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Please note the following corrections:

p. 283. Replace $p = 1.005$ with $p = 0.1005$

p. 284, Fig. 3 caption. Replace $p = 1.005$ with $p = 0.1005$

p. 289: Add at end of Acknowledgements: This is Paleobiology Database Publication 62.

Using a theoretical ecospace to quantify the ecological diversity of Paleozoic and modern marine biotas

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Abstract.—The process of evolution hinders our ability to make large-scale ecological comparisons—such as those encompassing marine biotas spanning the Phanerozoic—because the compared entities are taxonomically and morphologically dissimilar. One solution is to focus instead on life habits, which are repeatedly discovered by taxa because of convergence. Such an approach is applied to a comparison of the ecological diversity of Paleozoic (Cambrian–Devonian) and modern marine biotas from deep-subtidal, soft-substrate habitats. Ecological diversity (richness and disparity) is operationalized by using a standardized ecospace framework that can be applied equally to extant and extinct organisms and is logically independent of taxonomy. Because individual states in the framework are chosen a priori and not customized for particular taxa, the framework fulfills the requirements of a universal theoretical ecospace. Unique ecological life habits can be recognized as each discrete, n -dimensional combination of character states in the framework. Although the basic unit of analysis remains the organism, the framework can be applied to other entities—species, clades, or multispecies assemblages—for the study of comparative paleoecology and ecology. Because the framework is quantifiable, it is amenable to analytical techniques used for morphological disparity. Using these methods, I demonstrate that the composite Paleozoic biota is approximately as rich in life habits as the sampled modern biota, but that the life habits in the modern biota are significantly more disparate than those in the Paleozoic; these results are robust to taphonomic standardization. Despite broadly similar distributions of life habits revealed by multivariate ordination, the modern biota is composed of life habits that are significantly enriched, among others, in mobility, infaunality, carnivory, and exploitation of other organisms (or structures) for occupation of microhabitats.

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Ecological communities, however, do exist, but what are linked in them by biotic factors are not the faunistic units, the species, but the ecological units, the life forms.

—G. Thorson (1957: p. 470)

Though the technical difficulties are very great, they could probably be solved by anyone who really wanted to compare the furry growth of diatoms on a stone in a stream with the larger-scale patches of woodland that have about the same sort of uniformity when viewed from an airplane.

—G. E. Hutchinson (1965: p. 77)

Is the modern marine biota composed of the same life habits as ancient ones? Which biotas are ecologically more diverse, in terms of both the number of life habits and the disparity (similarity) of these life habits? These are basic questions that ought to be answerable quan-

titatively by comparative paleoecologists. I will argue below that the answers to these and similar questions are impeded by a methodological limitation in our ability to compare communities (or other ecological entities) when they are separated by vast expanses of time and space and when they share few or no evolutionary homologies. Their solution hinges on the ability to compare quantitatively all kinds of entities directly on the basis of their ecological capabilities.

Taxonomy has remained a typical yardstick for such comparisons. It has formed the dominant basis for comparing the structure of Paleozoic and Recent communities (Bretsky 1968; Ziegler et al. 1968; Walker and Laporte 1970; Levinton and Bambach 1975; West 1976; Miller 1988; Radenbaugh and McKinney 1998). Although all of these studies considered various ecological characters (e.g., trophic guilds, abundance), their primary impetus was the

presence of taxonomically similar entities. The underlying assumption when using taxonomy in this way is that the ecological characters of taxonomic groups are conserved during evolution, such that taxonomy acts as shorthand for ecology. Although this may be generally true at low taxonomic levels, and occasionally high ones (Webb et al. 2002), there are many exceptions. For example, Fauchald and Jumars (1979) noted stark population-level differences within individual species of polychaetes, and Stanley (1968, 1972) and Miller (1990) noted widespread life habit convergence among bivalve orders. As a general rule, Peterson et al. (1999) demonstrated that conservatism is less likely above the familial level. Thus, although taxonomic comparisons may be suitable for documenting the ecological organization of taxonomically similar communities, such a basis is not useful when comparing taxonomically disparate communities. In short, taxonomy is an indirect, and potentially misleading, proxy for getting at ecological questions.

Morphology has been another vehicle for ecological comparisons (Van Valkenburgh 1985, 1988, 1991, 1994; Foote 1996b; Wainwright and Reilly 1994; Van Valkenburgh and Molnar 2002; Lockwood 2004). The general premise of ecomorphology is that morphology can be used as a proxy for the ecological characters of organisms. Such correspondence has been well supported (e.g., Winemiller 1991; Wainwright 1994). However, there seems little potential in using these methods for large-scale comparisons spanning phyla and long time scales because of the lack of appropriate homologous characters. The most ambitious comparisons include Paleozoic and Recent arthropods (Briggs et al. 1992; Wills et al. 1994; Stockmeyer Lofgren et al. 2003) and animal skeletons (Thomas and Reif 1993; Thomas et al. 2000). There are few homologous (and even functionally comparable) morphological characters shared throughout benthic communities composed of green algae, foraminifera, corals, trilobites, bryozoans, brachiopods, and bivalves. It is essential to focus such comparisons on ecological characters directly, instead of on their underlying morphology or their consequences for taxonomy.

It is important here to understand what I mean by the term *ecological character*. We can start with the understanding that each organism exhibits unique phenotypic features (sensu Bock and von Wahlert 1965) that affect environmental interactions. Collectively, these phenotypic features endow each organism with ecological capabilities or characters (faculties sensu Bock and von Wahlert 1965). For now, I will focus on those autecological characters related to feeding, use of space, mobility, dispersal, reproduction, and body size; taken together, these describe an organism's basic life habit. Ecological diversity, regarded as the overall variety of life habits within some group, can be most easily assessed by richness, the number of unique life habits in this group. It can also be assessed by ecological disparity, a measure of how different each life habit is from others in this group (modified from Foote 1993a). I propose below a common framework for such characters and formal definitions for ecological richness and disparity.

Focusing on such ecological characters directly has two benefits. First, it avoids the problems of homology associated with morphological comparisons. Because distinct phenotypes can perform identical functions in numerous ways (Bock and von Wahlert 1965; Alfaro et al. 2004, 2005; Wainwright et al. 2005; Marks and Lechowicz 2006), there exists in nature an innate tendency for ecological convergence when emergent capabilities are beneficial. In a sense, such higher-order capabilities are "screened off" (sensu Brandon 1984) from their underlying morphological and functional causes. These characters are accordingly more suitable for large-scale ecological comparisons. This may diminish, although not eliminate, the role of phylogenetic effects (Felsenstein 1985b; Harvey and Pagel 1991). Second, compared with analyses using the proxies of taxonomy or morphology alone, such a focus better aligns results with the theoretical understanding of ecological diversifications (Grant 1999; Schluter 2000; Coyne and Orr 2004).

Such benefits motivated the development of the guild concept. Originally focused on comparisons among taxa sharing diet and foraging habits (Root 1967), it was later modified to

include other categories—microhabitat, locomotion, ecomorphology, timing of reproduction and daily activities, among others (Schoener 1974; Bambach 1983, 1985; Simberloff and Dayan 1991). Many studies have compared individual ecological characters over long time scales, including tiering (the stratification of infauna and epifauna; Thayer 1979, 1983; Ausich and Bottjer 1982; Bottjer and Ausich 1986; Droser and Bottjer 1989, 1993), insect feeding habits (Labandeira and Sepkoski 1993), energetic consumption (Vermeij 1999; Bambach 1993, 1999; Bambach et al. 2002), and body size (Smith et al. 2004), among others. Various individual characters related to escalation—chiefly carnivory, infaunality, and mobility—have been a recurrent focus (Vermeij 1977, 1987; Signor and Brett 1984; Kowalewski et al. 1998, 2006; Kosnik 2005; Madin et al. 2006; Aberhan et al. 2006).

The most ambitious multivariate guild attempt was conducted by Bambach (1983, 1985) in a series of studies comparing the ecology of Sepkoski's (1981) three evolutionary faunas. Using a three-dimensional framework defined by foraging habit, microhabitat, and mobility, he concluded that the timing of marine ecological diversification throughout the Phanerozoic was irregular and coincided with the diversification of successive evolutionary faunas, primarily resulting in increased utilization of previously vacant ecospace. These conclusions have withstood more recent analyses using broader ecological characters (Bambach et al. 2007; Bush et al. 2007). Bambach's framework has been influential (Aberhan 1994; Bottjer et al. 1996; Droser et al. 1997; Radenbaugh and McKinney 1998), but different qualitative frameworks also exist. For example, the Evolution of Terrestrial Ecosystems consortium (Behrensmeyer et al. 1992, 2003; especially Wing 1988; Wing and DiMichele 1992; Damuth et al. 1992) used a comprehensive framework for comparing terrestrial communities. Retallack (2004) also presented a framework focused on general ecological strategies.

Although such approaches are well suited to identifying synoptic ecological trends, they primarily are limited to making descriptive, qualitative comparisons or statistical comparisons of isolated ecological characters. A syn-

thetic quantitative framework, while also allowing such analyses, is preferable for several reasons. First, it facilitates more robust documentation of overall changes in ecospace utilization (Bambach 1983, 1985, 1993). This can benefit our understanding of the previously mentioned univariate trends because their causes are likely intricately related to other ecological characters that this method captures simultaneously. Second, quantification makes it possible to determine the structural components of individuals occupying ecospace (Van Valen 1974). That is, it allows measurement of the central location, dispersion (disparity), and distribution of all individuals' life habits in the multidimensional space defined by the ecospace framework. Of equal importance, it allows recognition of those ecological regions that are not occupied by individuals—either currently or in the past. Finally, quantification fosters the development of mechanistic null models that can test both the robustness of observed trends and distinguish among their possible causes (McShea 1994, 1998; Foote 1996a; Ciampaglio et al. 2001; Pie and Weitz 2005). The proposed framework marks the first framework suitable for such large-scale, quantitative comparisons.

Such motivations drove the quantification of morphological disparity (Gould 1989, 1991; Briggs et al. 1992; Foote and Gould 1992; McShea 1993; Wills et al. 1994). Given the success of these approaches (Saunders and Swan 1984; Foote 1991a,b, 1992, 1993a,b, 1994, 1995, 1996a,b, 1999; Thomas and Reif 1993; Wagner 1995, 1997; Wills 1998, 2002; Lupia 1999; Smith and Lieberman 1999; Eble 2000; Thomas et al. 2000; Ciampaglio et al. 2001; Ciampaglio 2002; Harmon et al. 2003; Stockmeyer Lofgren et al. 2003; McClain et al. 2004; Villier and Korn 2004; Collar et al. 2005), quantification of ecological diversity seems to offer profound benefits.

In this study, I propose a general method for quantifying ecological diversity that unites an extended framework of Bambach (1983, 1985) and the methodological advances of morphological disparity (see Foote 1991a; Wills 2002). The modified framework consists of 60 ecological character states that are universally applicable to extant or extinct organisms and

that are logically independent of taxonomy; in this sense, the framework constitutes a theoretical ecospace. It allows quantification of ecological richness and disparity directly for any entity—individuals, lineages, or entire communities. The framework and the methods used in analyzing it are suitable for answering many questions in comparative paleoecology. Here it is used to compare the ecological diversity of Paleozoic (Cambrian through Devonian) and modern biotas from deep-subtidal, soft-substrate habitats in terms of ecological (life habit) richness, disparity, and overall distributions of life habit gradients in ordination-space.

Paleozoic and Modern Data Sets

The biotas used here represent assemblages from deep-subtidal, soft-substrate habitats. The Paleozoic biota comprises 449 samples compiled from 167 references, including nearly 80,000 individual fossils (an underestimate considering only one-quarter of samples have abundance data) and more than 3500 species ranging in age from Cambrian through Devonian (Novack-Gottshall 2004). The modern biota comprises 50 samples compiled from three references in the literature. Ten samples were selected at random from comparable habitats along the western North Atlantic—five samples from the Mid Atlantic Bight (Lynch et al. 1979) and five from the Beaufort Shelf (Day et al. 1971)—totaling more than 8000 individual organisms and 450 species from the Boreal Province on an outer continental shelf margin. Although these samples are from the same habitat as the Paleozoic samples, the temperate, oceanic shelf does not represent the same latitude as most Paleozoic samples. To account for this difference, 40 samples were also selected at random from appropriate habitats in the tropical, epeiric Gulf of Carpentaria (Australia) (Long et al. 1995), totaling more than 91,000 individuals and 400 species.

The Ecospace Framework

The life habits of the taxa in the biotas were operationalized by using the following standardized ecospace framework criteria. It is important to note that although the frame-

work is well suited for comparing such marine biotas, it is equally well suited for characterizing the life habits of other ecological groups; the explanations that follow draw on examples from the full spectrum of life, both extinct and extant and representing most habitats.

Characters in the Framework.—The framework (Table 1; see also Appendix A online at <http://dx.doi.org/10.1666/pbio06054.s1>) includes 60 character states in 27 characters that describe the basic autecological capabilities of organisms. Characters include (1) resources, such as diet and microhabitat; (2) structures, behaviors, or other features related to the acquisition, maintenance, or defense of these resources, such as foraging, mobility, and substrate attachment; and (3) other important autecological characters, including body size, physiology, and reproduction. Depending on the scope of analysis, some researchers (especially macroecologists and paleobiologists) may be inclined to add geographic range, abundance, or other emergent (statistical, *sensu* Maurer 1999) group characters to this list (Peters 1983; Brown 1995; Gaston and Blackburn 1996; Maurer 1999). Adopting cladistic terminology, the term *character* refers to individual classes of ecological capabilities (faculties *sensu* Bock and von Wahlert 1965, whereas *character state* denotes the possible types of these capabilities (Swofford et al. 1996).

The characters were chosen according to four criteria. First, the characters must be ecologically important for living organisms. Habitat and dietary characters are given greater emphasis—that is, there are more characters—because of their recognized importance (Schoener 1974). Second, the characters must be logically independent of one another; that is, they refer to different components of life habits. This is a requirement of all theoretical multidimensional morphospaces (McGhee 1999) and even cladistics (Swofford et al. 1996). In reality, correlations may exist and can be investigated a posteriori, but the assumption here is that all character combinations are possible—even if never realized because of constraints (Seilacher 1970). Third, the characters must be assignable to ancient taxa, including long-extinct species with no

TABLE 1. Twenty-seven characters (bold) and 60 states (numbered) in ecospace framework. Characters listed in parentheses are not easily determined for many fossil groups.

<i>Binary characters</i>	
Reproduction	Primary feeding microhabitat
1. Sexual	30. Above primary substrate
2. Asexual/Clonal	31. Within primary substrate
(Development)	Immediate feeding microhabitat
3. Direct development	32. Above immediate substrate
4. Indirect, non-feeding development	33. Within immediate substrate
5. Indirect, feeding development	Diet
(Brooding)	34. Autotroph
6. Brooding	35. Microbivore
(Dispersal vector)	36. Carnivore
7. No vector	37. Herbivore
8. Fluid-dispersed	38. Fungivore
9. Organism-dispersed	Physical condition of food
10. Self-dispersed	39. Incorporal feeder
Mobility	40. Solution feeder
11. Sedentary	41. Particle feeder
12. Passively mobile	42. Bulk feeder
13. Facultatively mobile	Feeding habit
14. Intermittently mobile	43. Ambient feeder
15. Habitually mobile	44. Filter feeder
Substrate/medium composition	45. Attachment feeder
16. Biotic	46. Mass feeder
17. Lithic	47. Raptorial feeder
18. Fluidic	(Feeding selectivity)
Substrate consistency	48. Non-selective
19. Hard	49. Selective
20. Soft	50. Secondarily selective
21. Insubstantial	<i>Ordered, multistate characters</i>
Substrate relationship	51. Skeletal body volume
22. Attached	52. Primary stratification
23. Free-living	53. Immediate stratification
Primary microhabitat	54. Primary food stratification
24. Above primary substrate	55. Immediate food stratification
25. Within primary substrate	56. (Mobile velocity)
Immediate microhabitat	57. (Spatial patterning)
26. Above immediate substrate	58. (Dispersal distance)
27. Within immediate substrate	59. (Relative metabolic rate)
Support	60. (Life span)
28. Supported	
29. Self-supported	

living relatives or morphological analogues. Reliance on taxonomic information has been minimized by focusing on general—and consequently often convergent—ecological capabilities of organisms instead of on particular, often taxon-specific adaptations. Fourth, the individual states for each character must be fully subdivided. For example, a fluidic substrate (Table 1) is a valid substrate state because it represents a logical absence of a substrate, used by organisms that do not inhabit lithic or biotic substrates; see Appendix A for further examples.

The ecospace framework does not include synecological characters, except when an organism's autecological characters necessarily

imply some form of interaction. For example, carnivores are categorized only as meat eaters, and not with regard to their particular prey. In other words, character states referring to particular organisms—trilobite eaters, nectar eaters, and the like—were avoided because they limit comparisons to particular times when that dietary item was extant. This may limit the framework's utility for some comparisons, but it is a prerequisite if comparisons are to be made across wide taxonomical, morphological, and ecological ranges. Modifications of this framework are possible depending on the objectives of the study. A comparison spanning the history of life on Earth might find the character states carnivore, her-

bivore, and fungivore too restrictive; a replacement with chemoheterotroph might prove more useful.

Unlike the Skeleton Space (Thomas and Reif 1993; Thomas et al. 2000), this list is provisional and not intended to be fully inclusive. Although it is applied below to marine biotas, it is intended to characterize universally the significant autecological capabilities of all organisms in any habitat. Additional characters can be devised when such information is available or when a study requires them. Reproductive strategies, seasonality, daily cyclicity, food size, and numerous biogeochemical and physiological characters are important ecologically (Schoener 1974; Pianka 2000), but this information is not available for most fossil species, and so it is not included in the present treatment. Some possible candidates are listed here (Table 1 and Appendix A, in parentheses) with the hope they will be included in future comparisons. Similarly, it may sometimes be necessary to limit the number of characters and states if relevant information is not available. In the examples that follow, for instance, only 44 character states are used because of the current limitations of using fossilized species.

Coding of Character States.—Unless noted, the term *individuals* in the following refers to individual ecological entities—individuals or species—whereas the term *groups* refers to more inclusive groups—communities and lineages. Most character states are binary, coded 0 for absent and 1 for present. Several characters—body size, microhabitat stratification and others—are coded as continuous, ordered, multistate characters by using integers (or fractions if de-weighting is preferred; Sneath and Sokal 1973; Van Valen 1974). Such multistate characters are used only when there is a clear ordination among their states. When a state cannot be confidently assigned or is unknown currently, it can be coded as unknown. Such codings, however, reflect only a lack of knowledge rather than nonrelevance; in principle, all states can be coded.

This method of coding, in which multistate characters are the exception, might seem to warrant further explanation. In most cladistics or morphological disparity studies, the char-

acters are typically homologous, with each individual displaying a single phenotype. In contrast, individuals are more variable ecologically, marked by behavioral flexibility, generalism, and convergence with unrelated individuals (Peterson et al. 1999; Losos et al. 2003). This can be notably true for sexually dimorphic species (e.g., Pietsch 1976, 2005). The coding scheme used here accommodates such variability by allowing single individuals to be coded with multiple states in the same character. For example, semi-infaunal individuals, such as trees and some mussels, can be coded as living simultaneously above and within the sediment. (Other common ecological and behavioral capabilities best described by multiple character states for the same individual—hermaphroditism, parthenogenesis, substrate and microhabitat generalism, omnivory, among others—are discussed further in Appendix A.) In cases where individuals typically utilize a primary resource, even when capable of using others, only the primary resource is coded; this is the same method used to classify guilds (Root 1967). A limitation of such flexibility in coding is that every individual must exhibit at least one state for every character. In other words, no individual—while alive—lacks some diet, some microhabitat, or some body size. This has analytical consequences, namely that not every combination in the framework is possible.

Although individuals can undergo changes in their ecological characters throughout their life cycle—most notably due to metamorphosis or allometry—they are coded from the perspective of adult, sexually mature organisms, where ecological characters are usually most stable. Organisms with indeterminate growth are coded at the attainment of sexual maturity. Entire colonies are treated as individuals. Depending on the goals of a study, one could focus on each colony member individually, include individual genders or age or life stages separately, or code individuals within a population separately.

Some characters, such as absolute body size and microhabitat stratification, are scale-independent and coded according to absolute criteria. However, because the ecospace framework has an autecological focus, most char-

TABLE 2. Utility of ecospace for describing benthic microhabitats. If using just three characters (primary microhabitat, immediate microhabitat, and substrate) with several character states (in italics), it is possible to describe twelve unique microhabitat combinations. Although existing terminology exists for most combinations, the three characters are more succinct and more broadly applicable for describing them. Additional combinations are possible; for example, it is possible to occupy multiple states simultaneously. The same classification can be used for other focal habitats; in this example, the habitat is the benthic one with the sediment-water interface as the primary substrate. See text for further discussion. This ecospace framework allows the discovery of combinations that are unoccupied in nature, such as the microhabitat that is within the benthic sediment but above the water; although this may seem an unlikely life habit, it might be possible to imagine an organism that floats or flies in gas-filled chambers within a burrow network.

Primary microhabitat	Above S/W		Within S/W	
Immediate microhabitat	Above	Within	Above	Within
Substrate composition				
Biotic	Ectoparasite, epibiont	Endoparasite, borer, nestler	Ectoparasite	Endoparasite
Lithic	Epibenthos	Miner, cryptobiont	Burrowing endobenthos, subsurface miner	“Swimming” endobenthos
Fluidic	Atmobiont	Nekton, plankton	Unknown?	Interstitial meiobenthos

acters are coded from the perspective of the individual organism (or colony). An example is an organism’s immediate substrate, which may be rather different from the primary substrate of the focal habitat. Organisms that live cryptically within the cavities of coral reefs or endoparasitically within another organism may be both *above* substrates in a primary sense (i.e., situated above the sediment-water interface), but *within* substrates in an immediate sense (i.e., inhabiting a crevice or tissue). Because of this versatile perspective and the broad nature of the characters, the ecospace framework transcends the limitations of scaling; any ecological entity can be compared.

The Framework as a Theoretical Ecospace.— Ecological terms used in common classifications (e.g., Hunt 1925; Yonge 1928; Elton and Miller 1954; Turpaeva 1957; Jennings 1965; Walker 1972; Walker and Bambach 1974; West 1977; Bambach 1983; Merritt and Cummins 1996; Taylor and Wilson 2002) were used in the framework only when they were defined by a single character. For example, the common term *deposit feeder* was avoided because it conflates diet with feeding microhabitat, while implying aspects of mobility, resting microhabitat, foraging strategy, and sometimes even body size (Plante et al. 1990). The framework is versatile, however, in recognizing

such common life habits through combinations of relevant states.

In this way, the framework reduces the number of ecological terms needed to describe different life habits. Consider, for example, the number of words describing microhabitats (Elton and Miller 1954; West 1977; Taylor and Wilson 2002). If the substrate of the focal habitat is the sediment-water interface, three independent characters alone—primary microhabitat, immediate microhabitat, and immediate substrate—describe a dozen microhabitats (Table 2). Epibenthic organisms live on lithic sediment above the sediment-water interface in both a primary and an immediate (i.e., at the scale of the organism) sense. Cryptobionts and some miners live above the primary substrate, but within a lithic immediate substrate. The various parasites, epibionts, borers, and nestlers have similar relationships to a biotic substrate. Additional character states can further partition each broad microhabitat, with other combinations also possible; for example, semi-infaunal bivalves live above and within the primary sediment simultaneously (Stanley 1970). The same framework accommodates terrestrial and oceanic microhabitats by changing the primary substrate of the focal habitat from sediment-water interface to ground or water’s surface, respec-

TABLE 3. Example of ecospace framework coding. Taxa 1–5 are modern species and taxa 6–10 are Paleozoic species. Only 44 characters and states for which reliable information is available are used. The numbers and order of the character states follows that in Table 1 and Appendix A. For binary characters, a value of 1 designates the presence of an ecological character state. See Tables A1–6 for designation of multistate character states in characters 51–55; when measuring disparity in the text, such states have been deweighted to range from 0 to 1.

	1	2	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26
<i>Bugula neritina</i>	1	1	1	0	0	0	0	0	1	0	1	0	0	1	0	1	0	1
<i>Cancer irroratus</i>	1	0	0	0	0	0	1	0	1	0	0	1	0	0	1	1	0	1
<i>Cirolana polita</i>	1	0	0	0	0	0	1	0	1	0	0	1	0	0	1	1	0	1
<i>Glottidia pyramidata</i>	1	0	0	0	1	0	0	0	1	0	0	1	0	1	0	0	1	0
<i>Mitrella marquesa</i>	1	0	0	0	0	0	1	0	1	0	0	1	0	0	1	1	0	1
<i>Calceocrinus chrysalis</i>	1	0	1	0	0	0	0	1	1	0	1	0	0	1	0	1	0	1
<i>Isotelus maximus</i>	1	0	0	0	0	0	1	0	1	0	0	1	0	0	1	1	0	1
<i>Modiolopsis versaillesensis</i>	1	0	0	0	1	0	0	1	1	0	0	1	0	1	0	1	1	0
<i>Naraoia compacta</i>	1	0	0	0	0	0	1	0	1	0	0	1	0	0	1	1	0	1
<i>Zygospira modesta</i>	1	0	1	0	0	0	0	1	1	0	1	0	0	1	0	1	0	1

tively (see discussion of microhabitat characters in Appendix A).

This example demonstrates an additional feature of the framework: both realized and unrealized ecological combinations are noted a priori. For example, a microhabitat exists in Table 2 within the benthic sediment in a primary sense, but above water in an immediate sense. Although this may seem a logically impossible life habit, it is not. Imagine some organism that floats on the surface of—or perhaps flies in—gas-filled chambers in a submerged burrow network. Similarly unusual ecological habits and microhabitats are common in nature (Darwin 1875; Norell et al. 2001; Rubinoff and Haines 2005; Seilacher 2005).

The framework thus constitutes a theoretical ecospace, in the sense of a theoretical state-space defined by its character-dimensions. This is analogous to the term *morphospace* used by theoretical morphologists (Raup and Michelson 1965; Hickman 1993; Thomas and Reif 1993; Chapman et al. 1996; McGhee 1999; Thomas et al. 2000), with which they share similar methodological approaches and goals. The framework delineates, a priori, the domain of logically possible life habits that *could* be occupied by all organisms, and that is independent of the actual life habits occupied by organisms. When used in a comparative context, existing life habit complexes—such as deposit feeding—can emerge as outcomes of analyses comparing ecological entities (see below). With the exception noted above, the

framework can be fully occupied, at least in theory. By being unconstrained by the life habits occupied by *actual* organisms, it also points toward life habits that have yet to evolve, that are biomechanically nonfunctional or evolutionarily unfit, or that are developmentally impossible (Raup and Michelson 1965; Seilacher 1970; McGhee 1999).

Coding of Individual Organisms and Species.—The framework is equally suitable for coding extant and extinct individuals. For living species (such as those in the modern biota), inferences of basic autecological characters are straightforward, but not without some obstacles (Ricklefs and Miles 1994). Performance studies (e.g., Arnold 1983; Garland and Losos 1994; Wainwright 1994; Irschick 2002, 2003) have been used to great effect in determining how individual morphologies perform functionally. One important consequence of such studies is that the same function can be performed by multiple morphological designs (Alfaro et al. 2004, 2005; Wainwright et al. 2005); such convergence has been identified by using more general ecological characters as well (Marks and Lechowicz 2006). However, such formalized analyses are not usually necessary here because the framework characters are straightforward and often readily inferable (in much the same way as done by Marks and Lechowicz [2006]).

For fossils (such as those in the Paleozoic biota), direct observation of ecological characters is rare but not impossible (Boucot 1990; see obrution deposits in Brett 1984, 1990; Brett

TABLE 3. Extended.

27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	51	52	53	54	55
0	0	1	1	0	1	0	0	1	0	0	0	0	0	1	0	0	1	0	0	0	4	2	2	2	1
0	0	1	1	0	1	0	0	0	1	0	0	0	0	0	1	0	0	0	0	1	5	2	2	2	3
0	0	1	1	1	1	1	0	0	1	0	0	0	0	0	1	0	0	0	0	1	6	2	2	2	2
1	0	1	1	0	1	0	0	1	0	0	0	0	0	1	0	0	1	0	0	0	3	2	1	1	1
0	0	1	1	0	1	0	0	0	1	0	0	0	0	0	1	0	0	0	0	1	3	1	1	1	2
0	0	1	1	0	1	0	0	1	0	0	0	0	0	1	0	0	1	0	0	0	4	2	2	2	1
0	0	1	1	1	1	1	0	0	1	0	0	0	0	0	1	0	0	0	0	1	6	2	2	1	3
1	1	1	1	0	1	0	0	1	0	0	0	0	0	1	0	0	1	0	0	0	4	3	2	3	1
0	0	1	1	0	1	0	0	0	1	0	0	0	0	0	1	0	0	0	0	1	3	1	1	1	2
0	1	0	1	0	1	0	0	1	0	0	0	0	0	1	0	0	1	0	0	0	2	3	1	3	1

and Baird 1986). Barring direct evidence, ecological characters in fossils are inferred by bio-mechanical studies, analysis of environmental distribution, and comparison with relatives or living morphological analogues (Rudwick 1964; Stanley 1970; Alexander 1983, 1990; Hickman 1988; Plotnick and Baumiller 2000; Vogel 2003). Despite these varied sources, such inferences remain less powerful than those made with living individuals. Although specific procedures are not developed here, it is possible to test the sensitivity of results to such coding decisions (see Felsenstein 1985a; Foote 1993a). In cases where characters are unknown currently, states can be coded as unknown.

The life habits of all taxa in the databases were coded to the lowest taxonomic level—usually family or genus—for which reliable information was available. Coding decisions have been informed currently by 197 published references. Detailed examples of how two species—one extant and one extinct—were coded with the ecospace framework are found in Appendix B in the supplementary material (<http://dx.doi.org/10.1666/pbio.06054.s1>). Representative codings for ten arbitrarily selected extant and extinct species from the Paleozoic and modern biotas are reported in Table 3: the five extant species are the lingulate brachiopod *Glottidia pyramidata*, bryozoan *Bugula neritina*, crab *Cancer irroratus*, isopod *Cirolana polita*, and snail *Mitrella marquesa*; the five extinct, Paleozoic species are the trilobite *Isotelus maximus*, putative trilobite *Naraoia*

raoia compacta, crinoid *Calceocrinus chrysalis*, mussel *Modiolopsis versaillesensis*, and rhychnonellate brachiopod *Zygospira modesta*.

The Quantification of Ecological Diversity

Ecological Diversity of Organisms and Species.—Because the character states in the ecospace framework are all theoretically independent, the entire ecospace contains more than 106 quintillion unique combinations (1.069×10^{19}) that are theoretically possible (given the previous exception that all individuals occupy some state in each character). Using just the 44 character states that are currently practical with fossils still yields nearly 300 trillion possible combinations (2.993×10^{14}).

Once coded, these unique combinations serve as a basic unit of ecological (life habit) diversity that is theoretically independent of taxonomy and morphology. Because they are coded quantitatively, they furthermore offer a rich arsenal for comparative paleoecology. As one example, it is possible to compare the life habits of species from Table 3 as a dendrogram (Fig. 1). Prior to calculating distances, multistate characters were dewighted so each maximum state was equal to 1 and the distances were divided by the square root of 44 character states so that pairwise distances could range from a value of 1 (when two species share no character states in common) to 0 (when the species occupy the same life habit).

Although separated by at least 500 Myr, the modern predatory gastropod *Mitrella marquesa* and the Cambrian putative trilobite *Naraoia*

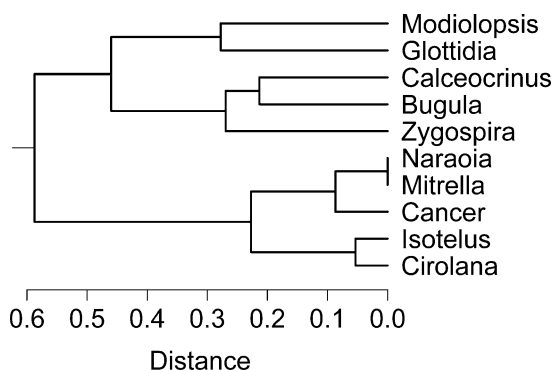


FIGURE 1. Dendrogram of ecological distances between marine taxa in Table 3. Cluster analysis used function `hclust()` in R 2.3.1 (R Development Core Team 2006) with the UPGMA method and Euclidean distance. Distances were standardized to range from 0 to 1 by deweighting of multistate characters and by dividing distance by square root of number of character states.

compacta can be seen to share the same life habit, defined by the ecospace framework (Table 3, Fig. 1). Such correspondence across 44 states is an important feature of this framework, allowing recognition of meaningful ecological similarities, even when the taxa share no such overarching similarities in body plan, morphology, skeleton, taxonomy, or temporal occurrence. This similarity, however, does not preclude other important distinctions in their specific niches. Speed of locomotion, size of prey, specific foraging strategies, and the like could all be different, but it is not possible to determine such distinctions for most fossil taxa. A virtue of this comparative approach is that it may point toward unanticipated ecological similarities or interactions among very distantly related taxa (see Brown and Davidson 1977; Janzen 1977; Reichman 1979) that can be tested with additional research.

Figure 1 reveals several other potentially unanticipated results. There are four life habits—represented by the *Mitrella/Naraoia* pair, *Cancer*, *Cirolana*, and *Isotelus*—that are similar to each other in being habitually mobile, epifaunal predators. *Glottidia* and *Modiolopsis* represent two similar life habits, sharing facultatively mobile, infaunal, filter-feeding abilities; *M. versailensis* is known also to nestle in arborescent bryozoans (Pojeta 1971). The three remaining habits—represented by *Zyg-*

ospira, *Bugula*, and *Calceocrinus*—are also similar, sharing sedentary, epifaunal, filter-feeding abilities. Each of these three basic life habit groupings includes modern and Paleozoic taxa, a similarity that would be unlikely if comparisons were based on evolutionary distances, or on their proxies in taxonomy and morphology. The ecospace framework allows analyses to focus solely on ecological characters, and it allows recurrently evolved and complex suites of life habits—raptorial predators, sedentary filter feeders, and the like—to emerge as *results* of the analysis, rather than assuming such life habit complexes exist a priori. Similar methods can be extended to compare entire biotas, such as the Paleozoic and modern.

Ecological Diversity of Multispecies Assemblages and Clades.—The simplest measure of ecological diversity for comparing groups of taxa is ecological richness, defined here as the number of occupied combinations (life habits) in the framework. This is more direct than species richness (Magurran 1988) because it measures actual ecological variation instead of using the proxy of taxonomy (Tilman et al. 1997; Díaz and Cabido 2001; Reich et al. 2004).

Another important component of ecological diversity is disparity, a measure of how different the life habits within a group are from one another. The ecospace framework can be used to measure the disparity of individuals within clades or multispecies assemblages (communities). Distance metrics—mean Euclidean distance, range, total variance, and the like (Sneath and Sokal 1973; Van Valen 1974; Foote 1991a; Ciampaglio et al. 2001; Wills 2002)—are most commonly used in the study of morphological disparity and can also be used here. For example, using mean Euclidean distance, the disparity of the modern “assemblage” (0.443, Table 3) is approximately the same as that of the Paleozoic “assemblage” (0.492). This method is used below for comparing entire biotas in the Paleozoic and modern.

At even larger scales, it is possible to use the ecospace framework to understand the macroevolutionary history and evolutionary paleoecology of entire lineages. An example is not provided here, but such an approach

might allow novel ways to measure ecological diversity, and especially disparity, during evolutionary radiations (Stanley 1968; Valentine 1969, 1995) mass extinctions (Jablonski 1986a; Valentine and Jablonski 1986; Jablonski and Raup 1995), and post-extinction recoveries (Hansen 1988; Jablonski 1998), as well as address the impact of ecological diversity on genus-level longevity (Kammer et al. 1998; Miller and Foote 2003; Liow 2004), onshore-offshore diversification (Jablonski et al. 1983; Sepkoski and Miller 1985; Westrop and Adrain 1998) and other macroevolutionary phenomena (Stanley 1979).

Comparative Paleocology of the Marine Biosphere: Do Paleozoic and Modern Biotas Exhibit Different Levels of Ecological Diversity?

It is a long-held impression that modern communities are more diverse ecologically than those of the distant past (Hutchinson 1959: pp. 155–156; Valentine 1969; 1973; Vermeij 1977, 1987; Bambach 1983, 1985). The goal here is to use the quantitative ecospace framework proposed above to assess the overall similarity in ecospace occupation in two large biotic groups from a single, deep-subtidal, soft-substrate habitat. This was done by pooling individual genera (using a randomly selected species for each genus) in the Paleozoic (Cambrian–Devonian) database and comparing it to the pooled genera in the modern database.

Important differences exist between the fossil and modern samples. For example, the modern ones are not fossilized and they were collected with benthic trawls and dredges. There are also many more Paleozoic samples, covering a much wider temporal duration. Although such differences limit absolute comparisons in ecological diversity (Foote 1992), standardizations used below provide a means to estimate the relative magnitude of ecological differences between Paleozoic and modern biotas. The impact of non-fossilizable organisms was evaluated by comparing the Paleozoic biota to untreated and taphonomically treated modern databases. All-Modern is the entire modern data set—including soft-bodied, fragile, and rarely fossilized taxa. The

Taph-Modern treatment includes those genera—primarily mollusks, crustaceans, tubicolous and jawed polychaetes, echinoderms, and bryozoans—nearly always or only occasionally expected to yield fossil representatives (Schopf 1978; Sepkoski 1982, 2002; Kidwell 2001, 2002).

First, the ecological diversity of groups is compared by using their ecological (life habit) richness: genus richness relationship based on 2000 bootstrapped iterations for each aggregate group sample. This rarefaction method (Sanders 1968; Hurlbert 1971; Bambach 1983; Foote 1992; Miller and Foote 1996; Gotelli and Colwell 2001) standardizes for differences in sample size both within samples—because all samples in each biota are combined—and between biotas, at least when observing differences between the shape of each resulting ecological richness/genus richness relationship. Error bars were calculated as the standard deviation of the distribution of means (Foote 1993b; Efron and Tibshirani 1993). Ecological disparity within each group was calculated as mean Euclidean distance after deweighting multistate characters and standardizing for number of character states. Significance of differences in richness and disparity was tested with 2000 bootstrap replicates (Efron and Tibshirani 1993). All tests are one-sided unless noted. All statistics and quantitative analyses used R 2.3.1 for Windows (R Development Core Team 2006).

Although the All-Modern biota has not been taphonomically treated, its ecological richness/genus richness relationship is only moderately above that for the Paleozoic biota (Fig. 2). This difference is not statistically significant at a standard richness of 400 genera (Fig. 3A; $\text{diff}_{\text{obs.}} = 13.40$, $\text{diff}_{\text{crit.}} = 18.00$, $p = 1.005$). This overall similarity is surprising because the fossil record filters out some life habits, differentially preserving ecologically similar taxa (Schopf 1978); this might greatly underestimate the richness of the original Paleozoic biota. The magnitude of such differences might be approximated by the reduced trend using the Taph-Modern treatment (Fig. 2), although the difference here is only marginally significant at a standard richness of 240 genera ($\text{diff}_{\text{obs.}} = 13.47$, $\text{diff}_{\text{crit.}} = 14.00$, p

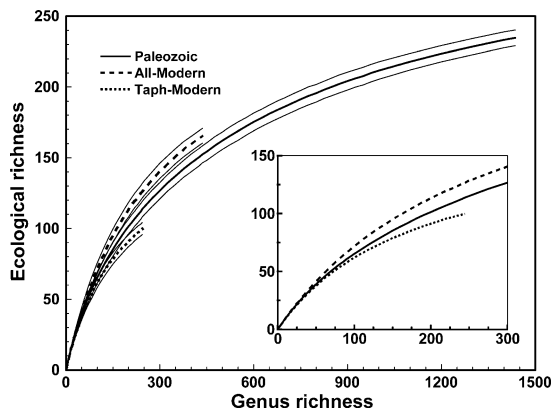


FIGURE 2. Ecological richness/genus richness relationship for modern and Paleozoic (Cambrian–Devonian) deep-subtidal, soft-substrate biotas. Ecological richness is defined as number of life habits. Each curve is a rarefaction (2000 bootstrap iterations) for all samples in the database, pooled by time and taphonomic treatment. Paleozoic includes all Cambrian–Devonian fossil taxa; All-Modern includes all modern taxa, including unfossilizable ones; Taph-Modern includes modern taxa expected to leave a fossil record; see text for further explanation. Error bars are one standard deviation from the distribution of 2000 bootstrapped means. Inset graph highlights relationship where error bars overlap; error bars are removed to clarify relationships. See text for statistical tests.

= 0.054). Measurement of ecological disparity offers a different result. Both when untreated and when taphonomically treated, the modern biota is significantly more disparate than the Paleozoic biota after standardizing for differences in genus richness (Fig. 3B; All-Modern at 400 genera: $\text{diff}_{\text{obs.}} = 0.065$, $\text{diff}_{\text{crit.}} = 0.014$, $p < 0.0005$; Taph-Modern at 140 genera: $\text{diff}_{\text{obs.}} = -0.058$, $\text{diff}_{\text{crit.}} = 0.019$, $p < 0.0005$).

It is increasingly well established (Vermeij 1977, 1987; Bambach 1983, 1985; Bambach et al. 2002; Aberhan et al. 2006; Kowalewski et al. 2006; Madin et al. 2006; Wagner et al. 2006) that the ecospace of modern biotas is rather different from those of Paleozoic biotas. This can also be examined here by using ordination to compare visually the distribution of genus life habits in these biotas. As a nonparametric ordination method, nonmetric multidimensional scaling (NMDS) is appropriate because the ecospace character states are categorical. Furthermore, NMDS is a robust and well-substantiated ordination method (Kenkel and Orłóci 1986; Faith et al. 1987; Minchin 1987), especially when resulting gradients are short, as is the case here because all ecospace states have a maximum distance of one unit, after

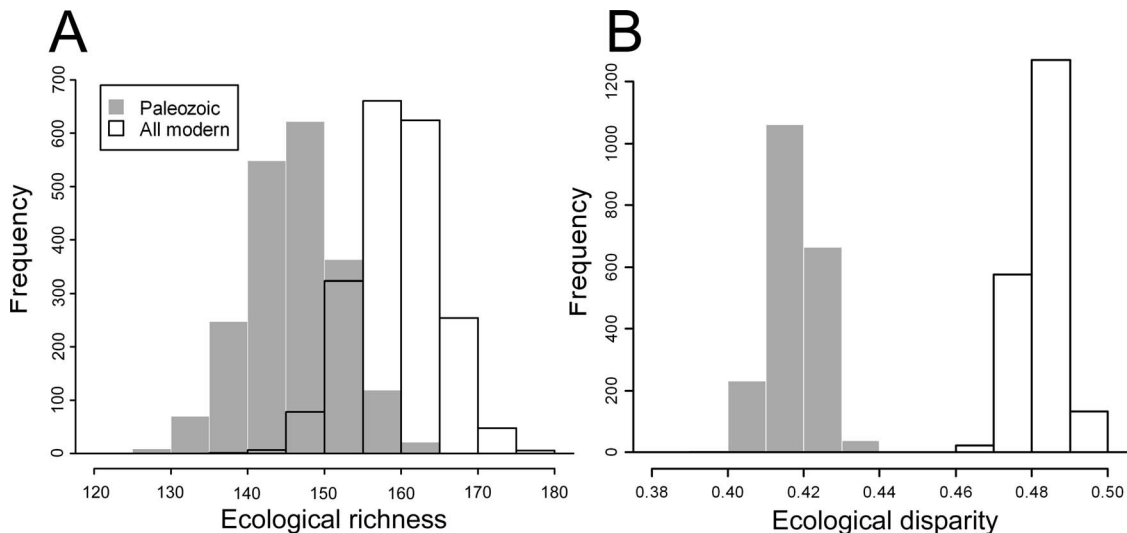


FIGURE 3. Ecological richness and disparity of modern and Paleozoic (Cambrian–Devonian) deep-subtidal, soft-substrate biotas. Modern communities include all taxa, including soft-bodied ones unlikely to be fossilized. Distributions produced from 2000 bootstrap iterations at constant genus richness of 400 genera. A, Ecological richness (life habit richness). Although modern communities contain slightly more numbers of life habits, the difference is not significant ($\text{diff}_{\text{obs.}} = 13.40$, $\text{diff}_{\text{crit.}} = 18.000$, $p = 1.005$), based on 2000 bootstrap iterations. B, Ecological disparity (mean Euclidean distance). Modern communities are significantly more disparate than Paleozoic ones ($\text{diff}_{\text{obs.}} = 0.065$, $\text{diff}_{\text{crit.}} = 0.014$, $p < 0.0005$) based on 2000 bootstrap iterations.

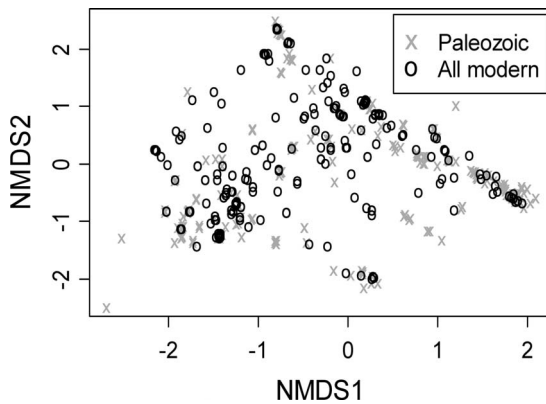


FIGURE 4. Graphical ordination ecospace for genus life habits in modern and Paleozoic (Cambrian–Devonian) deep-subtidal, soft-substrate biotas. Figure shows two axes from ordination of life habits coded with the eco-space framework. Nonmetric multidimensional scaling was conducted using function isoMDS() in R 2.3.1 (R Development Core Team 2006) with Euclidean distance. To avoid computational errors associated with species with identical life habits, the distance between such species pairs was made equal to one-half of the minimum observed distance between any other species pairs (see function metaMDS() in the vegan library; Oksanen 2006). There are 1376 Paleozoic taxa and 423 modern ones. Many points overlap—that is, taxa share identical life habits—but this overlapping does not obscure the graphical comparison because of the few life habits shared between the Paleozoic and modern biotas

deweighting. Metric ordination techniques resulted in nearly identical patterns despite vast algorithmic differences in methodology; the Procrustes sum of squares difference using principal components analysis was just 0.0000015 ($p < 0.001$ based on 1000 permutations; Peres-Neto and Jackson 2001).

The overall distribution of Paleozoic and All-Modern life habits is broadly similar in multivariate space (Fig. 4). Many points overlap in this ordination—that is, the taxa share identical life habits—but this overlapping does not obscure the graphical comparison because, as noted below, there are few life habits shared in common between the Paleozoic and modern biotas. To aid interpretation of axes using widely known taxa, Figure 5 demonstrates just the molluscan fraction of these biotas at the class level. In this two-dimensional, graphical ecospace, both axes represent gradients in suites of life habit combinations broadly interpretable as foraging strategies. High values along axis 1 are associated with taxa with sedentary, particle-feeding, filter-

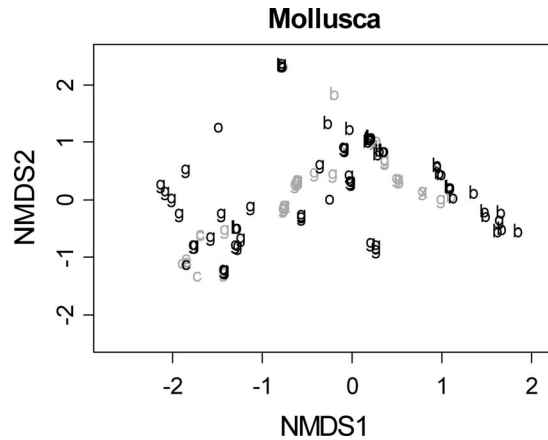


FIGURE 5. Graphical ordination ecospace for modern and Paleozoic (Cambrian–Devonian) mollusks only. Ordination is same as for Figure 4. Labels identify the major bivalve, cephalopod, and gastropod classes by first initial. Other classes are represented by symbols in Figure 4. There are 172 Paleozoic taxa and 114 modern ones, and the same circumstances for overlapping points apply as in Figure 4.

feeding strategies living attached to hard substrates, whereas those with low values are associated with free-living, habitually mobile, carnivorous, bulk-feeding raptors (see Appendix A for definition and discussion of ecospace states). High values along axis 2 are associated with intermittently mobile, microbivorous, particle-feeding mass feeders whose food source is located within primary and immediate substrates; low values are associated with carnivorous, bulk-feeding raptors with epibenthic food sources.

Taken together, these gradients delineate a rich variety of unique life habits. The broadly triangular distributions in Figures 4 and 5 provide end-members for each of the archetypal life habit complexes: sedentary, epifaunal filter feeders are found in the lower-right corner; intermittently mobile, infaunal, deposit feeders in the central apex; and mobile, epifaunal and swimming predators in the lower left. However, the gradients also accommodate those life habits that are intermediate between these extremes. For example, corals—those chimerically flower-like microcarnivores that have confounded categorization since Aristotle (Holland 2004)—cluster at the bottom center of the distribution (Fig. 4) because of their bulk-feeding carnivory, their fil-

ter-feeding foraging habit, and their sedentary, attached, epifaunal microhabitat.

A more complex gradient, apparent along the upper right side of the distributions seen in both Figures 4 and 5, describes the vast spectrum of particle-feeding microbivores. Using examples of modern molluscan genera (Fig. 5), this gradient delineates infaunal deposit feeders (such as nuculoid *Ennucula* and gastropod *Turritella*) at the apex through a region of siphonate deposit feeders (such as *Tellina*), mobile infaunal filter feeders (*Cyclocardia* and *Cultellus*), attached infaunal filter feeders (*Cucullaea*), and ends on the lower-right side with attached epifaunal filter feeders (such as semi-infaunal pteriid *Pinna*, adhesive gastropod *Crucibulum*, and ending with attached pteriid *Anomia*). Similarly, the gradient along the left side of this triangle delineates a mobility and predation spectrum dominated by gastropods, with intermittently mobile microbivores *Strombus* and *Xenophora* intersecting the particle-feeding gradient, continuing through facultatively mobile, attachment-feeding (and sometimes solution-feeding) carnivores and ectoparasites (*Volva*, *Eulimella*, and *Epitonium*), and ending at the lower-right corner with archetypal habitually mobile predators (such as *Murex* and cuttlefish *Sepia*). The predatory bivalve *Cuspidaria* also plots in this region. Similar gradient interpretations and the recognition of taxonomic overlap in life habits can also be observed in Figure 4. The same interpretations result when restricting analysis to the Taph-Modern treatment. Such categorically subtle but biologically real distinctions among life habits are not captured in most traditional ecospace frameworks (cf. Bambach 1983, 1985; Bambach et al. 2007; Bush et al. 2007). An important property of this ecospace framework is that it can make such rich and sometimes subtle life habit distinctions while still permitting the recognition of life habit convergence in unrelated taxa.

Despite the broad overlap in the distributions of Paleozoic and modern life habits, important differences remain. For example, although the entire modern biota is composed of 230 distinct life habits and the Paleozoic of 287, only 17 are shared, and seven result from taxa whose life habits could not be coded com-

pletely, such as "sponge indet." Such differences are expected given that modern biotas are enriched in predatory, mobile, and infaunal life habits compared to Paleozoic biotas (Vermeij 1977, 1987; Thayer 1979, 1983; Bambach 1983, 1985; Bambach et al. 2002; Novack-Gottshall and McShea 2003; Aberhan et al. 2006; Kowalewski et al. 2006; Madin et al. 2006; Wagner et al. 2006; Bambach et al. 2007; Bush et al. 2007). This can be substantiated by comparing the distributions of occupied states. The two biotas are significantly different in the occupation of half of the 44 character states (Table 4; Mann-Whitney two-sided tests, total $\alpha = 0.05$ after Bonferroni correction; but see warnings of reduced power [Underwood 1997]); this reduces to 15 significant differences when the Taph-Modern biota is used.

Compared with the Paleozoic biota, Taph-Modern is enriched in taxa whose life habits are mobile (although there is no difference among habitually mobile habits), are infaunal (in terms of both primary and immediate microhabitat), exploit other organisms (or structures) to occupy their specific microhabitat, live and feed on food that is further away from the sediment-water interface (either infaunally or epifaunally), are carnivorous, are feeding on dissolved food (frequently as parasites) or intact food, and forage by attaching to or taking in large quantities of food sources. Of these significant differences, only solution- and attachment-feeding should be viewed with caution because parasitism is sometimes difficult to identify in the fossil record. Because the comparisons are made among inhabitants of the same deep-subtidal, soft-substrate habitat, perhaps it is not surprising that characters related to substrate relationships (states 16–21) and the sources of food (states 30–33) are generally similar. Particulate, microbial diets (states 35 and 41) are the most common manner in which food is eaten in both biotas, but the manner in which this food is acquired is distinct, with Paleozoic taxa using filters and modern ones feeding en masse. Most of these differences are maintained with the All-Modern biota (Table 4), although several additional ones emerge.

Because these differences relate to many of

TABLE 4. Comparison of ecospace character-state occupation among Paleozoic and modern biotas. Mann-Whitney *U*-test used for comparing state distributions. Statistically significant differences after Bonferroni correction ($p < 0.00114$; total $\alpha = 0.05$) are noted with asterisks. Note that no unambiguous fungivores or herbivores were noted in the databases.

State	All-Modern	Taph-Modern	Paleozoic	Paleo/All-Modern		Paleo/Taph-Modern	
				<i>W</i>	<i>p</i> -value	<i>W</i>	<i>p</i> -value
1	100.0%	100.0%	99.9%	304717.5	0.4314	170922	0.5560
2	14.7%	12.3%	10.6%	293440	0.0208	168299	0.4380
11	12.2%	12.3%	46.9%	416635.5	<0.0001*	233046	<0.0001*
12	0.7%	0.8%	0.1%	309598	0.0530	173032	0.0448
13	18.2%	18.1%	6.5%	273473.5	<0.0001*	153286	0.0000
14	38.9%	40.3%	18.8%	240414.5	<0.0001*	132269	<0.0001*
15	30.0%	28.4%	26.1%	289682	0.1110	164826	0.4468
16	14.7%	14.0%	12.2%	286480	0.1634	161645	0.4304
17	91.5%	90.5%	86.9%	280947.5	0.0104	158854	0.1138
18	3.7%	3.3%	7.5%	314362	0.0050	176590	0.0165
19	19.8%	22.6%	25.9%	314111	0.0107	171199.5	0.2870
20	81.8%	78.6%	68.6%	256990	<0.0001*	149188	0.0017
21	3.7%	3.3%	7.5%	312472	0.0046	175528	0.0156
22	24.4%	25.5%	34.0%	338236	0.0002*	187497	0.0089
23	75.6%	74.5%	66.2%	279780	0.0003*	158535	0.0113
24	60.1%	58.0%	94.4%	408667.5	<0.0001*	232419	<0.0001*
25	50.7%	47.3%	7.6%	173123	<0.0001*	102671	<0.0001*
26	71.7%	62.6%	92.8%	368818.5	<0.0001*	222029.5	<0.0001*
27	37.3%	44.0%	15.2%	230776	<0.0001*	118092	<0.0001*
28	6.9%	9.9%	1.7%	293664	<0.0001*	159282	<0.0001*
29	93.1%	90.1%	98.3%	326088	<0.0001*	187722	<0.0001*
30	80.2%	86.4%	84.4%	313531	0.0418	165040.5	0.4101
31	27.2%	19.3%	21.2%	279390	0.0090	169495	0.5189
32	77.2%	82.7%	82.2%	310242	0.0217	164560.5	0.8342
33	31.1%	24.7%	25.5%	280765	0.0229	167880	0.7777
34	0.0%	0.0%	0.5%	313048	0.1434	175192	0.2737
35	67.5%	70.8%	76.9%	329322.5	0.0001*	178879	0.0385
36	51.6%	46.9%	27.1%	227227	<0.0001*	135145.5	<0.0001*
37	0.0%	0.0%	0.0%	N/A	N/A	N/A	N/A
38	0.0%	0.0%	0.0%	N/A	N/A	N/A	N/A
39	2.5%	2.0%	1.9%	309548.5	0.4127	174059.5	0.8666
40	2.8%	2.9%	0.0%	301519	<0.0001*	168622	<0.0001*
41	64.5%	67.1%	69.9%	317289	0.0338	173335	0.3724
42	46.5%	43.2%	29.6%	249862	<0.0001*	145518	<0.0001*
43	2.5%	2.1%	1.9%	308092.5	0.4053	173331.5	0.8599
44	31.1%	42.0%	49.1%	364421.5	<0.0001*	185250	0.0394
45	2.1%	3.7%	0.3%	304747.5	0.0003*	167800.5	<0.0001*
46	36.6%	35.0%	18.1%	242191	<0.0001*	138362	<0.0001*
47	43.3%	39.5%	30.1%	258377	<0.0001*	151021.5	0.0036
51	45.3%	53.3%	51.2%	348670	<0.0001*	152117.5	0.0509
52	45.0%	46.8%	42.3%	260628	0.0012	136988	<0.0001*
53	33.5%	39.2%	38.7%	334517	<0.0001*	156558	0.2287
54	34.9%	36.3%	34.2%	271897	0.1254	144861	0.0132
55	30.4%	35.1%	28.1%	288000	0.1956	140669.5	<0.0001*

the same general foraging characters defining the gradients in Figure 4, it should be expected that the distributions, despite much overlap, are distinct. Indeed, the Paleozoic biota has significantly greater values along the first axis than both All-Modern and Taph-Modern, marking a general shift from sedentary, epifaunal filter feeders to mobile predators

(Mann-Whitney one-sided test, All-Modern: $p < 0.0001$, $W = 3530443$; Taph-Modern: $p = 0.0002$, $W = 184677$). This difference is not observed along the second axis that demarcates deposit feeders and predators (All-Modern: $p = 1.0000$, $W = 245442$; Taph-Modern: $p = 0.9998$, $W = 138073$).

Such differences between the Paleozoic and

modern biotas can be due to several causes that the current analysis does not yet resolve. For example, it might be that such differences are the result of the combined accumulation of Paleozoic and modern samples spanning large geographic and temporal ranges. Finer geographic and temporal comparisons might reveal greater similarities (or differences) between modern and Paleozoic assemblages when restricted to certain regions or time intervals. Such temporal variation has been reported (Novack-Gottshall 2004; Madin et al. 2006; Bambach et al. 2007) during the Paleozoic interval considered here, especially from the Cambrian through Ordovician when many carnivorous habits were replaced by filter-feeding ones. The current method facilitates such finer-scale comparisons to be made quantitatively, even when there are no genera and but one family—the ubiquitous inarticulated brachiopod *Lingulidae*—shared in common among the ecological entities being compared.

Conclusions and Prospects

The composition of life has changed dramatically during its history (Valentine 1969, 1973; Bambach 1983, 1985; Vermeij 1987), and documenting this change and its ecological and evolutionary consequences remains an important goal. However, traditional methods to investigate these changes have been hindered by their focus on taxonomical or morphological comparisons alone. By focusing on ecological characters directly, the theoretical ecospace framework presented above serves as an important complement to these approaches.

When applied to deep-subtidal, soft-substrate Paleozoic (Cambrian–Devonian) and modern biotas, the framework describes a wide spectrum of important life habits observed in modern and ancient marine biotas. It does so in a standardized and taxon-free (*sensu* Wing 1988; Damuth et al. 1992) manner that is amenable to comparative analyses of ecological diversity using techniques previously used for morphological disparity. Although the comparison is a broad one, it suggests that the life habits in modern biotas are more ecologically disparate from one another,

on average, than were those in the Paleozoic, although both biotas shared generally similar numbers of life habits per genus. The distribution of these life habits overlaps broadly in ordination space, although the modern biota is enriched in carnivorous, actively mobile, and infaunal life habits, among others.

Because the ecospace framework ultimately is coded from the perspective of the individual organism, the framework is suitable for comparing ecological entities existing at extraordinarily different scales or living in different focal habitats. For example, it would be a simple task to compare the biota of the Southern Appalachian ecosystem (Hackney et al. 1992; Martin et al. 1993a,b) to that of a single lake or stream (Hutchinson 1965; Merritt and Cummings 1996; Benz and Collins 1998), interstitial benthic community (i.e., those living between grains of sand; Fenchel 1978), or even the gut fauna of a single individual (Hungate 1975; Plante et al. 1990). Despite major differences in spatial resolution and habitat diversity between these scales, there might be important similarities in terms of their structural organization.

But one might predict major differences between constituent organisms as well, primarily because of the influence of size on an individual's ecological capabilities (Peters 1983; Schmidt-Nielsen 1984; Bonner 2006). For example, to a first approximation, size determines whether the basic functions of life are governed by viscous or inertial forces (Vogel 1994, 2003). For many small organisms—such as agnostid trilobites (Müller and Walossek 1987) and copepods—their spinose or filamentous appendages function more like paddles than rakes (Koehl 1981; Koehl and Strickler 1981), making them *bona fide* raptors (*sensu* Appendix A) for their sizes (Vogel 1994). When found in much larger organisms, the same structures function very differently. Size should provide a dominant influence on the ecological constraints of organisms and the manner in which different organisms occupy ecospace.

At the largest scale, the ecospace framework offers a means to study the extent to which life—in its enormity—has occupied ecospace (*cf.* Thomas and Reif 1993). Little attention has

been paid to assessing the prodigious ecological varieties exhibited by organisms in this general, theoretical sense (McGhee 1999). Elementary—and essentially unanswered—questions abound. How extensively occupied is ecospace currently, and what degree of lability (*sensu* Losos et al. 2003) has it exhibited through time (Bambach et al. 2007)? To what degree is this occupation governed by convergent adaptation (Van Valen 1978; Moore and Willmer 1997; Losos et al. 1998; Vermeij and Lindberg 2000; Stayton 2006) and constraints of various kinds (Seilacher 1970; McPeck 2000)? How quickly and to what extent was ecospace filled during the Cambrian radiation and following the Late Permian mass extinction (Valentine 1969, 1995; Erwin et al. 1987; Droser et al. 1997)? Do mechanical constraints of anatomical design result in reduced levels of ecospace filling within terrestrial communities compared to marine ones (Thomas and Reif 1993)? Do equivalent taxonomic ranks—kingdoms, phyla, and classes—occupy similar levels of ecological diversity (Valentine 1969, 1980; Van Valen 1973; Valentine et al. 1991)? Such ideas deserve greater attention because they can point toward important, unrecognized explanations of evolutionary history.

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Appendix A

Definition of Ecospace Characters

This appendix presents and defines each of the ecological characters and character states in the ecospace framework, including discussion of examples, exceptions, and problematical issues. The following descriptions are not intended to offer a rationale for choosing each autecological character or to define common terms; rather, they justify how the various characters should be coded operationally and provide examples to explain their broad usage. Information available in introductory textbooks covering organismal ecology (e.g., Campbell and Reece 2004; Raven et al. 2004; Brusca and Brusca 2002) is not individually cited. Several of the terms are new or adapted from specific disciplines; these are defined. Several are in common usage (Lincoln et al. 1992) and are discussed only to note deviations from existing definitions. Neutral terminology is used whenever possible to keep jargon to a minimum. Characters set in parentheses are expected to be useful for future applications, but are not expected for immediate utility in studies including fossils. The ecospace framework as currently described here includes 27 characters (in bold) and 60 character states (numbered and italicized). The character brooding with a single alternative—present or absent—is treated as both a character and a character state. Unless noted, the term *individuals* in the following refers to individual ecological entities—individuals or species—while the term *groups* refers to more inclusive groups—communities and lineages.

Binary characters—Each of these characters is coded as 0 for absent and 1 for present, unless noted.

Reproduction—The reproductive mode of the individual. It is possible to be both sexual and asexual, whether via hermaphroditism (whether protandrous, protogynous, synchronous, or sequential), via periodic sexual reversal or parthenogenesis, or via having both asexual budding and sexual processes.

1. *Sexual*—Those individuals that reproduce sexually, whether individuation of offspring occurs or not.
2. *Asexual/Clonal*—Those genetically identical (barring mutation) individuals that reproduce asexually via fission, budding, or cloning, and that originate from a single individual (i.e., an ortet). Note that asexual individuals are defined solely by reproductive mode and not by the act of forming colonies, although such correlation may be common. Individuals that can regenerate portions of their body are not included here unless such capabilities regularly lead to fission or other reproductive processes.

(Development)—The mode of reproductive development for an individual. For marine invertebrates, this character is typically correlated with geographic and dispersal range (Jablonski and Lutz 1983; Jablonski 1986; Brown 1995). This character includes all aspects of development, whether larval development, insect metamorphosis, or plant alternation of generations. Not included is dormancy that occurs within an individual's lifetime and that is not directly related to reproductive development. In cases where individuals begin development as a lecithotrophic larva, becoming planktotrophic prior to settlement, it is appropriate to categorize the individual as both lecithotrophic and planktotrophic. Multiple character states can also apply when a species is developmentally plastic or can switch developmental strategies as a function of environmental condition.

3. *Direct development*—Direct-developing individuals, with or without brooding and with or without eggs, in which offspring are capable of self-sufficiency (barring sexual maturation) and resemble miniaturized adults (barring minor allometric

growth). Among insects, only ametabolous and hemimetabolous individuals are included in this character state.

4. *Indirect, non-feeding development*—Indirect-developing individuals (i.e., undergoing one or more life stages), with or without brooding and with or without eggs, in which offspring are sustained by yolk or other physically attached nutriment after birth. By this definition, all seed plants would be included in this character state.
5. *Indirect, feeding development*—Indirect-developing individuals (i.e., undergoing one or more life stages), with or without brooding and with or without eggs, in which offspring are capable of feeding self-sufficiently after birth. Holometabolous insects, spore-bearing plants, fungi, and slime molds are generally included in this character state.
6. **(Brooding)**—Individuals for which brooding, encapsulation, or any other form of post-birthing, direct parental process is involved with reproduction. Incubation, protection, and cultural transmission (teaching) are all included in this character state. Brooding can occur for both direct- and indirect-developing individuals. Common brooders include many mammals, birds, dinosaurs (Horner 2000), ostracodes and other crustaceans, and possibly some trilobites (Fortey and Hughes 1998).

(Dispersal vector)—The primary means by which larvae, spores, fertilized eggs, seeds, or other offspring (whether sexual or asexual) undergo dispersion. Dispersal can occur for both direct- and indirect-developing individuals. Although passive methods (states 8, 9) often involve the presence of structural or behavioral adaptations for dispersion, they are considered passive because they are not capable of self-sufficient dispersion. In the case of larvae with ciliary locomotion, the choice of character state depends on the relative efficacy of active locomotion versus passive dispersal. Multiple character states are possible, although emphasis is on the primary means of dispersal.

7. *No vector*—No dispersal vector is involved; offspring remain in the same location as the parent.
8. *Fluid-dispersed*—Offspring are entrained by wind or water currents and are transported passively.
9. *Organism-dispersed*—Offspring adhere to some organismal vector and are transported passively. This includes plants attached to animals as well as planktonic larvae attached to floating plants, algae, or animals (pleuston).
10. *Self-dispersed*—Offspring disperse actively via self-sufficient migration.

Mobility—The ability of an individual to move within its environment, regardless of any energy expended in such effort. These character states are tallied as binary because there is no unambiguous scale by which to logically order them. As above, passive methods do not denote the lack of structural or behavioral adaptations involved in mobility.

11. *Sedentary*—Immobile individuals, independent of attachment to substrate. These individuals will not change location even if disturbed, whether because of permanent attachment or inability to move. It also includes animals that move in place, such as pedunculate brachiopods that use muscular contractions to maintain orientation at sediment surface, to face feeding currents, and to shake off fouling individuals (Richardson and Watson 1975a,b; Richardson 1981). Note that this definition is modified from the more typical use of this term that often implies attachment. The term *sessile* has been avoided because of its dual connotation of immobility and attachment.
12. *Passively mobile*—Mobile individuals, but relying primarily on ambient flow for motion. This includes planktonic individuals that have some form of ciliary or buoyancy control

over depth stratification or orientations, but whose activities are insufficient to move against typical currents. In the aquatic realm, this encompasses planktonic individuals and occasional benthic epibionts, such as the bivalve *Pteria* attached to the upper arms of octocorralian corals (Stanley 1970). Terrestrial examples include tumbleweed; aerial examples include some insects, and the dispersal stages of many taxa (if such life stages are coded separately). Some deep-water pycnogonid chelicerates also would be included in this character state (Brusca and Brusca 2002).

13. *Facultatively mobile*—Individuals that are capable of mobility, but are typically immobile. Common examples include the inarticulate brachiopod *Lingula*, many byssate bivalves, and the deep-burrowing, pholadomyoid bivalves that can re-burrow when disturbed.
14. *Intermittently mobile*—Individuals that move about throughout their life, but that often remain in one location for appreciable durations. In most cases, mobility is associated with a change in feeding location. Common examples include tubicolous spionid and onuphid polychaetes and deposit-feeding tellinid bivalves, which remain in one location for extended periods, moving when local nutrition is depleted (Fauchald and Jumars 1979; Stanley 1970). This character state also includes generally sedentary individuals that limit movement to diurnal cycles, such as comatulid crinoids that move nocturnally from reef crevices to reef crests to feed and remain sedentary throughout the night (Meyer 1973). This character state is equivalent to the term “discretely motile” used by Fauchald and Jumars (1979) in classifying polychaetes.
15. *Habitually mobile*—Individuals that are primarily mobile (or vagile), although able to rest periodically. This vagility is independent of the medium in which motion occurs; thus, reptant (crawling on substrates), ambulatory (walking), cursorial (running), natant (swimming), burrowing, and flying individuals are all included here. This character state also includes individuals that rest within fluids (e.g., nektonic and demersal aquatic individuals and gliding aerial animals) as well as those that rest on substrates (e.g., aquatic nektobenthos). The distance moved is not a factor here; habitually mobile individuals that move freely, but within a spatially restricted domicile or trap (such as web-building and trapdoor spiders), are still habitually mobile.

Substrate/medium composition—The composition of an adult individual’s *immediate* substrate, whether attached to it or not. This character does not refer to the composition of the overall habitat; for example, individuals may attach immediately to shelled animals or algae within an overall liquefied chalk (Surllyk 1972). It also does not refer to the substrate of juvenile individuals, which may differ from that of adults (unless such life stages are coded separately). Only in cases where a substrate is not involved, such as involving plankton or nekton, should this character refer to the surrounding medium. There may not always be an unambiguous distinction between the biotic and lithic character states when referring to biogenic sediments and structures, such as calcarenites, oncoids, coals, rudites (reef stones), algal boundstones, and stromatolites (Taylor and Wilson 2002). When organisms do not make a substrate distinction between the shells of living organisms and fully degraded shell debris, coding both states may be appropriate. Many individuals, such as barnacles, are substrate generalists that can inhabit multiple substrates, whereas other individuals can have multiple substrates simultaneously. An example of the latter are many plants—especially lianas—that root into a soft, lithic soil, but support themselves in the forest canopy with tendrils around hard, biotic substrates (Givnish and Vermeij 1976; Putz

1984). This character is independent of the consistency of the substrate (see character states 19–21 below).

16. *Biotic*—Substrate consists of either living or recently dead, fissular or skeletal medium. This character state includes resting on or against another individual (e.g., the clinging, arboreal, epibiotic, and ectoparasitic habits) as well as active erosion (e.g., the boring habit), excavation (e.g., the mining habit), penetration (e.g., the endoparasitic habit), and passive entombment by the surrounding individual (e.g., the nestling habit).
17. *Lithic*—Substrate consists of chemically precipitated or physically eroded sediment, rock, soil, or other inorganic medium, regardless of whether microbial agents or other individuals were involved in the genesis of such material. This character state includes individuals that burrow within sediment, that live interstitially among sediment grains, that live within individual rocks, or that lie upon such substrates (e.g., the epibenthic habit). Long-dead shell debris, wood, algal mats, and other biogenic sediments and structures should only be included in this state when such material has been diagenetically altered and the organic fraction has been decomposed and leached.
18. *Fluidic*—The enclosing medium is primarily water (e.g., the pelagic or nektic habit) or air (e.g., the aerial, or atmobiotic, habit), although the individual may occasionally rest against other substrates (e.g., the nektobenthic and demersal habits). This character state also includes those neustonic individuals, such as water gliders, whose substrate itself is water.
19. *Insubstantial*—Flying, swimming, and planktonic individuals whose surrounding medium is a fluid and therefore lacks consistency.

Substrate consistency—The firmness of an adult individual’s immediate substrate, whether attached to it or not. As above, this character does not refer to the composition of the overall habitat or to the substrate of juveniles. This character is independent of the composition and elasticity of the substrate. A general guideline is whether an individual is able to penetrate the substrate without resorting to active excavation. For example, oligochaetes and plant roots that push through soils occupy a soft substrate, whereas insects that live on the surface of leaves or on the surface of water occupy a hard substrate. Note also that this character is scale dependent: a sandy substrate may be soft for benthic gastropods and hard for interstitial hydroids. Parasites will follow similar codings, often with ectoparasites (and gastrointestinal endoparasites) on hard, epithelial integument, and interstitial endoparasites in soft tissue. Multiple states are possible for the same species as well as for the same individual (see note on climbing plants in prior character, substrate/medium composition.)

20. *Soft*—Individuals whose immediate substrate is soft, including disaggregated, soupy, thixotropic, and unconsolidated sediments or soil.
21. *Hard*—Individuals whose immediate substrate is firm, including lithified, consolidated, or cemented sediments; caliche soil; shells, other skeletons, or other firm individuals; and the air-water interface, depending on the individual. For example, the water surface is a durable and impermeable substrate for water glider insects, but an insubstantial one for flying fish.

Substrate relationship—The relationship between an adult individual and its *immediate* substrate. Note that this character is independent of the nature of the substrate and an individual’s ability to move against or among its substrates.

22. *Attached*—Adult individuals that are physically attached to their immediate substrate, regardless of whether such at-

tachment is permanent and whether the attachment penetrates the substrate. For example, some tubicolous polychaetes and other individuals that construct tubes admixed with adjacent sediments are effectively attached, even though such individuals are occasionally able to relocate to additional domiciles (Fauchald and Jumars 1979). Excluded from this attached habit are those individuals, including many amphipods, that create tubes or other structures, that use a tube only for a stable domicile, that move about with their tubes, and that are otherwise free-living. Attachment can apply equally to individuals attached along their entire body surface (e.g., the adnate habit of encrusting individuals) as well as those attached only by an appendage or portion of the body (e.g., the tethered habit). Forms of attachment include rooting (the rhizomenal habit) as well as cementation, suction, clasping, clinging, or other ephaptomenal habits. Note that most colonial animals are attached, even if the attachment is of living individuals (whether zoaria, polyps, etc.) to the dead skeletons of prior generations. If coded from the perspective of adult individuals, attachment does not include those that are attached as juveniles but become free-living as adults (e.g., the liberose-sile habit of Bassett 1984).

23. *Free-living*—Adult individuals that are free-living (the planomenal habit) and that are not attached in any permanent or semi-permanent manner to substrates, regardless of their mobility. The free-living habit includes those individuals that never come in contact with substrates as well as those individuals that rest on substrates.

Primary microhabitat—The maximum typical resting location (or perching height) of an individual with regard to the *primary* substrate of the focal habitat. This character does not refer to the microhabitat in which food is acquired (see character states 30–33 below), nor to the maximum distance away from the substrate that the individual is capable of moving, unless such distances coincide with the typical resting position.

The primary substrate is dependent on the habitat being studied. For aquatic communities, this substrate will generally be the sediment-water interface; for terrestrial and aerial communities, it is the ground; for neustonic communities, it is the air-water interface; and for parasitic communities, it is the host's epithelium or appropriate tissular layer. Problems arise when considering those habitats lacking an obvious substrate. For practicality, atmobiotic and pelagic communities should be classified in relation to the closest ground and/or air-water interface; because few individuals are capable of living at the outer envelope of the atmosphere, this decision is obvious for atmobiotic communities. However, pelagic communities should be classified according to the focus of the study. If the focus is on marine epipelagic or lacustrine littoral-depth communities, then the appropriate substrate is the air-water interface; if the focus is on benthic communities, then the appropriate substrate is the sediment-water interface. If the habitat contains both sediment-water and water-air interfaces, as is found in many riverine, lacustrine, and littoral communities, the sediment-water interface should be used so that atmobiotic individuals can be coded as living above both the primary substrate and their immediate, fluidic substrate (see Table 2).

Individuals with significant portions of their bodies simultaneously within and above substrates should be classified in both character states. Typical examples include aquatic pleuston that float partially submerged at the water's surface, benthic, semi-infaunal individuals that are only partially submerged in sediment, and trees that have extensive root structures. Note, however, that not all rooted individuals must be classified by both character states. While such a correlation is likely for trees, this relationship reflects more the biomechanical constraints of

large, rooted individuals in terrestrial habitats than the ecological necessity of being rooted and having a significant portion of one's body in that rooting structure. A good counterexample is kelp, although these are less nutritionally dependent on their holdfast than are terrestrial trees (Dayton 1985). Individuals that live essentially above sediment but that sink passively into it, such as concavo-convex brachiopods and some scallops, should be coded as above the sediment unless they actively occupy both positions, such as some pectinid bivalves.

Note that this character is an *absolute* one, referring to the orientation of an individual in relation to the primary substrate of the entire habitat. The next character—*immediate microhabitat*—refers to the location of the individual from its own perspective. Individuals that live cryptically within the cavities of coral reefs or endoparasitically within another individual may be both above substrates in a primary sense (e.g., inhabiting a microhabitat situated above the sediment-water interface), but within substrates in an immediate sense (e.g., inhabiting a crevice or tissue). This character is further elaborated with continuous character 52 (primary stratification) below.

24. *Above primary substrate*—The individual lives above the primary substrate of the focal habitat. This character state includes superterranean, epibenthic, and epineustonic (i.e., living on the surface of water) individuals.
25. *Within primary substrate*—The individual lives within or below the primary substrate of the focal habitat. This character state includes subterranean and endobenthic individuals.

Immediate microhabitat—Typical resting location of an individual *relative* to its immediate substrate, whether geotropically oriented or not. Some individuals can simultaneously occupy both character states. The distinction with primary microhabitat is important, because many individuals, such as burrowing animals, live permanently within the substrate but also move freely within their burrow; such animals, therefore, would live above their immediate substrate, the burrow wall. Infaunal individuals that “swim” through substrates without creating a permanent burrow should be coded as living within their substrates. In contrast, planktonic, flying, and swimming individuals whose surrounding medium is fluid should be coded by the presence of both character states unless they only remain within a single stratum, in which case they should be coded as “within” their stratum. See further discussion under previous characters; this character is further elaborated with continuous character 53 (immediate stratification) below.

26. *Above immediate substrate*—The individual lives above its immediate substrate. This character state includes many epibiotic, ectoparasitic, and encrusting individuals.
27. *Within immediate substrate*—The individual lives within or below its immediate substrate. This character state includes subterranean, endobenthic, and endoparasitic individuals.

Support—Whether an individual supports itself or must rely on another structure (individual or material) to inhabit its primary microhabitat.

28. *Supported*—The individual relies on another structure to inhabit its primary microhabitat. Common examples include lianas (Givnish and Vermeij 1976; Putz 1984; Schnitzer and Bongers 2002), barnacles (Seilacher 2005), and other epibionts (Peters and Bork 1998) that use forms of attachment to maintain a different stratification state (characters 52–53) than they could otherwise, as well as infaunal burrow-dwellers that are unable to excavate burrows themselves. This excludes benthic individuals that attach to shells or other hard substrates as a source of attachment, but that do not gain a significant change in stratification. In this manner, it is independent of substrate relationship (character

states 22, 23 above). It can include free-living, mobile individuals if they position themselves atop structures to take advantage of particular stratification states. For example, many comatulid crinoids relocate atop reef crests during feeding (Meyer 1973); because their position depends on the reef framework, they are supported.

29. *Self-supported*—The individual inhabits its primary microhabitat without relying on other structures. This includes attached individuals that do not change their stratification state because of their attachment, as well as many free-living individuals. It includes mobile individuals, such as benthic gastropods and isopods, that roam over topographic features (and therefore stratigraphic states), except when the choice of substrate is conditional on a particular stratigraphic state that they could otherwise not attain themselves.

Primary feeding microhabitat—The location of an individual's food or where such food is acquired. Many individuals do not obtain food resources in the same location as their domicile. This segregation can be accomplished behaviorally by foraging (e.g., sea otters) or agriculture (e.g., leaf-cutter ants), or constructionally by manipulating feeding currents (e.g., serpulid polychaetes) or by setting traps (e.g., web-building spiders). As before, it is possible that some individuals can simultaneously derive food resources from both character states.

This character is an *absolute* one, referring to the orientation of an individual's food in relation to the primary substrate of the entire habitat. The next character refers to the location of the food from the individual's perspective. Thus, the food of leaf-mining insects may be above substrates in a primary sense, but also within substrates in an immediate sense. This character is further elaborated with continuous character 54 (primary food stratification) below.

30. *Above primary substrate*—The individual's food is above the primary substrate of the focal habitat.
 31. *Within primary substrate*—The individual's food is within or below the primary substrate of the focal habitat.

Immediate feeding microhabitat—The location of an individual's food *relative* to its immediate substrate as the individual is foraging, whether geotropically oriented or not. Unlike the immediate feeding stratification, this coding is made with respect to the immediate substrate (or medium). Some individuals can feed in both character states. Flying and swimming individuals that forage in a fluid should be coded by the immediate position of its food. For example, the epibenthic food of a carnivorous fish that forages while swimming would be classified as below (or within) its foraging level. See further discussion under previous character; this character is further elaborated with continuous character 55 (immediate food stratification) below.

32. *Above immediate substrate*—The individual's food resource is located above its immediate substrate.
 33. *Within immediate substrate*—The individual's food resource is located within or below its immediate substrate

Diet—The major dietary composition (largely carbohydrates) of an adult individual, regardless of the size of the food item. Character states are defined by the nutritional value of the diet, which generally parallels the cellular, metabolic, and organ-level diversity of taxonomic kingdoms. It is possible to subdivide this character to include more specific dietary types, including other taxonomic groups (algae, angiosperms, molluscs, fish, or culicids) or anatomical divisions (nuts, leaves, fruit, scales, or muscle). However, such divisions are not practical when comparisons are made across disparate habitats and large time scales.

Because most individuals are opportunistic to some degree, more than one character state often applies to the same individual; however, emphasis is on the primary dietary food items. An

omnivore might be classified as eating both plant and animal matter, whereas many carnivorous plants would be listed only as autotrophic, because insects primarily supplement nitrogen (Ellison and Gotelli 2001). Individuals that acquire a majority of their dietary needs from dissolved organic molecules or from decomposing other individuals could potentially be included in any of the heterotrophic character states depending on the organic source. Individuals with obligate photosymbionts—lichen (Lutzoni et al. 2001), zooxanthellate corals (Rowan 1998), and many others (Rowan and Powers 1991)—should be coded as microbivores (typically incorporeal and ambient feeding; see below) because a major source of their carbohydrates is derived from their cyanobacterial or dinoflagellate photobionts; these individuals should be coded simultaneously in other states if they have other diets (such as microcarnivorous, hermatypic corals). Only those individuals that are truly autotrophic and heterotrophic, such as phytomastigophoran protists, can be simultaneously both autotrophic and heterotrophic.

The common term *detritivore* has been redefined here as *microbivore*, referring solely to the dietary composition of detritus, which is dominantly bacterial and protistan in marine settings (Plante et al. 1990); plant and fungal matter may also dominate in terrestrial ones, but such diets should be described as herbivorous and fungivorous, respectively. This character state refers neither to the deposited location of the food (e.g., as in “deposit feeding”), nor to the particulate, fragmented condition of this food (e.g., as in particle feeding, see below).

34. *Autotroph*—Autotrophic individuals, whether photoautotrophic or chemoautotrophic, that assimilate carbon dioxide into complex biochemicals. This character state does not include heterotrophic individuals with obligate photosynthetic endosymbionts (see previous discussion of dietary character).
 35. *Microbivore*—Heterotrophic individuals that acquire the majority of their nutrition from bacteria and protists, whether corporeal or admixed with disintegrated, decomposed, detrital, or particulate matter, and regardless of whether the food is resting, deposited, or suspended in the environment. Food in this character state includes unicellular microbes as well as colonial protists, bacterial films, slime molds, and coenocytic, filamentous, and macrophytic algae (Sieburth 1976). In marine settings, yeasts and meiofaunal animals, including nematodes and turbellarians, are often eaten with these microbes but are not typically a foraged food item (Fenchel 1978; Barnes and Hughes 1988). This character state does not include those terrestrial detritus feeders whose diet consists primarily of fungal or plant material. In general, note that this character state, when referring to individuals that eat detritus, is restricted to the microbially rich nutritional composition of detritus and not the physical condition of that food (see next character).

The term *microbivore* is preferred over *detritivore* as a dietary character state because most detritus contains essentially no nutritive content aside from its affiliated microbial biota, and because many suspension feeders share the same diet as detritus feeders (Hunt 1925; Plante et al. 1990). Also included in this character state are fungi, protists, and bacteria that feed on other microorganisms, as well as organisms with endosymbiotic microbes (Plante et al. 1990). This character state could be subdivided into bacterivore (or bacteriophage) and protistivore character states when such information is available.

36. *Carnivore*—Heterotrophic individuals (including fungi) that eat organic matter of animal origin, regardless of whether the food resource is alive or dead when acquired and ingested.
 37. *Herbivore*—Heterotrophic individuals (including fungi) that

eat organic matter of plant origin, regardless of whether the food resource is alive or dead when acquired and ingested.

38. *Fungivore*—Heterotrophic individuals (including fungi) that eat organic matter of fungal origin, including yeasts, regardless of whether the food resource is alive or dead when acquired and ingested.

Physical condition of food—The physical condition of nutritional material acquired by an individual, regardless of the size of the food. Like many characters here, there is a strong element of scale-dependence (Hutchinson 1965). What may appear to be a particle feeder from our anthropomorphic perspective, such as a small, infaunal gastropod, may actually be a bulk feeder of nematodes and diatom films; amoeboids feeding on the same diatoms may also be bulk feeders. These character states are logically independent of the diet and foraging habit of the individual, although there may be a high correlation. These states are essentially identical to those described by Schmidt-Nielsen (1997), although he treats dissolved organics and sulfur-reducing bacteria as additional states.

39. *Incorporeal feeder*—Individuals that are able to self-sufficiently utilize ambient or dissolved radiant or inorganic chemical energy, without acquiring nutrients directly from other organisms. Lichens and other individuals with obligate photosymbionts that rely primarily on their photosymbionts for nutritional needs are included in this character state. Also included is the bivalve *Solemya* (Reid and Bernard 1980; Powell and Somero 1986), some olenomorph trilobites (Fortey 2000), and several epidermal-feeding crinoids (e.g., Silurian *Pygmaeocrinus*, *Paracolocrinus*, and microcrinoids [Brett 1984]) that lack or have significantly reduced mouthparts and digestive systems, that utilize sulfur-reducing bacterial symbionts, or that acquire a majority of their nutrition from dissolved organic matter.
40. *Solution feeder*—Individuals that acquire most of their nutritional requirements via dissolved nutrients, typically via diffusion or sucking, and without regard to the origin of the dissolved organic matter. Examples include decomposing fungi, saprophytic plants, many parasites and insects, vampire bats, lepidopterans, and hummingbirds. If individual life stages are included, nearly every juvenile mammal will be included in this state (Schmidt-Nielsen 1997). Fungi, arachnids, some insects, and other individuals with extracorporeal digestion are not included if they are in direct contact with their food source.
41. *Particle feeder*—Individuals that acquire most of their nutritional requirements via degraded, decomposed, or particulate organic matter. Note that this term is new and not to be confused with detritivory, microbivory, or deposit feeding. Particle feeding refers strictly to the particulate condition of the food; detritivory (and its form used here, microbivory) refers to dietary composition; and deposit feeding refers to the physical location of that food, sometimes also referring to the foraging behavior used to feed on such material (as its form used here, mass feeding) (Plante et al. 1990). In fact, many suspension feeders and deposit feeders eat the same particulate food items, differing solely in their foraging habits (Hunt 1925; Plante et al. 1990). Microorganisms—intact bacteria, protists, and fungi—are included here as particulate organic matter when they are freely distributed in a foraged environment.
42. *Bulk feeder*—Individuals that obtain most of their nutritional requirements via nutrients stored in portions of, or entire bodies of, macroscopic organisms *en bloc*, whether animal, plant, fungal, protistan, or algal (i.e., macrophytic algae), alive or dead, but which have not undergone significant decomposition or fragmentation. This character state can include a variety of foraging habits, including many predat-

tors, grazers, burrowers, and suspension feeders. Metazoan microbivores may be included here when the microorganismal flora constitutes mats, films, molds, syncytia, or other aggregated masses that require food-handling abilities to be eaten. If the focal habitat is not macroscopic, then individual microorganisms may be considered as bulk food.

Feeding habit—The means by which food is acquired, whether via direct manipulation, physical contact, or indirect acquisition. For mobile animals, this is synonymous with foraging behavior. This character also includes all individuals that acquire nutrition without active movement, although some degree of adaptation, whether genetic or ecophenotypic, is generally involved. Feeding habits generally involve the processes of food detection, incapacitation, and manipulation. Thus, these behaviors are complex and generally require numerous coordinated structures and behaviors. Although this character is not subdivided into discrete subcharacters related to each of these processes, it is intended that the following character states accurately characterize the primary methods in which individuals acquire food.

43. *Ambient feeder*—Individuals that acquire nutrients across body walls without active attachment to or manipulation of a food source. Although plants and some other sedentary individuals do not actively detect food, competition still causes mortality of saplings, seeds, or other juveniles that are not capable of meeting basic nutritional requirements. Optimization of energy intake can still take place in sedentary autotrophs via growth and movement of leaves, stalks, zooxanthellate carrier cells, cellular pigmentation, and other energy-harvesting structures. This character state also includes numerous endoparasites and other individuals that acquire nutrients or dissolved organic molecules via diffusion across a body wall, but without active attachment to their host.
44. *Filter feeder*—Individuals that acquire nutrients, regardless of dietary composition and condition, suspended in some fluid through the use of sieves and nets, fibers, setules, mucous traps, pores, or other filters (Rubenstein and Koehl 1977). These individuals may use a variety of active means by which to capture, entrain, or direct nutrient-laden feeding currents by these structures, although passive suspension feeders are also included by this definition (LaBarbera 1984). Included are diverse individuals: carnivores—including corals; microbivores—including sea pens and brittlestars; more renowned filter feeders—from crinoids to bivalves; and less renowned ones as well—including arachnids and mysticete whales. Some traditional deposit feeders are also included here, including some polychaetes and aquatic insect larvae (Vogel 1994). Note that not all suspension feeders use a filter to capture nutrients (see raptorial feeding below).
45. *Attachment feeder*—Individuals that acquire nutrients, regardless of dietary composition and condition, by actively and directly attaching to the food source, regardless of the duration of attachment. The prey or food item is typically larger than the feeding individual, although this is not necessary. Examples include ectoparasitic insects and arachnids, coprophagous platyteratid gastropods that position themselves above the anus of crinoids (Keyes 1888; but see Gahn and Baumiller 2003), agnathan fish, saprophytes, and some fungi.
46. *Mass feeder*—Individuals that acquire nutrients, regardless of dietary composition and condition, by capturing edible, and sometimes inedible or not eaten, material *en masse*. In all cases, the primary criterion is that multiple food items are processed simultaneously, through ingestion, systematic harvesting, or food manipulation. The prey or food item is sometimes larger than the feeding individual, such as leaf-mining insects and some fungi and parasites. Individuals are often adapted for continuous feeding or temporary

TABLE A1. Ordered scale for skeletal body volume.

State	Volume (ml)	Code
Hectolitic	≥100,000	9
Decalitic	10,000–100,000	8
Litric	1,000–10,000	7
Decilitric	100–1000	6
Centilitric	10–100	5
Millilitric	1–10	4
Submillilitric	0.1–1	3
Supramicrolitric	0.01–0.1	2
Microlitric	0.001–0.01	1
Submicrolitric	<0.001	0

storage of food items. Individuals that ingest or churn up substrates to extract food, and some browsers and grazers that ingest mass quantities of herbage, are also included here. Individuals feeding on carrion or other necrolyzed, fragmented, or decomposed matter, or on food living within such matter, may be included here when active raptorial methods are not evident, such as occurs in jawless amphinomid polychaetes (Fauchald and Jumars 1979). Examples of typical mass feeders include earthworms, nuculoid bivalves, artiodactyl mammals, and many polychaetes, holothurians, and some trilobites. A less obvious example includes rodents that gather food within cheek pouches and store it in caches or middens. Because this state is independent of selectivity (see next character), it is understandable that sediment ingestion or food gathering often is followed by selective storage, regurgitation, or mass defecation of inedible material if the ingestion is not selective.

47. *Raptorial feeder*—Individuals that acquire nutrients, regardless of dietary composition and condition, by actively seizing and manipulating individual food items. Unlike the previous state, the primary criterion is that feeding is concentrated on individual food items; thus, specialized detection, incapacitation, and manipulation structures and behaviors are required. This character state includes most predators (motile stalkers, ambush predators, and sessile opportunists) as well as some grazing and browsing herbivores, microbivores, and scavengers that have specialized means of selecting and acquiring food items. It also includes those suspension-feeding animals—such as scan-and-trap copepods and tentacular corals (Koehl 1981; Koehl and Strickler 1981; LaBarbera 1984)—that seize individuals without the use of a filtration device. Although most individuals in this character select their prey prior to seizing it (see feeding selectivity next), this is not necessary. A less selective example is the sawfish, which, in part, chaotically thrashes its toothy saw into a school of fish to wound its prey before eating (Breder 1952; Bigelow and Schroeder 1953; McEachran and de Carvalho 2002).

(Feeding selectivity)—The degree to which food resources are selected for consumption.

48. *Non-selective*—Food resources are not sorted during consumption, often with mass excretion of inedible material.
49. *Selective*—Food resources are sorted from non-food items prior to consumption, whether through direct selection, mechanical sorting, or immediately prior to ingestion, such as occurs in the production of bivalve pseudofeces. This character state also applies in the case of autotrophic individuals that have the ability to sort usable from unusable energy through the use of photoreceptive pigmentation or other means.

TABLE A2. Ordered scale for stratification. The same scale is used for primary and immediate stratification, as well as for the stratifications of food source.

Distance (cm)	Code
≥100.0	4
10.0–100.0	3
1.0–10.0	2
0.1–1.0	1
<0.1	0

50. *Secondarily selective*—Food resources are sorted after consumption, typically involving mass consumption of food and non-food items followed by regurgitation of inedible material.

Ordered, multistate characters.—These characters are coded according to the scales noted below.

51. **Skeletal body volume**—The body volume of the skeleton (or easily fossilized hard parts) of adult, sexually mature individuals. It would be preferable to use the more meaningful character of body mass; however, such a measure is not possible with most fossil taxa (but see Powell and Stanton 1985). While body volume is intended as a proxy for body mass and the relative energy utilization of a fossil individual, it is more accurately used here as a measure of spatial allocation. This altered meaning still incorporates scaling information relevant to mobility, defense from predators, diet selection, and the manner in which individuals negotiate their environment (see Novack-Gottshall in press). Body volume includes the space enclosed by the skeleton that may or may not include living tissue. The scale (Table A1) and allometric equation (A1) are based on empirical observations on the body volume of taxonomically and morphologically diverse taxa inhabiting deep-subtidal, soft-substrate habitats during the Cambrian through Devonian (Novack-Gottshall in press).

$$\text{Volume} = 0.544(\text{ATD})^{0.896} \quad (\text{A1})$$

where ATD is the product of the three major body axes (the anterioposterior, transverse, and dorsoventral axes) measured in units centimeter. This equation may not be appropriate for other taxa, or for those outside the range 0.01–1000 ml. For further discussion, including estimation of confidence intervals and standard error, see Novack-Gottshall (in press).

52. **Primary stratification**—The typical maximum distance (Table A2) that an individual inhabits away from the primary substrate of the focal habitat, regardless of whether the individual lives above or within the substrate. This character supplements primary microhabitat (character states 24, 25); refer there for further details. In many ecological studies, primary stratification is also known as the stratum or tiering layer (Elton and Miller 1954; Turpaeva 1957; Ausich and Bottjer 1982; Bottjer and Ausich 1986). Because this character does not distinguish between individuals that live above and within substrates, it refers equally to stratification of forests (i.e., ground story, understory/midstory, and high canopy), epibenthos (i.e., reclining, elevated, and highly elevated), and endobenthos (shallow and deep infaunal) if coding with respect to the sediment-water or sediment-air interfaces.

Note that this character refers to the primary metabolic mass of a typical, sexually mature (if applicable) adult individual and not to any supportive, reproductive, protrud-

TABLE A3. Ordered scale for spatial patterning.

Spatial patterning	Mean/variance	Code
Uniform	$\gg 1.0$	2
Random	~ 1.0	1
Aggregated (gregarious)	$\ll 1.0$	0

sive, or attaching organs or appendages; typical examples of such masses include tree canopies, crinoid calyces, tetrapod trunks, and fungal vegetative mycelia. In many cases, this distance will correspond to one of the principal body size axes, but this is not necessary.

Note that this character is an *absolute* one, referring to the maximum height of an individual from the primary substrate of the entire habitat. The next character refers to the height of the individual relative to its immediate substrate. Thus, birds and bromeliads that live habitually within the high forest canopy may be both highly elevated in a primary sense (i.e., more than 10 m above the forest floor), but reclining in an immediate sense (i.e., inhabiting the surface or crevices of branches). See further discussion for immediate stratification (character 53) and Table 2 (in text).

The scale (Table A2) was selected from empirical observations on the stratification of taxa inhabiting deep-subtidal, soft-substrate habitats during the Cambrian through Devonian. The same scale is used for characters 53–55. Extrapolations or modifications can be made in future studies depending on their requirements.

53. **Immediate stratification**—The typical maximum distance (Table A2) that an individual generally inhabits away from its immediate substrate, regardless of whether the individual lives above or within the substrate. This value typically corresponds to the diameter of individuals that live within their immediate substrate. Unlike the previous character that is typically measured as a vertical distance, this distance can assume any orientation. This character supplements immediate microhabitat (character states 26, 27); refer there for further details. Corals that build robust frameworks should be coded only by the thickness of the living polyp layer; they are stratified in a primary sense (character 52) by the thickness of the entire multi-generational, skeletal framework. The coding scheme (Table A2) is the same as for character 52 (primary stratification).
54. **Primary food stratification**—The typical maximum distance of an individual's primary food resources from the primary substrate of the focal habitat, regardless of whether the individual lives above or within the substrate. When food is found in multiple microhabitats, this character refers to the maximum distance at which any dominant food item is found. Although many food items in a habitat are allochthonous in origin (e.g., particulate organic matter and some carrion), this character is concerned only with the location of food where it is utilized by the individual and not with its origin. For autotrophic (i.e., chemosynthetic and photosynthetic) individuals, this character records the location where energy oxidation occurs and not the location of the sun (i.e., photoautotrophic) or the earth's interior (i.e., deep-sea chemoautotrophs). This character supplements primary feeding microhabitat (character states 30, 31); refer there for further details. The coding scheme (Table A2) is the same as for character 52 (primary stratification).
55. **Immediate food stratification**—The typical maximum distance of an individual's typical food source away from itself, regardless of whether the individual lives above or within

TABLE A4. Ordered scale for relative metabolic rate.

Relative metabolic rate	MSMI (L O ₂ h ⁻¹ kg ⁻¹)	Code
Energetic	$\gg 1.0$	2
Moderate	~ 1.0	1
Inactive	$\ll 1.0$	0

the substrate. Note that this is measured not from a substrate but from the food handling portion of the individual. For individuals that move while foraging, this character is the typical search distance involved in finding its food. For example, a mass-feeding polychaete that swallows food-bearing sediment would be coded as 0 if it feeds in place, whereas a hawk that searches for prey from the sky could be coded as 4 or greater. This character supplements immediate feeding microhabitat (character states 32, 33); refer there for further details. The coding scheme (Table A2) is the same as for character 52 (primary stratification).

56. **(Mobile velocity)**—The typical maximum speed used in moving, or a measure of energy expended in the act of mobility. This character could be subdivided to reflect either self-propelled velocity or the actual velocity of the individual regardless of energy expended (as in the case of epibiotic or planktonic individuals). This character is not feasible currently with most fossil individuals, and so an appropriate scale is not proposed.
57. **(Spatial patterning)**—Description of the spatial patterning of populations of individuals. Different populations of the same species can display different degrees of spatial patterning, but a single pattern should be found for each species in a single sample. Following convention (Hayek and Buzas 1997) (Table A3), spatial patterning is defined by the ratio of the mean density of individuals within samples to the variance of that estimate. More powerful statistical methods might be preferable (Hurlbert 1990). Common examples of gregarious individuals include Silurian *Pentamerus* brachiopod assemblages (Ziegler et al. 1966), ophiuroid assemblages, bryophyte mats, and birch assemblages. A uniform distribution can imply a negative interaction among individuals (Hayek and Buzas 1997).
58. **(Dispersal distance)**—The typical dispersal distance of an individual. Although this may correspond to geographic range for many planktotrophic marine species (Jablonski and Lutz 1983; Jablonski 1986; Brown 1995), this is not always the case for terrestrial species (Howe and Smallwood 1982; Sutherland et al. 2000). This character is not feasible currently with most fossil populations, and so an appropriate scale is not proposed.
59. **(Relative metabolic rate)**—The absolute metabolic rate (or rate of oxygen consumption) of an individual often scales with body mass to the power of 0.75 (Schmidt-Nielsen 1997). When such observations are available, the mass-specific metabolic index (MSMI) can be calculated:
- $$\text{MSMI} = \text{metabolic rate}/(\text{body size})^{0.75}. \quad (\text{A2})$$
- When such estimates are not available, the following approximate coding (Table A4) can be used. In many cases, an approximate metabolic rate of extinct taxa can be estimated from living relatives (Powell and Stanton 1985; Bambach 1999; Bambach et al. 2002).
60. **(Life span)**—The typical life span of an individual. This character is not available readily with most fossils, and so an appropriate scale is not proposed.

Appendix B

Demonstration of Coding for Extinct and Extant Species

The following two examples—one extant and one extinct—demonstrate how species can be coded with the ecospace framework. In both instances, only 44 characters and states from the larger ecospace framework were used for which reliable information was available for living and fossil biotas (Table 3). All other taxa in the Paleozoic and modern databases were coded using similar criteria.

The living, inarticulated brachiopod *Glottidia pyramidata* (Stimpson) (Family Lingulidae) belongs to one of the oldest living families (West 1976; Kowalewski et al. 1997). *G. pyramidata* is sexual and gonochoristic (Williams et al. 2000; Paine 1963). As an adult, *G. pyramidata* lives within the sediment (its primary microhabitat) at a typical depth of 0 to 5 cm in a U-shaped burrow with the anterior commissure at the sediment surface (Paine 1963; Thayer and Steele-Petrović 1975). This burrow is not typically cohesive, and so the brachiopod lives within its immediate, unconsolidated substrate. It is able to move by means of a muscular pedicle when disturbed—either withdrawing into its burrow or physically changing locations—but it remains sedentary typically, with the pedicle impermanently attached to sediment; thus, it is facultatively mobile, self supporting, and attached. Suspended food particles (primarily phytoplankton, although animal larvae, sand, and detritus are sometimes found [Paine 1963]) are brought from the overlying water with the lophophore; it is a particle-feeding microbivore that acquires food with a filter (in the broad sense, cf. Vogel 1994). A typical specimen has an estimated skeletal body volume of approximately 0.714 ml (using measurements from Williams et al. 2000 and equation A1).

Isotelus maximus (Family Asaphidae) was a massive trilobite found throughout present-day eastern North America during the Late Ordovician (Harrington et al. 1959). From the buttressed hypostome with posterior notch, Fortey and Owens (1999) inferred that it had a predatory habit and that the hypostome likely was used to manipulate prey. This predatory conclusion is supported further by trace fossils, with *Rusophycus* corresponding to the genus superimposed on a *Palaeophycus* worm burrow (Brandt et al. 1995; Fortey and Owens 1999). These *Rusophycus* do not demonstrate a churning behavior, instead showing raptorial attacks with evidence of large appendages. The absence of other attributable trace fossils—for an otherwise distinctive trilobite—argues that this was a generally epibenthic, free-living, habitually mobile animal that did not burrow into sediment except superficially when feeding. It is unclear how high in the water column it swam, but it was likely primarily benthic, judging from its large size and flattened profile. It perhaps fed on benthic prey items at or above the sediment-water interface; the large, raised eyes are evidence that it could locate prey from a distance. There are no known asexual trilobites, and it was likely gonochoristic. A typical specimen of the species has an approximate skeletal body volume of 269 ml (using measurements from Feldman 1996 and equation A1).

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