2001
<i>FD_{div}</i> : Functional divergence	Average distance of species from the PCoA trait-space centroid.	Villéger et al. 2008
Spacing		
<i>FE_{zc}</i> : Functional evenness	Evenness of minimum-spanning-tree lengths between species in PCoA trait-space.	Villéger et al. 2008

and dispersal limitations—such as competition–colonization trade-offs that allow poorer competitors to resist extinction by virtue of higher dispersal rates—can maintain redundancy by restricting opportunities for local competitive interactions (Hastings 1980; Tilman 1994; Cornell 1999; Kinzig et al. 1999; Clark et al. 2007; Olszewski 2011). Such spatial and demographic complexities can be extended more broadly to mitigate most forms of competition (Hubbell 2001), and this argument is discussed below in the neutral model. It is worth emphasizing that Hubbell’s (2005) assumption of “functional equivalency” in neutral theory is not the same concept as functional redundancy used here, as is clarified below. Recent simulations have demonstrated that complex competitive interactions involving many species can even promote redundancy (Scheffer and van Nes 2006), an idea later termed the emergent neutrality theory (Holt 2006; Vergnon et al. 2009, 2012). A common criticism of claims of apparent redundancy is that they are superficial, an artifact of focusing on relatively few traits that obscure recognition of ecologically more important differences (Clark et al. 2007; Barabás et al. 2013; Kraft et al. 2014).

Competitive interactions are not the only factor relevant to functional redundancy. A simple process such as habitat filtering (Southwood 1977; Keddy 1992a; Poff 1997; Podani 2009; Kraft et al. 2015), wherein the strictures of settlement to or existence within a particular habitat acts as a first-order control on community membership, can restrict community membership to species sharing particular functional traits. This can be considered a form of ecological canalization. Over longer, evolutionary timescales, redundancy can also result from niche conservatism accompanying speciation events (Mayr 1942, 1963; Peterson et al. 1999; Webb et al. 2002; Wiens and Graham 2005), although this is widely expected to result in subsequent divergence (Brown and Wilson 1956; Losos et al. 2002). A weakened form of redundancy is implicit in discussion of adaptive peaks and adaptive optima (Eldredge 1989; Hansen 1997; Marshall 2006; Novack-Gottshall 2007a; Mahler et al. 2013). Convergent evolutionary pressures (Losos 2011; Segar et al. 2013;

Winemiller et al. 2015) can promote such functional redundancy, but convergence is typically only discussed when comparing geographically vicariant biotas, instead of within the individual communities considered here (but see Scheffer and van Nes 2006; Vergnon et al. 2012). It is clear that although reconciling functional redundancy with ecological theory remains among the most contentious areas of ecological research, there is little doubt that apparent redundancy is a common feature in many communities. The presence of such redundancy, regardless of its causes, has been claimed as an important factor for stabilizing ecosystems and increasing their resilience in the face of disturbances (Plotnick and McKinney 1993; Díaz and Cabido 2001; Fonseca and Ganade 2001; Guillemot et al. 2011; Gerisch 2014).

Paleoecological Examples.—Few explicit discussions of functional redundancy exist in the paleoecological literature, perhaps because of its initially poor advocacy in classical ecological theory. In an editorial of this history, Stanley (2008) argues that most benthic primary consumers are broadly functionally redundant but the high predation and disturbance prevents competitive exclusion from occurring. The concept of redundancy is most commonly invoked when discussing resilience of biotas in the face of environmental disturbances (Nagel-Myers et al. 2013), especially mass extinctions. For example, a recent study (Foster and Twitchett 2014) claimed little net ecological impact from the late Permian mass extinction because all but one life habit persisted globally into the Early Triassic. (But see Dineen et al. [2014, 2015], who used a more multidimensional ecospace framework to demonstrate substantial differences in functional richness and evenness during these intervals.) Redundancy, or lack thereof, has been a broadly implicated causal factor in the extinction of individual lineages (Dick and Maxwell 2015) and entire biotas during mass extinctions (Roopnarine et al. 2007; Mitchell et al. 2012). At larger scales, many discussions of provinciality, sea level, habitable shelf area, and relationships between alpha and beta diversity as drivers of global diversity (e.g.,

Valentine and Moores 1970; Valentine 1973; Bambach 1977; Boucot 1983; Sepkoski 1988; Peters 2008; Holland 2010; Hautmann 2014; Na and Kiessling 2015) have assumed implicitly that vicariant populations retained similar life habits during geodispersal.

Partitioning Model

Model Dynamics.—The model of partitioning (Table 1) occurs when successive species in a community occupy life habits intermediate to those previously occurring in the community. The general structural topology (Fig. 1C) depends in part on how “intermediate” is defined. A “strict” definition produces distinct life-habit gradients, whereas a “relaxed” definition progressively fills in the central region of the ecospace (functional-trait space), although in both cases new species are occupying previously unoccupied portions of remaining ecospace (Bush and Novack-Gottshall 2012). Dynamically, the slope of H on species richness will be <1 initially, reaching an asymptote when potentially inhabitable life-habit gradients become saturated. In the relaxed version, this rate is just slightly <1 , whereas it is substantially less in the strict model. Because successive species inhabit more finely intermediate life habits, disparity metrics (such as V and $FDis$) will decrease asymptotically as a function of increasing species richness, generally with a faster decline in the more constrained strict version. Like the redundancy model, occupied ecospace will remain nearly constant and increase asymptotically at low to intermediate rates because overall community ecospace is not substantially enlarged by successive species. Statistics sensitive to internal structure ($FDiv$ and D) will generally decrease asymptotically, as later species occupy life habits increasingly similar to previously inhabited ones. At large values of species richness, when relatively few unoccupied portions of intermediate ecospace still exist, the dynamics of partitioning models (and especially those implemented in weakened versions) may resemble those of weakened versions of the redundancy model because new species will be functionally rather similar to preexisting ones.

Mechanisms.—Local competition among species for limited resources is widely expected to produce niche partitioning, a limiting similarity among species in their resource requirements (Gause 1934; Hutchinson 1959; MacArthur and Levins 1967; MacArthur 1970; Schoener 1974; Fox 1987). In a generalized sense, this partitioning is a form of resource specialization (Futuyma and Moreno 1988) that can take many forms, including dietary (Grant 1986), foraging strategy (Schoener 1971; Stephens and Krebs 1986), behavioral timing (Kronfeld-Schor and Dayan 2003), habitat specialization (Hutchinson 1959; McPeck 1996), and polymorphisms within individual populations (Araújo et al. 2011). Coevolution (Ehrlich and Raven 1964; Futuyma and Slatkin 1983; Brooks and McLennan 1993), ecological fitting (Janzen 1985; Zamora 2000; Agosta and Klemens 2008), and other mechanisms that facilitate diversification through specialized interactions with other taxa can also promote specialization (but these mechanisms could also promote redundancy if the functional traits of descendent species are phylogenetically conserved). Although these mechanisms span a range of scales and specific processes, the critical outcome in the model of partitioning is one of progressively closer packing of species according to life habits (i.e., specialization). Mathematical models have predicted unrealistically tight packing of species (Kinzig et al. 1999) in some circumstances, but Schwilck and Ackerly (2005) have shown this concern is ameliorated when demographic stochasticity (especially in immigration rate) and environmental heterogeneity occurs, both of which are predicted to increase the likelihood of limiting similarity. Partitioning has been relatively understudied by functional ecologists, but Mouillot et al. (2007) found no evidence for partitioning in lagoonal fish communities.

Paleoecological Examples.—Explicit tests of local-scale partitioning within individual fossil assemblages are rare, perhaps reflecting the expectation (Huntley et al. 2008) that such local processes are unlikely to be recorded in the fossil record. Across synoptic scales, the most explicit discussion of niche partitioning in fossil communities involves tiering (Ausich and Bottjer 1982; Bottjer and Ausich 1986), in

which benthic marine suspension feeders spanning many taxonomic groups were hypothesized to have subdivided epifaunal and infaunal microhabitats. Although their explanation for this partitioning includes multiple causes (including increasing body size and predator avoidance), I include it here because its primary mechanism is one of niche partitioning according to distance from seafloor. This pattern has been extensively demonstrated in paleocommunities (e.g., Peters and Bork 1998; Morris and Felton 2003; Wang et al. 2012; Brower 2013; McLean and Lasker 2013).

James Valentine (1969, 1995; Walker and Valentine 1984) has been the leading proponent of specialization as the dominant ecological trend in Phanerozoic diversification, a trend he termed “progressive canalization of ecospace” (1969). His conclusion was based primarily on the increasing proportion of lower taxa within higher taxonomic groups in the global biota, interpreting it as one of increasing Phanerozoic specialization, in which earlier genus-poor, presumably generalized classes were succeeded by genus-rich, more specialized classes. He later supported this conclusion using the stochastic tesseræ model (1980; Walker and Valentine 1984), which demonstrated that logistic diversification within an empty ecospace should restrict later lineages to intermediate life habits. Although Valentine (1973) conceded that the total ecospace of the marine biota has increased, the dominant pattern according to his model is one of increasing specialization.

This view of an ecologically generalized Cambrian biota was echoed by Sepkoski (1979) in his analysis of early Paleozoic diversification, and he later developed this argument in his analysis of increasing beta diversity during the Paleozoic (Sepkoski 1988). Recent research on the Cambrian radiation (Na and Kiessling 2015), based largely on theoretical relationships between alpha, beta, and gamma diversity (Hautmann 2014), reiterates that niche partitioning was an important contributor to the Cambrian radiation. Many aspects of post-Paleozoic diversification are hypothesized to have resulted from increasing specialization among motile predators

(e.g., Vermeij 1987; Bambach et al. 2002; Aberhan et al. 2006; Stanley 2008), and Nürnberg and Aberhan (2015) demonstrated a positive relationship between global diversity and environmental (habitat) specialization throughout the Phanerozoic. While the partitioning of ecospace implied by most of these paleoecological patterns was originally intended to explain global diversity patterns, all imply that progressive specialization should occur within individual assemblages, both as a cause of and as a response to increased species richness.

Expansion Model

Model Dynamics.—The model of expansion (Table 1) occurs when successive species in a community occupy progressively more novel life habits that did not occur previously in the community. The general structural topology (Fig. 1D) is one of progressive divergence toward more extreme life habits (Bush and Novack-Gottshall 2012). Except for *FDiv*, this model produces the largest statistical values of the four models. *H* will increase asymptotically at a rate faster than for any other model (including the neutral model) because the expansion model rule actively pursues novel life habits, constrained only by what life habits are deemed theoretically possible. The asymptote and rate of increase (or the slope for small sample sizes) will vary depending on the structure of the ecospace framework used, with the asymptote equal to the maximum number of unique life habits allowed by the framework. In those frameworks that allow less than approximately 5000 unique life habits (typically a result of specifying few numbers of functional traits), *H* will have an initial slope slightly <1 with species richness, whereas frameworks allowing more unique life habits will remain equal to sample size through approximately 200 species. Disparity statistics (*V*, *M*, *FDis*, *FRic*) will display the most rapid rates of increase as the extremes of the potential ecospace are explored, after which they will reach large asymptotes as the exploration of life habits attenuates. Statistics sensitive to internal structure will have varying dynamics, depending on the nature of the ecospace

framework (see companion article [Novack-Gottshall 2016] for details). For example, *FDiv* will typically decrease asymptotically (perhaps after rising during the initial phase of rapid expansion), whereas *D* will remain relatively constant or perhaps increase or decrease asymptotically. Evenness statistics (*FEve*) will likewise remain relatively constant or increase asymptotically if the life habits of originating species began the simulation clustered into a small region of the ecospace.

Mechanisms.—The primary mechanism for the expansion model is one of active divergence among life habits. Within the context of community ecology, the basic mechanism promoting such novelty is niche divergence (Brown and Wilson 1956; MacArthur and Levins 1967; Schluter 2000; Losos et al. 2002; Brousseau et al. 2013), which is often extrapolated to larger evolutionary scales to explain adaptive radiations (Schluter 2000; Losos 2010). Alternative hypotheses, initially termed “forbidden species” or “checkerboard” patterns (Diamond 1975) but subsumed within the broader “niche-versus-neutral” debate (cf. Weiher et al. 2011), explain divergence patterns through biased immigration of species with niche traits not found previously within a community. Recent research on adaptive radiations suggests that many claims of character displacement are unsubstantiated (Stuart and Losos 2013) and that a shifting mosaic of adaptive peaks may be a better explanation than ecological divergence writ large (Estes and Arnold 2007; Harmon et al. 2010). Whatever the cause, such diversifications are widely considered to result in elevated evolutionary rates during their initial phases, a pattern termed the “early-burst” model (e.g., Rabosky and Lovette 2008; Harmon et al. 2010; Ingram et al. 2012; Wagner and Estabrook 2014; Knape et al. 2015), but widely discussed in the paleontological literature on evolutionary rates (Simpson 1944; Raup 1983; Walker and Valentine 1984; Lee et al. 2013; Hautmann 2014) and morphological disparity (Gould 1991; Briggs et al. 1992; Foote 1994; Erwin 2007), especially in the context of the Cambrian and other fossil radiations. The statistical dynamics of the expansion model noted above fit these

predictions well and are borne out in simulations.

Critical to all such concepts is the ecological-opportunity hypothesis (Gavrilets and Vose 2005; Losos 2010; Mahler et al. 2010), which preconditions divergence on the availability of novel resources, previously uninhabited life habits, or ecological release from prior constraints. James Valentine has long advocated this idea (Valentine 1969, 1995; Walker and Valentine 1984; Erwin et al. 1987) to explain the uniqueness of the Cambrian radiation, and its roots go back to Darwin (1859). The evolution of novel morphological (“key”) innovations (Stanley 1968; Erwin 1994; Hunter 1998; Gavrilets and Vose 2005; Vermeij 2006) is a commonly inferred driver of such opportunities. Colonization of new habitats (or major changes to previous ones, either inhabited or regionally adjacent) is also thought to play an important role in divergence, as it can lead to increased nutrient and biogeochemical fluxes, novel ecosystem interactions, and ultimately new adaptive pressures (Losos et al. 1997; Price and Clague 2002; Herrel et al. 2008). The effects of such environmental changes are increasingly well studied in modern disturbed settings (Hooper et al. 2005; Lotze et al. 2006; Worm et al. 2006; Kidwell 2007, 2015; Villéger et al. 2010; Boyd and Hutchins 2012; Mouillot et al. 2013), and frequently invoked for unique “natural experiments” throughout geological history (see below). Depending on how generally they are manifested, some niche-construction and ecosystem-engineering processes may also induce positive-feedback dynamics that result in inhabitation of novel portions of ecospace (Jones et al. 1994, 1997; Laland et al. 1999; Wright et al. 2002; Odling-Smee et al. 2003; Scott-Phillips et al. 2013; Berke 2015). I also include escalation facilitated by new predators and Red Queen coevolution as examples of such positive-feedback mechanisms (Van Valen 1973; Vermeij 1987; Liow et al. 2011) that can facilitate life in previously uninhabited portions of ecospace.

Note that my usage of “novel” in this context is distinct from the concept sometimes embodied by the term “specialized,” which I restrict to those new variations intermediate

in some manner to preexisting traits (as represented above in the partitioning model); instead, here I use “novel” in the strict sense of life habits distinct and more extreme from those preexisting within the community. It is also worth emphasizing that not all key innovations, newly colonized habitats, or diversifications of newly originating taxonomic lineages must result in divergent, expansion dynamics (Erwin 2011). These events, if occurring as unique contingencies, are perhaps best not included in this model, which is intended as a generalized and persistent bias within diversifying biotas. Such contingency-driven patterns may be better cast as positive- or negative-feedback models (Bush and Novack-Gottshall 2012), discussed in more detail below.

Paleoecological Examples.—Like the partitioning model, most relevant paleoecological examples focus on synoptic Phanerozoic-scale trends instead of analyses of individual assemblages. Because diversity and inhabited ecospace have undoubtedly increased in all ecosystems since the Ediacaran and Cambrian (Bambach et al. 2007; Bush et al. 2011; Laflamme et al. 2013; Knope et al. 2015), most synoptic paleoecological hypotheses can be characterized as examples of the expansion model. The most cogent advocate for the role of continued expansion throughout the Phanerozoic is Richard Bambach (1983, 1985), who compared the ecological strategies of Sepkoski’s (1981) three evolutionary faunas using the first-ever ecospace framework (functional-trait space), defined by diet, tiering, and activity. Because successive evolutionary faunas utilized greater numbers of life habits, his primary conclusion was that the evolution of novel adaptive strategies was a primary driver of taxonomic diversification. This general pattern has held up well to additional scrutiny (Bambach et al. 2007; Bush et al. 2007a,b, 2011; Novack-Gottshall 2007b; Bush and Bambach 2011; Knope et al. 2015), although Bambach has allowed a subsidiary role for specialization, especially for predators (Bambach 1983). He later expanded these ideas with his “seafood through time” theory (Bambach 1993), in which ecospace expansion was facilitated by improvements to organismal physiology and energetics, aided not only by mass extinctions (Knoll et al. 1996, 2007;

Bambach et al. 2002;) and major environmental changes (Bambach 1999; Bush and Bambach 2011; Knope et al. 2015), but also as a persistent tendency during background intervals (Knoll and Bambach 2000; Bush and Bambach 2011).

Another influential advocate of continuous innovation throughout time is Geerat Vermeij (1977) and his theory of enemy-driven escalation. Although initially envisioned to explain that Mesozoic predation-resistant adaptations—primarily thicker, more armored shells and increased mobility—were triggered by the evolution of durophagous predators (Vermeij 1977; Vermeij et al. 1981; Schindel et al. 1982), the concept of asymmetric coevolution was later generalized by Vermeij to explain a wide range of performance-enhancing adaptations across all of life, including metabolic rates, bioturbation, vertebrate dentition, herbivory (Vermeij and Lindberg 2000), body size, and planktonic habits (Signor and Vermeij 1994), among many other innovations. The basic patterns have been exceptionally well documented, especially the trend of increasing frequency of (and presumably more disparate) predatory life habits during the Phanerozoic (Vermeij 1987; Aberhan et al. 2006; Kowalewski et al. 2006; Bambach et al. 2007; Bush et al. 2007a; Huntley and Kowalewski 2007; Novack-Gottshall 2007b; Stanley 2008; Bush and Bambach 2011; Kosnik et al. 2011). Evidence also exists for Phanerozoic increases in exploitation of other organisms as substrates or domiciles (Vermeij 1987; Taylor and Wilson 2003; Novack-Gottshall 2007b). Vermeij's comprehensive argument remains that the environment—primarily acting on productivity but also including an important role for energy-producing oxygenation (Vermeij 2011)—and energy-intensive dominant taxa—primarily through their powerful effects on interacting taxa—are the primary factors facilitating opportunities for evolutionary novelties and controlling the structure of ecological (economic) systems (Vermeij 1995, 1999, 2011, 2013). In his perspective, mass extinctions, smaller disruptions, and other historical events can affect the timing of these system-wide reorganizations (both positively or negatively), but there exists a persistent tendency for such improved performance throughout the

history of life (Vermeij 1987). Although his explanations are not phrased in the terminology of expansion used herein, his focus on performance-enhancing innovations driving revolutionary ecological reorganizations is consistent with this model.

Most of these claims have been demonstrated at synoptic scales, but Bambach (1977), Vermeij (1987, 2008), and others have repeatedly encouraged their application to local assemblages. Many such studies have been conducted on predation and escalation dynamics (e.g., Schindel et al. 1982; Hansen and Kelley 1995; Hoffmeister and Kowalewski 2001; Kelley et al. 2003; Kelley and Hansen 2006; Huntley and Kowalewski 2007; Kowalewski and Leighton 2007; Sessa et al. 2012; Tyler et al. 2013). More studies need to be conducted examining ecospace and functional traits at local scales; examples include Walker and Laporte (1970), Levinton and Bambach (1975), Radenbaugh and McKinney (1998), Behrensmeyer et al. (2003), Bambach et al. (2007), Xiao and Laflamme (2009), Bush et al. (2011), Villéger et al. (2011), Laflamme et al. (2013), Mitchell and Makovicky (2014), Miller et al. (2014), Dineen et al. (2014, 2015), and O'Brien and Caron (2015).

Biotic responses to habitat colonization and transformation that have occurred throughout the Geozoic history of life (sensu Kowalewski et al. 2011) remain a major focus of paleoecology and biogeochemistry and are widely expected to drive ecospace expansion. Examples include infaunalization (Thayer 1979; Tarhan and Droser 2014; Kloss et al. 2015); creation of marine reefs and hardgrounds (Guensberg and Sprinkle 1992; Wood 1993; Taylor and Wilson 2003; Servais et al. 2010); colonization of the open ocean (Signor and Vermeij 1994; Butterfield 1997; Klug et al. 2010); terrestrialization, plant diversification, and concomitant changes to weathering and erosion (Algeo and Scheckler 1998; Bateman et al. 1998; Bambach 1999; Labandeira 2005; Sahney et al. 2010; Zanne et al. 2013; Edwards et al. 2015; Sundue et al. 2015); and many other biogeochemical revolutions (Bambach 1993; Vermeij 1995; Martin 1996; Bush and Pruss 2013; Allmon and Martin 2014). Although these environmental changes are not required to result in novel life habits and ecospace

expansion, such an invocation is implicit in most discussions (e.g., Droser et al. 1997; Bambach 1999; Bush and Bambach 2011; Vermeij 2011).

Neutral Model

Model Dynamics.—Unlike the previous three driven (or active) models (sensu McShea 1994), community membership in the neutral model (Table 1) occurs without regard to life habit. It is a passive model of life-habit diversification (Bush and Novack-Gottshall 2012) that can serve as a process-free null model (Gotelli and Graves 1996). Unlike the three driven models, in which the functional traits of later species depend on the traits of species already present within a biota, the neutral model is in essence non-Markovian in that species are added independently and their functional identities are ignored. The general structural topology (Fig. 1A) is one of random inhabitation of life habits, in which most of the ecospace becomes inhabited at high levels of species richness, given sufficient numbers of species (Bush and Novack-Gottshall 2012). Similar to other scenarios involving passive and driven models (Stanley 1973b; Gould 1988; McShea 1994; Wang 2001; Hunt 2006), the dynamics of the neutral and driven expansion (but not other) models are often quite similar; sufficiently powerful analyses are needed to discern them. As in the expansion model, H will increase asymptotically at a slope close to 1 with species richness, becoming saturated as the number of potential life habits allowed by the ecospace framework is exhausted; the rate of increase will be very slightly less than that in the expansion model (although the difference will be negligible except for analyses with high statistical power). Disparity statistics (V , M , $FDis$, $FRic$) will also increase asymptotically until number of life habits becomes saturated, but generally at a rate less than that for the expansion model (i.e., these statistical dynamics offer greater opportunity to distinguish the expansion and neutral models than do the dynamics of H), the difference also a function of the number of life habits allowed by the ecospace framework. Statistics sensitive to internal structure will

have varying dynamics, with $FDiv$ generally decreasing (or increasing, if originating species share similar functional traits/life habits and begin in a small region of ecospace). D will remain approximately constant, as will evenness statistics ($FEve$), as successive species continue to have life habits unrelated to (or assigned at random from) prior species.

Mechanisms.—In large part a reaction to the assembly-rule debate (Diamond 1975), community ecologists have exerted enormous effort developing null models that are both appropriate and sufficiently statistically powerful to distinguish relevant models of community assembly (cf. Connor and Simberloff 1979; Gotelli and Graves 1996; Weiher and Keddy 1999; Gotelli 2000; Gotelli and Ulrich 2012). This methodological focus has only intensified in response to Hubbell's (2001) neutral theory, which has refocused the assembly debate to one of niche-versus-neutral models. Functional ecology has offered important perspectives (and powerful statistics) on this debate, and null models are generally tested using simulations or permutation tests of individual statistics suitable to a particular model.

Recent sensitivity analyses (Mouchet et al. 2010; de Bello 2012; Maire et al. 2015) have demonstrated how performance of functional ecology null models depends highly on data structure (such as the number and type of functional traits used), characteristics of the species pool, and power of statistics used to discriminate assembly models. Defining the proper species pool for an analysis is a particularly important decision (Cornell 1999; Patzkowsky and Holland 2003; Knape et al. 2012; Cornell and Harrison 2014; Gerhold et al. 2015; Mittelbach and Schemske 2015). It is now generally recommended that tests be tailored to each particular study (de Bello 2012)—not prohibitive given modern computing resources (cf. Kowalewski and Novack-Gottshall 2010)—and that statistical conclusions be drawn using appropriate criteria (White et al. 2014). A major unresolved question is how to incorporate multiple statistics into single model-selection tests, as many statistics are correlated (Mouchet et al. 2010) and there often exists ambiguity about which statistic—if

one exists at all—is most appropriate for distinguishing the range of assembly models under consideration (Ciampaglio et al. 2001; Mouchet et al. 2010; Maire et al. 2015). Another concern is that most tests only consider a single model, either supporting a stochastic process or rejecting it in favor of an alternative model; few functional ecology studies consider multiple-candidate models and explicit model-selection criteria (Burnham and Anderson 2002; Johnson and Omland 2004; Grueber et al. 2011). The companion article (Novack-Gottshall 2016) suggests a novel and powerful solution to this impasse: the use of classification trees as a form of model selection.

The stochastic neutral model introduced here occurs when the other three driven models are not enacted, and it is formulated in a manner different from many used in community ecology and functional diversity. Rather than drawing species from a (biologically real) species pool, it creates samples of species whose life habits (functional traits) are drawn at random and independently from a theoretical ecospace framework/functional-trait space (e.g., Novack-Gottshall 2007b). This process allows *any* theoretically possible life habit to exist within the neutral sample (similar to the process used in Raup and Gould 1974; Foote 1999). Although many of these life habits are going to be logically impossible or perhaps never realized in biological history (Hutchinson 1957; Valentine 1969; Bambach 1983; Bush et al. 2007a), this null model is useful in identifying important constraints (such as patterns of covariation among traits, empty regions of the ecospace, or perhaps particular habitat filters) that restrict real organisms from actual communities (Raup 1966; Seilacher 1970; Thomas and Reif 1993). The model can be modified (see companion article [Novack-Gottshall 2016]) to weight the assignment of functional traits based on their frequency of occurrence in a supplied species pool and thus to provide better approximations to the realized ecospace of the sampled species pool. It can also be modified to serve as a simple permutation test, the null model used in most functional diversity analyses, if desired, by forcing sampling to occur only from a species pool.

It is worth emphasizing that this neutral model, aside from acting as a process-free, non-Markovian null model in which functional differences are ignored, is mechanistically different from the neutral model of Hubbell (2005, 2006; Rosindell et al. 2012). The two primary characteristics in Hubbell's (2005, 2006) model are "functional equivalence" among species in their per-capita demographic rates (i.e., birth, death, dispersal, speciation rates) and a spatially structured habitat in which dispersal from a regional species pool only occurs when a patch becomes available. The four models described herein focus explicitly on the functional traits of organisms: the neutral model ignores these traits (operationally using a different definition of "functional equivalence") when assembling communities (that is, it is a "neutral theory," *sensu* Rosindell et al. 2012), whereas the three driven models can be considered models of "niche theories" (*sensu* Rosindell et al. 2012). The four models herein also lack spatial structure; any species whose life habit is allowed by the ecospace framework and model rules (or in the case of the neutral model, any life habit allowed by the ecospace framework) is guaranteed entry into the community.

Paleoecological Examples.—Paleontology has a long history—stemming in large part from the MBL simulations (Raup et al. 1973; Raup and Gould 1974; Gould et al. 1977)—of using stochastic null models to test whether observed patterns differ from those expected by stochastic processes. Valentine's tesseræ model (1980; Walker and Valentine 1984) simulated stochastic taxonomic diversification within an empty ecospace. The simulation demonstrated that major taxonomic groups (those with distinct functional traits) would arise quickly at first, but subsequent originations would only represent diversification within these early clades. Once equilibrium species richness was reached, new species (and thus new life habits) could only be added after extinction of prior species. By comparing the per-species rate of extinction within a clade (a measure of species turnover) to that clade's intrinsic rate of speciation, they were able to estimate that approximately 30% of the potential ecospace was unoccupied at any time. Although they interpreted the pattern in terms of progressive specialization, the general

patterns are likely similar to the dynamics described above for the neutral model, albeit their analyses explicitly incorporated a Markovian phylogenetic structure.

This tradition of stochastic modeling has been well embraced in studies of morphological disparity (e.g., Foote 1991; Ciampaglio et al. 2001; Korn et al. 2013; Mitchell and Makovicky 2014) but has only rarely been employed in analyses of ecological disparity. The only two studies (that I am aware of) include Mitchell and Makovicky (2014), who demonstrated that the functional diversity (ecological disparity) of Early Cretaceous bird assemblages was significantly lower than that for later bird assemblages, which expanded into unfilled portions of the Mesozoic ecospace. Miller et al. (2014) demonstrated that the functional ecospace of the Amboseli mammalian death assemblage was statistically indistinguishable from a random draw from the living species pool, despite a bias toward larger species in the death assemblage.

Other Models

The four models discussed above can serve as informative and generalized end members of a wide spectrum of patterns that might result from ecological and evolutionary processes, but they are not intended to be exclusive (cf. Foote 1996). Others have been introduced in the paleontological literature and are briefly discussed here. The contraction model (Bush and Novack-Gottshall 2012) occurs when ecospace contracts. Especially relevant to discussion of extinctions, it could serve as a useful model when considering any reduction in species richness (Mouillot et al. 2013). Depending on the extent of functional selectivity and taxonomic loss involved, the dynamics are expected to follow the same as those presented above, but in reverse. Positive- and negative-feedback models (Bush and Novack-Gottshall 2012) occur when the introduction of one life habit influences the range of life habits other taxa can inhabit, either through ecosystem engineering, habitat modification, or other processes (e.g., for discussion of ecosystem engineering in the context of the Ediacaran–Cambrian radiation, see Erwin et al. 2011; Erwin and Tweedt 2011;

Laflamme et al. 2013; Darroch et al. 2015). These feedback models can be envisioned as particular forms of the expansion and contraction model, but ones in which subsequent life habits are biased toward particular regions of the ecospace. They could be modeled as mixtures of the above models by specifying a change in model rules (and/or modification of the ecospace framework) at a particular point in a simulation or by adding linkages between functional traits. A migration model (Dick and Maxwell 2015) has also been introduced recently, in which there is a wholesale shift in the occupation of ecospace; this model shares some similarity with the feedback models but lacks an obvious candidate for what causes the shift to occur. It could be modeled by allowed the ecospace framework to change (either in a specified manner or through a Brownian motion random walk) during a simulation. Inclusion of such phylogenetic structure would form a useful and interesting modification to the four models above, which currently have been formulated to focus only on functional identities of species and not their phylogenetic relatedness. For example, depending on implementation, inclusion of phylogenetic structure might cause the dynamics of all models to approach the redundancy model, as phylogenetic conservatism further constrains the exploration of ecospace. Because of their reliance on particular contingencies of timing, effect, and implementation, the variants discussed here are less generalizable than the four simpler models that are the focus of this article, and their predicted dynamics would likely vary, depending on the particular processes, interactions, and constraints involved.

Distinguishing among the Models: Trends in Phanerozoic Marine Ecological History

These four general models of ecological diversification can accommodate a wide range of processes in ecological and evolutionary theory (Table 1) and can be applied to any temporal or spatial scale at which these processes might operate, from individual assemblages to the entire biosphere. Their dynamics offer a useful benchmark when

interpreting patterns of ecospace (functional) utilization. In particular, statistics used in morphological (ecological) disparity and functional diversity studies provide easily measured and informative metrics for identifying these models. In the discussion that follows, I summarize the most efficient ways to distinguish these models, emphasize important (and sometimes overlooked) dynamics, and discuss (sometimes playing devil's advocate) how these dynamics may inform past and future analyses of ecological disparity.

Each of these four models produces predictable dynamics as a function of species richness. Most statistics, across models, display asymptotic behaviors, rising or falling quickly at low sample sizes as ecospace is colonized and reaching asymptotes as the model rules follow their course and the ecospace becomes saturated. Thus, evidence of such behavior, by itself, is insufficient to identify the process producing the pattern. In general, the expansion model produces the largest values for disparity and evenness statistics, followed closely by the neutral model, and the redundancy model tends toward the lowest values. Partitioning model dynamics are intermediate, with the strict version generally displaying lower values than its relaxed counterpart because of its more tightly constrained behavior. If models are followed in weakened forms, the dynamics will converge toward those of the neutral model.

The particular value for any statistic by itself is uninformative; it is the dynamics across varying levels of taxonomic richness that are needed to distinguish each model. It is critical that simulations are conducted—for each distinct ecospace framework used, and perhaps for each analysis—because the statistical power to distinguish the dynamics of each model depends on the data structure of the ecospace framework used (e.g., the number and type of functional traits) and to a lesser extent how each model is implemented (Mouchet et al. 2010; de Bello 2012; Maire et al. 2015). See companion article (Novack-Gottshall 2016) for additional details on variation in dynamics using different ecospace frameworks and recommendations for implementing simulations and conducting model selection.

Guidelines, however, do exist to assist distinguishing these models in general circumstances (Table 1). The most diagnostic criterion for the redundancy models is having life-habit richness (H) values far lower than species richness (and especially so if relatively constant). Because this behavior is not expected in most actual circumstances, the redundancy model can also be distinguished by the combination of generally low H values and declining or low, nearly constant disparity values. This model can also be visually detected by the presence of discrete clumps of life habits in ordinations of the functional-trait space (Fig. 1). The partitioning model is diagnosed by generally declining trends in all statistics (except for certain disparity statistics, such as $FRic$ and M , that will increase slowly) and relatively constrained ecospace occupation in ordinations, especially if linear gradients are present. The tightly restricted occupation of ecospace for the redundancy and partitioning models can present challenges to distinguishing these models in practice, especially when the rules for one or both models are implemented in a weakened state. In large samples, there will be very tight packing of life habits in both models. The primary distinction (aside from their fundamentally different causes) is the degree of differentiation among life habits; in redundancy, there exist discrete spaces between clumps, whereas life habits for partitioning are more continuously distributed. This behavior causes H to be less for the redundancy model and some disparity statistics (such as $FRic$ and M) to have contrasting dynamics, although the differences may be subtle.

The dynamical similarities (Table 1) between the driven expansion model and the passive neutral model are worth discussing in more detail given their opposite causes. In both cases, overall ecospace enlarges as new life-habit combinations occur, increasing both the maximum range and dispersion of the biota. The rate of increase will be slightly greater for the expansion model, but the difference will only be able to be distinguished using powerful statistical methods (or large ecospace frameworks with many characters). Both models will also share generally constant

evenness dynamics. Notably, sensitivity analyses in the companion article (Novack-Gottshall 2016) demonstrate that the Bush and Bambach ecospace framework (Bambach et al. 2007; Bush et al. 2007a, 2011; Bush and Bambach 2011) may be insufficiently powerful to distinguish these two models statistically. In ordinations of the driven expansion model (Fig. 1), early species will typically have centrally located positions, with successive species in more extreme positions; the centroid will often (but not always) be empty as the model progresses. Species will also disperse from central positions in the neutral model, but the centroid will typically be occupied and later life habits will occur throughout the ecospace. This behavior, at least for small to moderately large sample sizes, mimics McShea's (1994) "test of the minimum" for distinguishing passive from driven models.

Because biotic ecospace has expanded through the Geozoic, both at the scale of individual assemblages (Bambach et al. 2007; Bush et al. 2011; Villéger et al. 2011; Mitchell and Makovicky 2014) and throughout the entire biosphere (Bambach 1983; Bush et al. 2007a; Novack-Gottshall 2007b; Bush and Bambach 2011), there is broad consensus for the expansion model and its mechanism of novel divergence as a dominant pattern for the history of life. In particular, Bush et al. (2007a), using abundance data from individual marine assemblages, demonstrated significant increases in individual functional traits during the Phanerozoic. Using the test of the minimum, they claimed that the predation pattern was consistent with a diffusional process (because predators remained uncommon within assemblages throughout time), whereas the patterns for increasing infaunality among suspension feeders and active motility were more consistent with driven processes (because most animals in modern assemblages are motile and most suspension feeders are infaunal). Bush and Bambach later (2011) claimed similar tendencies for increases in energetics and ability of animals to disturb other animals in their habitat (often caused by an interaction between motility and infaunality). There is little reason to question the veracity of these patterns given their

overwhelming empirical (Vermeij 1987; Aberhan et al. 2006; Huntley and Kowalewski 2007; Novack-Gottshall 2007b; Bush and Bambach 2011) and theoretical support (Vermeij 1987, 2011, 2013; Stanley 2008).

But a similar argument could be made in support of the model of redundancy, in which ecospace exists as clusters of crowded, canalized clumps. It is interesting to note that the modal marine life habits have not changed throughout the Phanerozoic. Whether examined taxonomically at the scale of Sepkoski's three evolutionary faunas (Bambach 1983, 1985) or at finer scales (Bush and Bambach 2011), including proportional occurrences in local assemblages or across global aggregates (Bush et al. 2007a; Novack-Gottshall 2007b), most marine animals have always been either epifaunal, attached suspension feeders; shallow infaunal, mobile deposit feeders; or mobile predators or algae eaters. The recurrence of these canonical life habits across multiple taxonomic groups throughout the Geozoic—despite many variations on the themes and supplemented by changes in how these life habits have been enacted—could be claimed as evidence that these strategies are ecological attractors (*sensu* Thomas and Reif 1993; Wagner and Erwin 2006), adaptively basic ways of living essential to how marine communities function. The relatively few life habits tallied—in all attempts to comprehensively do so thus far—remain trivially low compared with the number of life habits that is at least theoretically possible given the number of species represented in such ecospace frameworks (*cf.* Kowalewski and Finnegan 2010). This low ratio provides compelling evidence that the redundancy model (or at least a weakened version of it) should be considered a viable candidate model for life's history.

A compelling argument could as easily be made for the partitioning model, in which progressive specialization is the overriding tendency. The strongest evidence is the markedly linear gradients found in an ordination of the life habits of Paleozoic (Cambrian–Devonian) and Recent marine taxa (Novack-Gottshall 2007b: Figs. 4,5). Not surprising, the end members of these gradients fall within the three canonical strategies just

mentioned. Much of the gradation is a result of variation in body size and tiering, but it also reflects transitions in mobility, substrate relationships, and food preferences, which could be interpreted as intermediately specialized variations on these basic strategies. Similar linear patterns are also apparent in the occupation of “cubes” in the Bush and Bambach framework (Bambach et al. 2007; Bush et al. 2007a, 2011; Bush and Bambach 2011), especially in the categories of suspension feeding, predation, and motility, all of which gain progressively more variation throughout the Phanerozoic (i.e., the lines of cubes become more “connected” to adjacent cubes through time). Similar patterns of increased packing have been claimed for Phanerozoic bivalves (Mondal and Harries 2015): diversification after the Ordovician radiation involved closer packing among life habits, with bivalves never inhabiting more than ~30% of the available ecospace. Many of the best-documented paleoecological patterns—predation (Stanley 1973a, 2008; Vermeij 1987; Baldomero et al. 2014) and tiering (Ausich and Bottjer 1982; Thayer 1983; Bottjer and Ausich 1986)—have consistently been interpreted as examples of increasing specialization. Simulation-based analyses in the companion article (Novack-Gottshall 2016) support the partitioning model for ~75% of well-preserved Late Ordovician samples from the type Cincinnati (the remainder are supported as redundancy models). However, this by itself is insufficient to establish whether this model continues to be upheld in later periods as a general Phanerozoic trend.

And yet many of these patterns are equally consistent with a pattern of stochastic diffusion from an initial ecological structure begun in the Cambrian or Ediacaran (Bush and Bambach 2011), perhaps punctuated with mass extinctions associated with major taxonomic turnovers, but in which ecological disparity generally increases with the addition of new species, and with many new species assured to have life habits functionally intermediate to, similar to, and often convergent with, already existing species. We do know that modern biotas are functionally more disparate than Paleozoic ones (measured as *D* by Novack-Gottshall [2007b] and as *FRic* by

Villéger et al. [2011]), but this alone is insufficient to identify whether this is caused by a driven or passive diffusional process. The simple truth is that we do not yet know which model is statistically best supported by these patterns. However, the data that exist are strong, and sufficiently powerful statistical analyses are available to answer this question.

Acknowledgments

I thank A. Bush, D. W. McShea, A. I. Miller, V. L. Roth, W. G. Wilson, and G. A. Wray for discussion of ecological models; and G. Spencer and the staff at the Myrin Library (Ursinus College), where much of the manuscript was written. Research and manuscript support was facilitated with a sabbatical leave provided by M. J. de la Cámara and Faculty Development (Benedictine University). This review is based, in part, on a portion of my doctoral dissertation at Duke University. This paper was strengthened by thoughtful reviews from M. Foote, S. M. Holland, and G. Hunt.

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