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General models of ecological diversification. II. Simulations and empirical applications

Philip M. Novack-Gottshall

Abstract.—Models of functional ecospace diversification within life-habit frameworks (functional-trait spaces) are increasingly used across community ecology, functional ecology, and paleoecology. In general, these models can be represented by four basic processes, three that have driven causes and one that occurs through a passive process. The driven models include redundancy (caused by forms of functional canalization), partitioning (specialization), and expansion (divergent novelty), but they also share important dynamical similarities with the passive neutral model. In this second of two companion articles, Monte Carlo simulations of these models are used to illustrate their basic statistical dynamics across a range of data structures and implementations. Ecospace frameworks with greater numbers of characters (functional traits) and ordered (multistate) character types provide more distinct dynamics and greater ability to distinguish the models, but the general dynamics tend to be congruent across all implementations. Classification-tree methods are proposed as a powerful means to select among multiple candidate models when using multivariate data sets. Well-preserved Late Ordovician (type Cincinnatian) samples from the Kope and Waynesville formations are used to illustrate how these models can be inferred in empirical applications. Initial simulations overestimate the ecological disparity of actual assemblages, confirming that actual life habits are highly constrained. Modifications incorporating more realistic assumptions (such as weighting potential life habits according to actual frequencies and adding a parameter controlling the strength of each model's rules) provide better correspondence to actual assemblages. Samples from both formations are best fit by partitioning (and to lesser extent redundancy) models, consistent with a role for local processes. When aggregated as an entire formation, the Kope Formation pool remains best fit by the partitioning model, whereas the entire Waynesville pool is better fit by the redundancy model, implying greater beta diversity within this unit. The 'ecospace' package is provided to implement the simulations and to calculate their dynamics using the R statistical language.

Philip M. Novack-Gottshall. Department of Biological Sciences, Benedictine University, Lisle, Illinois 60532, U.S.A. E-mail: pnovack-gottshall@ben.edu

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Introduction

Understanding the causes of ecological diversification remains an important goal in paleontology, ecology, and evolutionary biology. Andrew Bush and I recently introduced (2012) several models of diversification in ecospace (functional-trait space) that are useful for conceptually representing a broad range of diversifications, whether at the scale of ecological assembly of communities or whether shaping entire biotas over evolutionary timescales. The models share many similarities with hypotheses used by community and functional ecologists (Villéger et al. 2010, 2011; Mouillot et al. 2013; Vogt et al. 2013; Gerisch 2014) and those used by paleontologists studying morphological, and increasingly ecological (functional), disparity (Dineen et al. 2014, 2015; Miller et al. 2014; Mitchell and Makovicky 2014; Dick and Maxwell 2015; Knope et al. 2015). Most of these ideas invoke the processes of ecological canalization, specialization, and/or divergence during diversification. In a companion article (Novack-Gottshall 2016), I described four of these models in more detail and discussed their usefulness as general models of ecological diversification. The redundancy model occurs when successive species occupy similar regions in ecospace as previously existing species, and can be considered a form of ecological canalization. The partitioning model occurs when successive species progressively subdivide ecospace, such as occurs in niche partitioning and specialization. The expansion model occurs when successive species progressively explore novel portions of ecospace, such

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as occurs during niche divergence. Despite their mechanistic differences, these three models are all driven (sensu McShea 1994) by particular causes. In contrast, the fourth neutral model occurs as a passive model, in which ecospace is inhabited at random.

The ecospace that becomes structured during each model's implementation can be envisioned as a landscape (or multivariate ordination) defined by the life habits (functional-trait combinations) of constituent organisms (Fig. 1). Because each model ecospace is associated with distinct distributions of life habits (ecological structure) that can be quantified using various disparity statistics, the models also suggest promise as the basis for quantitative tests if implemented through computer simulations. In the companion article (Novack-Gottshall 2016), I summarized the expected dynamics for these models, using a range of metrics from the morphological disparity and functional diversity literature. Sensitivity analyses (Ciampaglio et al. 2001; Villier and Eble 2009; Mouchet et al. 2010) have demonstrated strengths and weaknesses inherent to each metric, and it remains to be demonstrated how sensitive these dynamics are to different implementations of the models and to different data structures (ecospace frameworks). More important, it remains unclear how to select among alternative models when using multiple, interdependent statistics (Burnham and Anderson 2002; Johnson and Omland 2004; Grueber et al. 2011).

In this second of two companion articles, I demonstrate how these models can be implemented as stochastic simulations. Sensitivity analyses are conducted to evaluate how differences in number of characters (functional traits), character types, and various implementations of the simulations affect resulting statistical dynamics. Because the life habits theoretically allowed by any ecospace framework will always be greater than those that exist in reality (either by logical, biological, or other constraints), the simulation results suggest several ways they can be made more realistic, that is, they can better approximate actual assemblages. The use of classification trees (Breiman et al. 1993) trained on multivariate Monte Carlo data sets (simulations) is proposed as a novel method for selecting among multiple models. As a case study, these methods are applied to well-preserved fossil assemblages from the type Cincinnatian (Upper Ordovician of Ohio, Indiana, and Kentucky). Because the samples hierarchically span multiple localities and stratigraphic levels, they offer useful tests of the generality of the models. In addition to their application for fossil samples, the methods proposed here have value to those studying functional diversity in modern communities, where debate continues regarding the best manner to test important hypotheses on ecological structure.

Implementing the Models using Monte Carlo Simulations

Statistical dynamics for the four models can be obtained using Monte Carlo simulations, which are provided here for a range of ecospace frameworks. The simulations were programmed using R (R Development Core Team 2015), and a package—ecospace: Simulating Community Assembly and Ecological Diversification Using Ecospace Frameworks (Novack-Gottshall 2015)—is provided to allow others to implement them for their own purposes. In the discussion that follows, single quotation marks (' ') refer to control parameters or variables called within the package functions.

Theoretical Ecospace Framework

Prior to each simulation, a theoretical ecospace framework is defined (with the function 'create_ecospace') that specifies the realm of possible life habits that all species can inhabit during the simulation. This step is flexible, allowing any number of characters and character types used by functional ecologists (e.g., Mouchet et al. 2010; Villéger et al. 2011), paleoecologists (e.g., Bambach et al. 2007; Bush et al. 2007; Novack-Gottshall 2007), and those studying morphological disparity (e.g., Foote 1994; Ciampaglio et al. 2001). Examples include factors (e.g., diet can be autotrophic, carnivorous, herbivorous, or microbivorous), ordered factors (factors with a specified order, such as for mobility: habitual > intermittent > facultative > passive > sedentary), ordered numerics (discrete or continuous numeric

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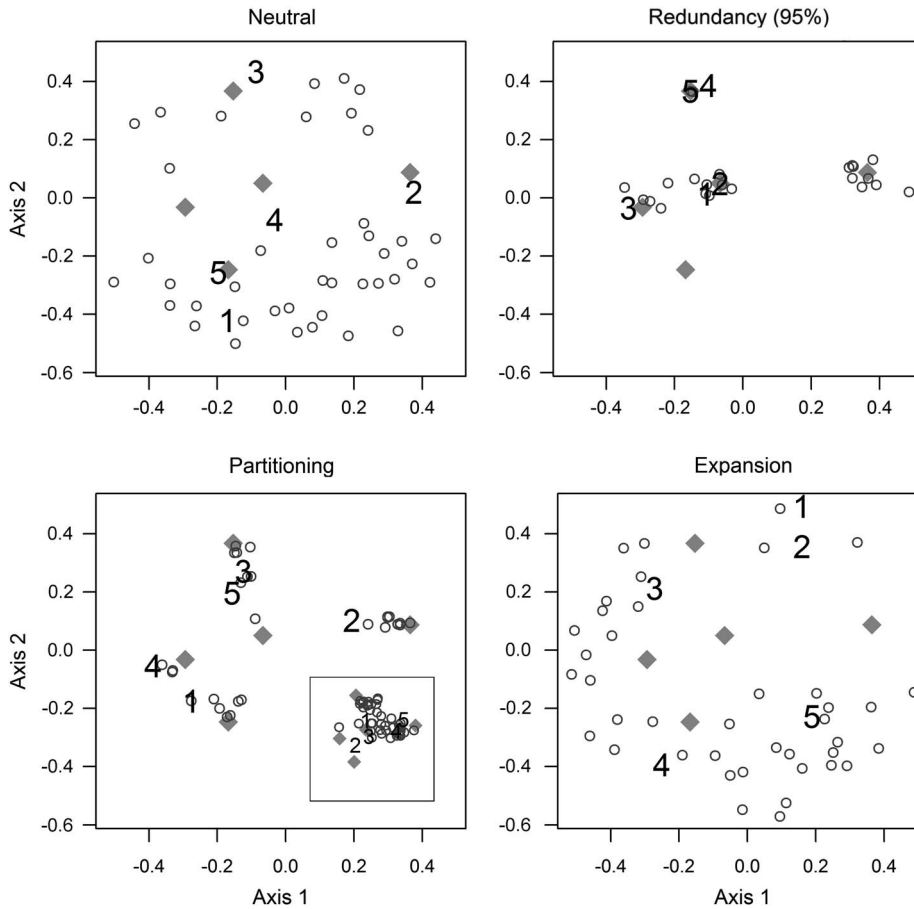

FIGURE 1. Typical examples of simulated 50-species assemblages produced by the four model rules. Assemblages are plotted on a common, nonmetric, multidimensional-scaling ordination space of functional traits to allow comparative evaluation of model behavior. Five gray diamonds represent common "seed" species whose life habits were assigned stochastically using an 18-character (functional-trait space) ecospace framework (modified from Novack-Gottshall 2007), imposing a realistic constraint that each life habit could have at most two character states within a given character. Numbers illustrate the addition of five species to each assemblage (after seed species), with the remaining 40 species as hollow circles. All model rules, except redundancy, were enacted at 100% rule following for each simulation; redundancy rules were weakened such that all successive species have habits 95% similar to preexisting ones; at 100% enactment, later life habits are limited to the "seed" species. In the neutral model, functional traits of all species are chosen independently at random, and the entire ecospace becomes inhabited through passive processes. In the redundancy model, new species have life habits similar to preexisting ones, producing an ecospace with distinct clusters. In the partitioning model, new species inhabit life habits intermediate to preexisting ones. This model can be enacted in a strict form (larger image), in which new species are restricted to gradients between preexisting species (typically leaving the center empty), and a relaxed form (inset), in which new species progressively fill in empty regions of the space originally defined by the seed species. In the expansion model, new species progressively inhabit novel life habits, producing an ecospace that expands its breadth over the simulation, while leaving the original region uninhabited. Figure 2B shows the average dynamics of eight structural statistics when such simulations were repeated 1000 times.

values, such as body size), and binary/numeric character types. Binary states can be treated individually (present = 1/absent = 0) or can be treated as multiple states within a single character. For example, the character "reproduction" can be treated as including two states [sexual, asexual] with exclusively sexual habits coded as [0,1], exclusively asexual as [1,0], and hermaphrodites as [1,1]. This coding strategy is preferable over the use of discrete factors (sexual, asexual, hermaphroditic) in allowing flexibility for possible (and biologically

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frequently occurring) state combinations, while maintaining logical functional distances (in a Euclidean or other metric sense), such that hermaphrodites would be closer to sexual and asexual habits than either exclusive mode is to the other. (This example is trivial, as it could easily be coded as an ordered factor, but such binary coding schemes can be extended to additional character states in which such factorial options are no longer practical.) See Novack-Gottshall (2007) and Supplementary Appendix 1 for additional discussion and examples of the value of multiple binary states within a single character (functional category). When such multiple binary characters are included, subsequent simulations (and the ecospace framework that controls them) specify that "all-absences" are impossible (i.e., an organism cannot be neither sexual nor asexual, [0,0]). This behavior can be controlled with a 'constraint' parameter, which can allow any combination (e.g., [1,1,1]) or specify a maximum number of "multipresences" (e.g., setting 'constraint = 2' allows [1,0,0], [0,1,0], [0,0,1], [1,1,0], [1,0,1], and [0,1,1] as state combinations, but excludes [1,1,1]; setting 'constraint = 1' only allows the first three of these combinations).

Another feature when defining the ecospace framework is the ability to weight character states, such that certain states occur more often than others. This constraint can be imposed using customized weights or calculated automatically using empirical samples (such as a regional species pool) to assign weights based on their frequency of occurrence. A weight of 0 excludes that character state from inclusion in the ecospace framework, and thus from simulations based on it. Although not explored here, these weights could be used, with some care, in linking covariation among states across different characters and offer potential to extend these simulations to studies of morphological disparity, in which nonapplicable character states—for example, glabella shape for a mollusk—are frequently encountered.

Simulations and Implementation as Algorithms

All simulations are implemented as Monte Carlo processes in which species are added iteratively to assemblages, with all added species having their character states specified by the model rules below (Fig. 1). Aside from these model rules (and whatever inherent constraints are imposed by the ecospace framework), there are no deterministic components to the stochastic simulations. Simulations begin with the seeding of a specified number of species, chosen at random (with replacement) from either the species pool (if provided) or following the neutral-rule algorithm (if not). Once seeded, the simulations proceed iteratively (character by character, species by species) by following the appropriate algorithm until terminated at a prespecified species-richness value (sample size). A 'strength' parameter can be used to specify the probability that a simulation follows each rule, with possible values ranging from 1.0, in which the model rule is always followed, to 0.0, in which the model rule is never followed (and during which the simulation switches to the default neutral model rule). Although not explored here, it might be profitable in future analyses to modify the model-selection analyses into an optimization routine so that the 'strength' parameter is treated as a free parameter to be estimated by the data rather than chosen as an arbitrary value.

Neutral Rule.—Here we iteratively add species independently, assigning characters character by character as random multinomial draws (with probabilities assigned by character-state weights, if assigned) from the theoretical ecospace framework. If weighting was assigned to the ecospace framework, character states are assigned in proportion to those weights, on average.

This "rule" is not technically a rule, but the absence of other rules: all further simulations default to this neutral algorithm when, for example, a simulation is implemented with a strength parameter of 0, and converge on this model when implemented at strengths <1. It is important to note that the neutral rule is not a simple permutation (randomization) test (Kowalewski and Novack-Gottshall 2010), drawing at random from the species pool (except for the seed species, if a species pool is provided). Most tests in the functional ecology literature use such simple permutation tests, and such a test can be enacted in the neutral

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model by setting the number of seed species to a sufficiently large value, such as the size of the species pool. The life habit of each new species is built character by character from the realm of theoretically possible states allowed by the ecospace framework. Thus, new species can occupy combinations of character states that did not occur in the species pool (if provided). This is an important feature of the simulations, allowing the entire theoretical ecospace to be explored by the neutral model if given sufficient numbers of species. If it turns out that the actual species pool is structurally different from a similarly parameterized neutral model, it can be concluded that there is an important mechanism controlling how the actual sample was composed.

Redundancy Rule.—In this instance, we pick one existing species at random and create a new species using that species' characters as a template. A character is modified (using a random multinomial draw from the theoretical ecospace, as in the neutral rule) according to the strength parameter. When the strength parameter is set to 1, all species will be functionally identical to the original seed species; when set to 0, the simulation is identical to the neutral rule. Because new character states can be any allowed by the ecospace framework, there is the possibility of obtaining redundancy greater than that specified by strength parameters <1.0 (if, e.g., the new randomly chosen character states are identical to those of the template species).

Partitioning Rule.—Here we calculate distances between all pairs of species, using Euclidean distance if all characters are numeric/binary or ordered numeric types and using Gower distance if any character type is an ordered or unordered factor. There are two algorithms to choose from for the next step, a 'strict' (and default) partitioning implementation and a 'relaxed' implementation. In the strict (or "minimum distant-neighbor") implementation, identify the maximum distances between all pairs of species (the "most-distant neighbors"); the new species will have character states based on the pair of species that represents the minimum of these distances. This implementation progressively fills in the largest parts of the ecospace that are least occupied between neighboring species and on average partitions the ecospace in straight-line gradients between seed species. In the 'relaxed' (or "maximum nearest-neighbor") implementation, identify nearest-neighbor distances between all pairs of species; the new species will have character states based on the pair that represents the maximum of these distances. This implementation places new species in the most unoccupied portion of the ecospace that is within the cluster of preexisting species, often the centroid. (See Fig. 1 for a visual portrayal of these alternate implementations.) In both cases, the life habit for each new species is built as a resampled combination of the character states of the chosen neighbor pair, with probabilities controlled by the 'strength parameter.' Ordered, multistate character partitioning (whether factor or numeric) can include any state equal to or between the observed states of existing species. Each newly assigned character is compared with the ecospace framework to confirm that it is an allowed state combination before proceeding to the next character; if the newly built character is disallowed from the ecospace framework (i.e., because it has "dual absences" [0,0], has been excluded based on the species pool, or is not allowed by the ecospace 'constraint' parameter), then the character-selection algorithm is repeated until an allowable character is selected. When simulations proceed to very large sample sizes (>100), this confirmatory process can require long computational times and produce "new" intermediate species that are functionally identical to preexisting species. This can occur, for example, when no life habits, or perhaps only one, exist that form an allowable intermediate between the selected neighbors. This behavior mimics the "pathologically" tight packing of species that has been demonstrated in large sample–size simulations of niche partitioning (Kinzig et al. 1999). This behavior also causes dynamics at such sample sizes to share important similarities with weakened implementations of the redundancy model (see "Simulations, Constraints, and Model Selection" below).

Expansion Rule.—In this instance, we calculate distances between all pairs of species, as done in the partitioning algorithm, and identify the species pair that is maximally

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distant. The newly added species has character states chosen at random that are equal to or more extreme (if ordered or numeric character types, or that are the same or different for unordered factors) than those in this species pair, with the strength parameter controlling the probability of following this rule. As with the partitioning rule, each newly assigned character is confirmed to be an allowed character-state combination before proceeding with remaining characters and species. Like the partitioning rule, this algorithm can take long computational times to run to completion for large sample sizes and shares the similar property that functionally identical life habits may occur by virtue of saturation of ecospace-allowable life habits.

Other Simulation Assumptions and Limitations.—The simulations explicitly assume that dispersal is guaranteed to all species, provided that new species have appropriate character states as proscribed by the ecospace framework and the model rules. This is an important distinction from Hubbell's neutral model (2001) and many other spatially structured models in community ecology but consistent with how many species pools are defined in ecological studies (Cornell and Harrison 2014). Extinction, speciation, and emigration are not allowed during the course of a simulation (although they can play important roles in the definition of the original species pool). All species that immigrate to the assemblage remain there, with their character states retained, throughout the course of the simulation. Such ecological and evolutionary processes (character displacement, competitive exclusion, habitat filtering, etc.) are only present as implemented by the model rules governing addition of new species to the assemblage.

The framework and simulation algorithms currently do not incorporate relative abundance (cf. Bush et al. 2007; Deline 2009; Deline et al. 2012), life-history characteristics, population demographics, dispersal and local extinction, spatial structure, speciation and evolution, or other constraints on the regional pool. The incorporation of relative abundance could be especially worthwhile for ecological studies, as it would allow the simulations to better mimic the assembly of ecological communities. For example, abundance plays an important role in immigration from regional species pools (Hubbell 2001; Patzkowsky and Holland 2007; Cornell and Harrison 2014), and abundant taxa can have larger influences on the composition of functional traits within communities and a greater impact on the functional identity of taxa that settle later (Fargione et al. 2003; Guillemot et al. 2011). Functional diversity studies increasingly incorporate relative abundance (Villéger et al. 2008; Laliberté and Legendre 2010; Fontana et al. 2015), but the models used here are limited to presence/absence data, which some functional ecology studies (e.g., Ackerly and Cornwell 2007) have demonstrated produce results similar to those studies that incorporate abundance data.

The simulations also currently do not incorporate phylogenetic structure in an explicit sense. The three driven models are Markovian in that preexisting taxa affect which functional traits can enter at later stages of the simulation, but there is no explicit assumption of heritability or phylogenetic relatedness among simulated species. In contrast, the neutral model is non-Markovian in that all taxa are added independently of one another, without regard to their functional traits. The lack of such phylogenetic structure perhaps hinders the application of these models to diversification within individual, evolving lineages, but the models are intended as reasonable approximations of large-scale evolutionary diversifications involving many disparate lineages, and the focus is on the ecospace structure of the overall biota. The existing simulations could be modified to include such features, which would prove worthwhile for future studies.

Calculating Functional Diversity and Ecological Disparity Statistics

As each simulation proceeds, the theoretical ecospace (functional-trait space) becomes progressively filled with new species having combinations of character states (life habits) selected by the model rules (Fig. 1). Because the mechanisms controlling community assembly vary among models, it is expected that the statistical dynamics will likewise vary. These model-specific dynamics can be calculated as a

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function of species richness. Here, eight widely used statistics are calculated, drawn from the morphological disparity and functional diversity literature (Ciampaglio et al. 2001; Wills 2001; Villéger et al. 2008; Mouchet et al. 2010).

The four morphological (here ecological) disparity measures include the following (Foote 1993; Ciampaglio et al. 2001; Wills 2001). Unique trait-combination (life-habit) richness (*H*) measures the number of unique life habits within each sample. Mean distance (*D*) and maximum range (*M*) measure the mean and maximal distance, respectively, in functional-trait space among species, using Euclidean distance if all characters are numeric/binary or ordered numeric types, or using Gower distance (1971) if any character type is an ordered or unordered factor. Total variance (*V*) measures the sum of variances for each character state across species (Van Valen 1974); when using factor character types, this statistic cannot be measured and is excluded.

The four functional diversity measures include the following (Mason et al. 2005; Anderson et al. 2006; Villéger et al. 2008; Laliberté and Legendre 2010; Mouchet et al. 2010; Mouillot et al. 2013). Functional richness (*FRic*) measures the minimal convex-hull volume in multidimensional principal coordinates analysis (PCoA) ordination trait space. Functional evenness (*FEve*) measures the evenness of minimum-spanning tree lengths between species in PCoA trait space. Functional divergence (*FDiv*) measures the mean distance of species from the PCoA trait-space centroid. Functional dispersion (*FDis*) measures the total deviance of taxa from the circle with radius equal to mean distance from PCoA trait-space centroid. *FRic* and *FDiv* use a subset (here set to 3 by default) of the PCoA axes for their calculation (because their convex hull–volume calculation requires more species than functional traits), whereas the other two use the entire PCoA space.

These statistics are calculated with the function 'calc_metrics' wrapping around function 'dbFD' in the 'FD' package (Laliberté and Shipley 2014) to calculate functional diversity statistics. The four functional diversity statistics are not calculated for samples having less than four unique life habits, for the same reason just explained. The calculation of *FRic* can be computationally demanding and has proven truculent to many users when dealing with idiosyncratic data structures (see Help file in Laliberté and Shipley 2014). Some of these issues are resolved in the implementation here. Specifically, the package defaults to three PCoA axes ('m = 3') as a generally useful and computationally tractable number of axes; defaults to Lingoes correction (Legendre and Anderson 1999) when non-Euclidean PCoA axes are calculated; has corrected (starting with 'FD' Version 1.0–12) a previously unnoticed rounding error in the calculation of PCoA scores that caused computation problems with highly redundant data sets; and has been optimized to prevent overwriting errors (of temporarily stored vertices files) when used in a parallel-processing computer environment. Although including more PCoA axes allows greater statistical power (cf. Villéger et al. 2011; Maire et al. 2015), the use of 3 here provides satisfactory resolution for the often functionally redundant data sets in these simulations. This choice is also warranted because such statistics are calculated directly from multivariate PCoA trait spaces (instead of dendograms) and because the ecospace frameworks used here have few factor-character types (which are especially sensitive to few axes). Three PCoA axes also provide the largest computationally tractable number to allow calculation of these statistics across all sample sizes and models considered.

Sensitivity analyses of these statistics (Ciampaglio et al. 2001; Mouchet et al. 2010; Novack-Gottshall 2010; Maire et al. 2015) have concluded that, despite much correlation among them, each statistic has its strengths for particular uses and contexts. *H*, *M*, *V*, *FRic*, and *FDis* are all useful measures of disparity (or dispersion of species within functional-trait space). *D* and *FDiv* are useful for characterizing internal structure (i.e., clumping or inhomogeneities within the trait space). *FEve* is useful for characterizing the extent of spacing among species within the trait space. Such sensitivity studies consistently recommend that all are useful for particular purposes, with selection left to the researcher, a solution that is decidedly indecisive. Below, I demonstrate

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that classification trees (trained on all statistics from simulated data sets) offer a productive solution to this subjectivity.

Model Selection

A difficulty in implementing model selection with these simulations is that every simulation iteration (i.e., each addition of a species) yields eight statistics. This lack of statistical independence is typically addressed through model-fitting procedures (such as likelihood-ratio tests or the Akaike information criterion [AIC]; Anderson et al. 2000; Burnham and Anderson 2002; Johnson and Omland 2004; Grueber et al. 2011) that incorporate dependency relationships explicitly (such as for a multivariate normal model). However, these methods become prohibitively complicated when the statistics involved are not approximately normally distributed. In this case, H is a discrete binomial distribution. Depending on the model, several statistics are highly skewed, with D best fit by gamma distributions and M and V best fit by Weibull distributions (confirmed using maximum-likelihood goodness-of-fit tests); in contrast, the four functional diversity statistics are all reasonably well fit by normal distributions. Most functional ecology studies thus use one (or a few) of these statistics for a particular test, subjecting them to a simple permutation test to reject a particular null hypothesis. Because all functional diversity/disparity metrics contribute potentially useful information on functional (ecospace) structure (Ciampaglio et al. 2001; Villier and Eble 2009; Mouchet et al. 2010), there is value in retaining all suitable metrics when possible. The obstacle is doing so while simultaneously considering multiple-candidate models (Johnson and Omland 2004; Grueber et al. 2011).

Here I propose a novel and simple method to conduct model fitting in such cases. Classification trees are a powerful and flexible tool for classifying complex data sets with nonlinear, localized, and other complicated relationships among variables (Breiman et al. 1984; Cutler et al. 2007), and they are being increasingly used by ecologists (De'ath and Fabricius 2000; De'ath 2002; Sullivan et al. 2006; Cutler et al. 2007; Boyer 2010; Durst and Roth 2012) and paleontologists (Finnegan et al. 2012, 2015). The basic algorithm is to recursively subdivide heterogeneous data sets (e.g., composed of different classes/models) into subsets that are as homogeneous as possible, using whatever values of variable(s) are most powerful to do so. The result, often portrayed visually as a decision tree, is a statistical model in which values of predictor variables are used to classify the original class/model identities. Studies demonstrate that the method (and its continuous-variable counterpart regression trees) performs as well as nonlinear (generalized additive and linear model) regressions and constrained ordination and is exceptionally well suited to scenarios involving complex (heterogeneous) classifications (Prasad et al. 2006; Cutler et al. 2007). Performance can be improved using "random-forest" variants, in which replicate trees are made, each time leaving out random subsets of variables and data, until a stable model solution is achieved (Prasad et al. 2006; Cutler et al. 2007). This variant also prevents overfitting of the model and allows ranking of predictor variables by their overall importance. (Use of alternate tree-building algorithms below confirmed that random forests performed best for the current analyses.) When applied to new data sets (either a validation/test set to test the tree's classification performance or empirical samples), each resulting tree in the forest casts a vote for the class (here, model) into which each sample should be classified. The proportion of votes for particular models, which scale from 0 to 1, can be used as a measure of support for particular candidate models, analogous to how Akaike weighting allows candidate models to be compared by their relative support (Anderson et al. 2000; Johnson and Omland 2004; Grueber et al. 2011).

The typical workflow to implement classification trees as a form of model fitting includes the following steps. See Supplementary Appendix 2 for technical details on how these steps were implemented in analyses below.

1. Simulate training data sets: Run many simulations of the candidate models (here, the four ecological diversification models) to be considered, calculating relevant summary statistics (here, the eight disparity and

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functional diversity statistics) for each iteration. This large Monte Carlo data set serves as a training data set to train the classification tree.

2. Build a classification tree: Use random-forest classification to identify which combination of variables and their statistics are most predictive of each original model: model ~ $S + H + D + M + V + FRic + FEve + FDiv + FDis$
3. Test the tree with a validation data set: Test the tree's performance using validation data sets, additional simulation data sets of known models that were not included when training the tree. A general (nonoverfit) classification tree should perform approximately as well on a validation data set as it did on its training data set.
4. Classify empirical samples using the random-forest tree: Submit empirical samples (with calculated disparity/diversity statistics but unknown model identity) to the tree for classification, treating the proportion of votes cast for each model as a relative measure of model support.

Methodological analyses (Supplementary Fig. 9) demonstrate that classification trees perform well as model-fitting methods. When conducted across a variety of ecospace frameworks (spanning different numbers of characters, seed species, and character types and incorporating weighting by empirical species pools), trees were able to classify 75–97% of their training data sets correctly (Supplementary Appendix 2); validation tests showed similar performance, with ~2% fewer samples being classified correctly. When applied to more complex cases, such as the ability to distinguish nine models of subtly distinct dynamics (neutral model, four [including both strict and relaxed partitioning versions] process-driven models with 100% rule following, and the four process-driven models with 50% rule following), the training trees still classified 90% of training data correctly (84% of validation data), even when the dynamics of the models were quite similar. This performance extends across all sample sizes, with the classification tree still sufficiently powerful to distinguish these models >33% of the time correctly at sample sizes as small as six (the minimum sample size when the models could be classified, as five species were seeded without any assembly rules). In nearly all cases, the correct model also received the largest proportion of classification votes.

The trees were also successful in identifying samples produced from simulations quite foreign from those used to train the sample (Supplementary Fig. 9). When trained on the nine 50% and 100% rule-following models, the resulting tree generally classified validation data sets produced at 95% and 90% rule following as members of the 100% models, with some votes for the alternate 50% rules. Validation samples produced at 75% generally were classified with mixed support for both the 100% and 50% models. (This generality declines at sample sizes >30–40, as dynamics reach stable asymptotic values; at larger sample sizes, it is worthwhile to consult more complex classification trees to identify the strength of these models.)

These results demonstrate that classification-tree votes can provide a measure of model-selection support, and this support can be extended, at least in this case, beyond the particular training models. Whether trained on nine training sets (as in Supplementary Fig. 9) or on larger numbers (13- or 21-model training sets, if adding 75%- or if adding 75%-, 90%-, and 95%-strength models), the correct model consistently achieves support levels >0.20, from which it is possible to recommend this support value as a benchmark of "substantial" support for the correct model, and values above 0.40 tend to be associated with "unambiguously strong" support for the correct model. (In other words, support values of 0.2 and 0.4 here can serve analogous roles as the 0.1 and 0.9 Akaike-weight benchmarks used in AIC-based model selection.) Although 0.4 may seem low compared with 0.9, the difference can be explained by the large number of candidate models [9, 13, or 21] being considered here, and the fact that the correct model in these tests often achieves support values much greater than 0.4, whereas poorly supported models tend to receive far fewer votes. It is recommended that future analyses using different model implementations run sensitivity

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analyses to validate the generality of these benchmarks, as they likely depend on the number and dynamical similarity of models being considered.

The classification-tree approach to model selection shares several similarities with the methods recently termed approximate Bayesian computation (ABC) in that model selection can proceed without a known likelihood function or an understanding of the dependence between variables (Beaumont 2010; Slater et al. 2012). However, ABC is primarily used when estimating one or a few parameters and often within structurally similar or hierarchically nested models; it is not well suited for choosing among models with distinct parameters (such as is the case here). ABC also performs poorly when considering many summary statistics simultaneously, the "curse of dimensionality" (Beaumont 2010) (and also the case here, where eight interdependent statistics are used). In contrast, classification trees are powerful and flexible methods that were developed to classify such heterogeneous data sets using many predictive variables (Breiman et al. 1993). Although they have not been used before for multivariate model selection, they perform remarkably well and appear to be well suited to this goal.

Simulation Dynamics and Sensitivity to Different Ecospace Frameworks

The four models can be distinguished by examining the dynamics of the functional diversity/disparity statistics as a function of species richness. These dynamics are examined here across a range of ecospace-framework simulations in order to understand their general dynamics, their sensitivity to different ways of creating ecospace frameworks, and their statistical power in model inference when models are known to operate in simulations.

Popular Ecospace Frameworks

Figure 2 illustrates the dynamics for two influential ecospace frameworks, that of Bush and Bambach (Bambach et al. 2007; Bush et al. 2007, 2011; Bush and Bambach 2011) and Novack-Gottshall (2007), which have been adapted for a variety of studies (e.g., Xiao and Laflamme 2009; Bush and Novack-Gottshall 2012; Ros et al. 2012; Bush and Pruss 2013; Laflamme et al. 2013; Dineen et al. 2014, 2015; Aberhan and Kiessling 2015; Dick and Maxwell 2015; Mondal and Harries 2015; O'Brien and Caron 2015). Bambach's original ecospace framework (1983, 1985) consisted of 3 factor characters (diet, activity/motility, and tiering, with the last ordered) and 11 character states, allowing 48 possible unique life habits. The Bush and Bambach ecospace framework retained these 3 characters, but added additional character states (totaling 19) and reformulated motility as an ordered factor. With the addition of osmotrophy as a diet category (Laflamme et al. 2009; Bush and Bambach 2011; Bush et al. 2011), this yields 252 possible unique life habits. The Novack-Gottshall framework more finely subdivides life-habit dimensions according to substrate relationships, microhabitat, motility, diet, and foraging habits and is modified here to include 18 characters (6 ordered numeric and 12 multistate binary) and 37 character states, yielding nearly 3.6 trillion possible life habits (see Supplementary Appendix 1 for list of characters and states). In all three frameworks, many of these theoretically possible life habits are unlikely to ever be realized given logical or functional constraints (cf. Bambach et al. 2007).

Model dynamics for both ecospace frameworks are congruent, despite their rather different structures. In both cases, life-habit richness (H) increases as a function of species richness (S) for all models except redundancy, with the values for strict partitioning (and for Bush and Bambach, also relaxed partitioning) reduced compared with the other models. The neutral and expansion model slope for Bush and Bambach is also reduced slightly compared with that of Novack-Gottshall, as the smaller realized ecospace becomes saturated more quickly. Trends for mean distance (D) are also similar, with neutral remaining stable, expansion increasing slightly (more so for Novack-Gottshall), and the others declining asymptotically to varying extents. Total variance (V) is highly correlated with D for

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Novack-Gottshall, although the presence of factor character types in Bush and Bambach precludes its measurement. Maximum range (*M*) is quite distinct across frameworks, with all Bush and Bambach simulations quickly filling the available ecospace. The Novack-Gottshall framework, in contrast, does not reach asymptotic limits within 50 species, with the rank order of model dynamics generally paralleling that for the other disparity metrics (*D* and *V*): expansion has the greatest range values; followed closely by neutral, significantly greater than both partitioning models; and with redundancy remaining constant at low range. Functional richness (*FRic*) increases for all models, except redundancy for Novack-Gottshall, which decreases, with the greatest values for expansion and neutral models, intermediate for strict partitioning, and least for redundancy. For Bush and Bambach, relaxed partitioning produces the largest *FRic* values of all models, whereas it remains intermediate for Novack-Gottshall. Functional evenness (*FEve*) remains nearly constant for neutral and expansion and declines asymptotically for the other models, and the rank order is similar in both cases: expansion and neutral at the top, followed by both partitioning models, and redundancy at the bottom. Functional divergence (*FDiv*) has generally nonlinear dynamics. Its dynamics increase in both frameworks for redundancy, whereas they decrease for other models, with relaxed partitioning generally decreasing at the fastest rate (although eventually crossing neutral and expansion models into an intermediate value at high sample sizes for Novack-Gottshall). Functional dispersion (*FDis*) has similar dynamics to *D* (and *V*), although the dynamics for the expansion and neutral models increase asymptotically instead of remaining constant.

That these two quite different frameworks share generally similar dynamics is good news for those seeking to apply these statistics for model inference. The most important differences include nearly continuous overlap between the neutral and expansion models in the Bush and Bambach framework, whereas the expansion model generally has greater values and more distinct dynamics for Novack-Gottshall. This is an important consideration if the goal (cf. Bush et al. 2007) is to distinguish an active process (expansion) from a passive process (neutral). Trend dynamics generally also have smaller error margins for the Novack-Gottshall framework, which enables more powerful model selection.

This statistical power can be evaluated using classification-tree methods, by training a random-forest tree on the simulation statistics and counting the proportion of an independently simulated (validation) data set that is classified correctly. The Bush and Bambach framework was able to correctly identify 73% of validation samples correctly. (See Supplementary Appendix 2 for details and classification rates.) Greatest variable importance (in order from most to moderate importance) was awarded to *H*, *FEve*, *FDis*, *D*, and *FRic*. This ranking is consistent with Figure 2A, where these dynamics generally overlap least with those of other models. Confusion matrices, which illustrate both the frequency at which the correct model was selected and which models were misclassified, reiterate that the tree had difficulty distinguishing the expansion from neutral dynamics in the Bush and Bambach framework, with ~50% of expansion samples misclassified as neutral (and vice versa). In contrast, the two partitioning models were correctly classified more than 80% of the time (and usually confused with the alternate partitioning parametrization), and the redundancy model was nearly always properly classified.

The Novack-Gottshall framework provided greater power to distinguish the models, with 89% classified correctly using a validation data set. Variable importance rankings rated *FEve* the most important, followed in order by *D*, *H*, *FDiv*, and *FDis*, four out of the five of which were also considered most important in the Bush and Bambach tree. The confusion matrix also demonstrates some difficulty distinguishing the expansion and neutral models, but to a much lesser extent: ~75% of expansion models were correctly distinguished from the neutral models (and vice versa), with 98% of partitioning and exactly 100% of redundancy models correctly classified. Thus, the more multidimensional Novack-Gottshall framework, albeit more complicated and less

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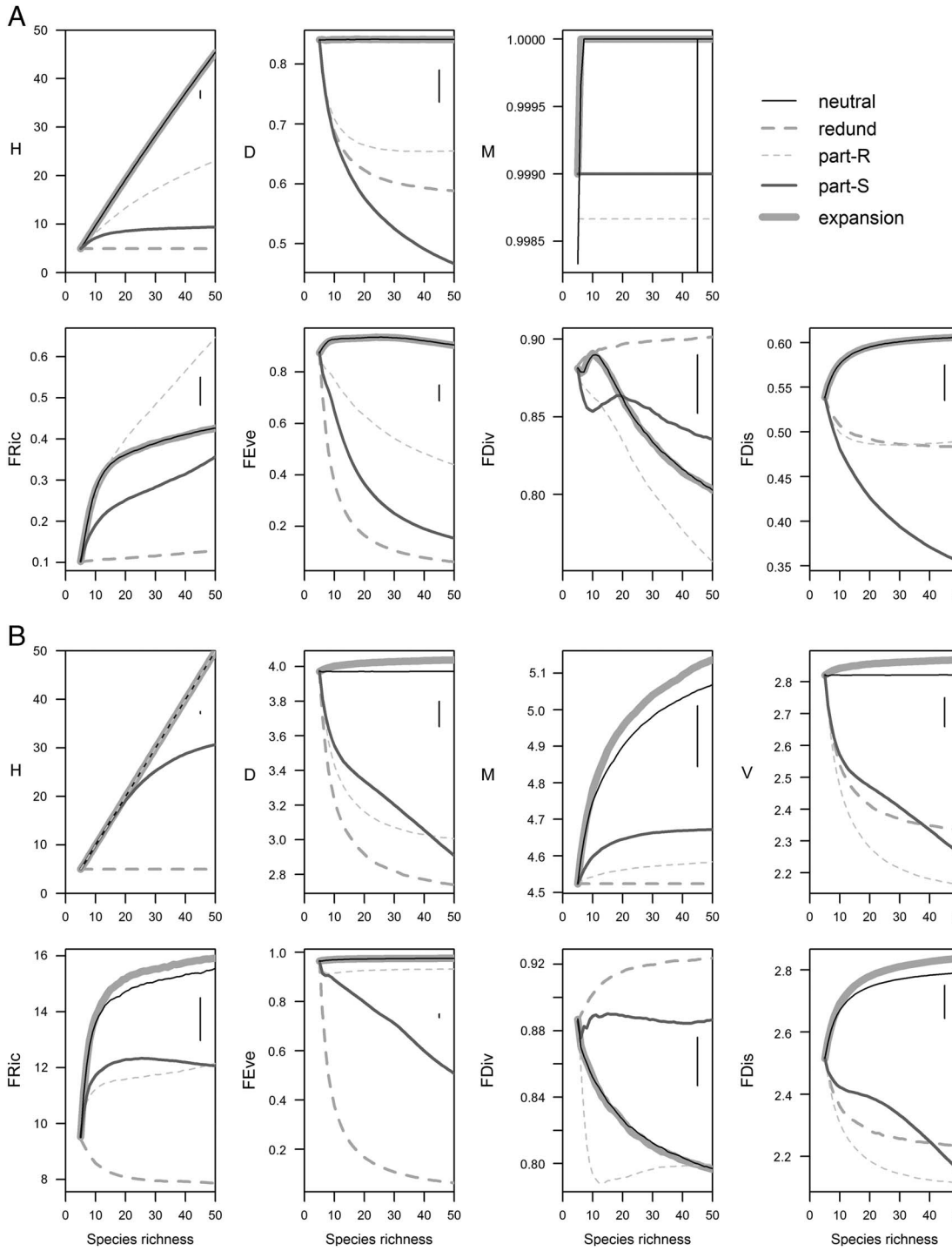
intuitively appealing for general summary applications, provides greater statistical power for inferring important ecological and evolutionary models.

These results can be generalized by examining other ecospace frameworks to identify what forms of ecospace framework choices are most likely to provide informative results for future



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analyses. The most important differences between these two ecospace frameworks concern differences in number of characters and character types; thus it is worth examining the effect of these variables. In addition, analyses also examine the effect that number of seed species has on dynamics and the ability to distinguish resulting models.

Number of Ecospace Characters

Ecospace frameworks with more characters and states ought to have greater opportunities for the models to be distinguished, and thus be more powerful frameworks. Simulations—implemented using ecospace frameworks with 5, 15, and 25 characters of mixed character types—bear this out, but only to a modest extent (Supplementary Fig. 6). The dynamics across simulations are generally similar, in much the same way as for the frameworks discussed above (Fig. 2). In particular, the smaller 5-character simulation (Supplementary Fig. 6A) strongly resembles the dynamics of the Bush and Bambach framework (Fig. 2A), whereas the larger 15-character simulation strongly resembles the dynamics of the Novack-Gottshall framework (Fig. 2B), attesting that many of the differences result from differences in the numbers of characters in each framework. However, the classification rates improve only modestly as additional characters are added (83%, 85%, and 86% of models, respectively), suggesting that number of characters is not the primary driver of performance between the two frameworks. This conclusion reiterates one made in prior sensitivity analyses of functional diversity (Maire et al. 2015), which likewise found that number of characters accounted for limited improvement in performance. Examination of confusion matrices (Supplementary Appendix 2) demonstrates that most of the improvement in the larger simulations was the result of improved performance at distinguishing the partitioning models, both from each other and from the other models, made possible because the larger number of characters allows for greater opportunities for intermediate life habits.

Character Types

Another important difference between the two frameworks considered above is their character types, with the Bush and Bambach framework using ordered and unordered factors and the Novack-Gottshall framework using ordered and unordered numeric (binary) characters. Maire et al. (2015), using sensitivity analyses involving simulated data sets, concluded that character type carried the second-most importance in the performance of functional-trait spaces (ecospace frameworks), subordinate only to whether statistics were calculated via a multidimensional ordination versus a functional dendogram, a comparison not considered in the current study (where all functional diversity metrics are calculated using the more powerful ordination method). They

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FIGURE 2. Model dynamics for eight functional diversity statistics for the ecospace frameworks of (A) Bush and Bambach (Bambach et al. 2007; Bush et al. 2007, 2011; Bush and Bambach 2011) and (B) Novack-Gottshall (2007). In both cases, all models are enacted at 100% rule following with five seed species. The second case (B) also stipulates that each life habit can have at most two character states within a given life-habit character (see text for explanation of 'constraint' parameter). Dynamics are reported as a function of increasing species richness, up to 50 species (i.e., there is a common abscissa in all graphs); the ordinate has been truncated to focus on the trend lines for each statistic. Statistics include life-habit richness (*H*), mean distance (*D*), maximum range (*M*), total variance (*V*), functional richness (*FRic*), evenness (*FEve*), divergence (*FDiv*), and dispersion (FDis); see text for description of each statistic. Trend lines are the average of 1000 simulations. Vertical bars near the top right of each graph illustrate the average standard deviation around each set of trends; the standard deviation for mean distance in the Bush and Bambach framework equals 0.0117 and extends beyond the borders of the graph. Part-S and Part-R represent the strict and relaxed versions of the partitioning model; redund in caption is an abbreviation for the redundancy model. The variance trend in (A) is omitted because the characters in the Bush and Bambach framework are all factorial, preventing its calculation. The uppermost *H* trend line in (B) is an overlap between the neutral, relaxed partitioning, and expansion trend lines. Despite their rather different structures, the model dynamics for each ecospace framework are quite similar. Notable differences include total overlap between neutral and expansion models in the Bush and Bambach framework and generally smaller error margins for the Novack-Gottshall framework, which allows more powerful model selection using classification-tree methods (89% of validation models classified correctly vs. 73% with the Bush and Bambach framework).

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demonstrated that continuous and ordinal (ordered numeric) character types performed best, and discrete categorical (unordered factor) types performed worst. This conclusion is partially borne out here (Supplementary Fig. 7) using simulated ecospace frameworks built from 15 characters of varying types: factors, ordered factors, ordered numeric, and binaries (unordered numeric). Again, dynamics are generally similar across simulations, with the greatest difference occurring with ordered factors (Supplementary Fig. 7B), which have rather distinct dynamics from the other frameworks for *D*, *M*, *FDiv*, and *FDis*, and to a lesser extent for *FRic*. The dynamics for factors and ordered and unordered numeric (binaries) are all quite similar. Thus, there is negligible difference caused by the distance metric used, with Gower distance used for both factor types and Euclidean distance for both numeric types. Classification rates on ordered factors were also substantially improved (94% of trained models classified correctly) compared with the other character types (78% for unordered factors, 79% for ordered numerics, and 81% for binaries), with most of the difference due to improved ability of the ordered-factor tree to distinguish the neutral and expansion models. (See Supplementary Appendix 2 for additional details, including confusion matrices.) Overall, ordered character types, and especially ordered factors, perform better than the other character types, although the improvement is modest.

Number of Seed Species in Simulations

Actual ecological communities do not normally start with prespecified numbers of initial colonizing "seed" species; thus, selecting how many to choose in a simulation should reflect knowledge of the ecological and evolutionary scenarios one seeks to mimic. It is worthwhile to evaluate the effect that this arbitrary choice might have on resulting simulations. Supplementary Figure 8 demonstrates that the effect can be substantial for some models, although the dynamics for the neutral and expansion models are essentially invariant across implementations tested here. The greatest difference occurs for *FDiv*, with the partitioning dynamics dramatically changing behavior across the three scenarios: with three seed species, the dynamics are relatively constant at low values; with five seed species, the strict version decreases and the relaxed version remains constant after an initial decrease; and with 10 seed species, both trends decrease at different rates. In all cases, however, the strict version has values greater than the relaxed one. The statistic *M* and to a lesser extent *FRic* also vary with number of seed species, with the redundancy and partitioning values substantially suppressed when seeded with three (and to a lesser extent five) species and substantially increased when seeded with 10 species. Although some dynamics vary dramatically due to differences in seed species, the classification rates are less variable. The simulation seeded with three species classified 85% of training data correctly (or 82% when excluding the redundancy model, in which many statistics were absent, because the functional diversity statistics require a minimum of five unique life habits), 85% for the simulation seeded with five species, and 75% for the simulation seeded with 10 species (see Supplementary Appendix 2 for details, including confusion matrices). Confusion matrices demonstrate that the neutral and expansion models are most difficult to distinguish in all three simulations, with the 10 seed species simulation also showing greater difficulty distinguishing the other models. Thus, it is worthwhile—assuming the ecological and evolutionary context justifies it—to use moderately few numbers of species to seed the simulations, because using larger numbers impedes the simulations from following the model rules. Although not entirely justified by the overall classification-tree results, the dynamics suggest that using too few species to seed the simulations can suppress the dynamics of the partitioning and redundancy models, which are explicitly constrained to exploring the part of the ecospace seeded by the initially occurring species.

Which Statistics Are Most Valuable?

Another benefit of using random-forest classification trees as a form of model selection is that they provide an explicit mechanism to evaluate which statistics are most valuable in classifying the models. As discussed earlier,

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this is accomplished by excluding some variables at random from the tree-training algorithm (somewhat analogous to bootstrap support in cladistics), which prevents overfitting of the model and aids in evaluating the relative variable contribution to the final tree model (Prasad et al. 2006; Cutler et al. 2007; Strobl et al. 2007). Variable importance rankings for the classification trees used with these simulations considered *FEve* the most valuable statistic, on average, for distinguishing the models, followed by *D*, *H*, and *FDis*. In models in which *V* could be included, it was considered the fourth most important variable. *FDiv* and *FRic* consistently had intermediate (but worthwhile) value, and *M* and *S* consistently had low value. The poor ranking of *S* is reassuring, as it is the independent variable in all models and only useful in combination with other statistics. This ranking is intuitive, as the high-value statistics tended to have the least overlap among models in the simulations presented above (Fig. 2, Supplementary Figs. 6–8). Although functional ecologists focus almost exclusively on their newly invented statistics, those traditionally used in morphological disparity are often just as powerful (or more so) and also computationally more straightforward to measure. Thus, they ought to be considered more frequently in functional diversity studies. However, a benefit of using classification trees as a basis for model selection is that one ultimately does not have to choose which statistics to include (cf. Mouchet et al. 2010). The tree algorithm is sufficiently powerful and flexible to "learn" which variables to rely on in each circumstance: it always sees the forest through their trees.

Model Inference of Late Ordovician Samples and Effect of Geographic and Temporal Scale

Empirical Samples

These methods are applied to a case study of well-preserved fossil biotas from the type Cincinnatian (Late Ordovician) Kope and Waynesville formations of southwest Ohio, northern Kentucky, and southeast Indiana. Lithologically, these units are composed of shales interbedded with thin limestone tempestites, representing offshore, soft-substrate conditions below storm-wave base in the Cincinnati Arch epeiric sea (Holland 1993). Taphonomic conditions are excellent, with preservation by obrution deposits, and most assemblages include evidence of fossils preserved in life position, articulated specimens, and autochthonous and parautochthonous communities (Frey 1987a,b; Schumacher and Shrake 1997; Hughes and Cooper 1999; Aucoin et al. 2015). The shelly and trace-fossil biotas are also extensively well studied, with much attention given to their life habits (Pojeta 1971; Richards 1972; Frey 1987a,b; 1989; Brandt et al. 1995; Lescinsky 1995; Brandt 1996; Feldmann 1996; Sandy 1996; Schumacher and Shrake 1997; Leighton 1998; Gaines et al. 1999; Meyer et al. 2002; Morris and Felton 2003; Novack-Gottshall and Miller 2003; English and Babcock 2007; Freeman et al. 2013). These two formations were selected for analysis as a case study because they represent exemplary preservation within a single depositional environment, but the results are likely to apply to other type Cincinnatian units.

A total of 218 collections from the Kope and Waynesville formations (totaling 2322 occurrences; min = 2, mean = 8.2, median = 8, max = 23 taxa) were downloaded from the Paleobiology Database (www.paleobiodb.org), only including those that included the entire biota. Source references include Dalvé (1948), Browne (1964), Frey (1987a, 1988, 1989), Novack-Gottshall and Miller (2003), and Holland and Patzkowsky (2007). The size of each collection was confirmed to represent a typical field sample (i.e., a hand sample, slab, or small bedding plane). All stratigraphic members were included, as they are defined more by biofacies than by major differences in depositional environment (Holland et al. 2001; Holland and Patzkowsky 2007).

A set of 92 Kope samples were collected from eight stratigraphic sections (roughly equivalent to outcrops) spanning the Fulton, Economy, Southgate, and McMicken members; the 126 Waynesville samples represented 15 sections spanning the Fort Ancient, Clarksville, and Blanchester members and their informal "trilobite shale" and "*Treptoceras duseri* shale" facies. Analyses were conducted at multiple scales: individual samples (representing

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autochthonous local communities), stratigraphic sections, members, and each formation in aggregate. Because the analyses hierarchically span multiple localities and stratigraphic levels, they offer useful tests of the generality of the models. If the ecological models presented above provide good fits for the functional structure within individual samples, then we might expect different structures (and models) to be recorded at the spatially and temporally mixed scales of the larger aggregate levels where regional and evolutionary processes are more likely to play out.

Ecospace Framework and Ecological Disparity

Life habits (functional traits) of 237 unique Kope and Waynesville taxa were coded into a modified ecospace framework from Novack-Gottshall (2007) that included 18 characters (6 ordered numeric and 12 multistate binary) and 37 character states. Given the sensitivity analyses noted above, the large number of characters and the presence of these character types ought to be sufficient for distinguishing the relevant models. Life habits were coded according to inferences of functional morphology, body size, ichnology, *in situ* preservation, biotic associations recording direct interactions, and interpretation of geographic and depositional environment patterns, in consultation with 67 peer-reviewed, published references, many studying this fauna directly. Body-size measurements were made using the methods of Novack-Gottshall (2008b), primarily from Feldmann (1996), supplemented with the *United States Geological Survey Professional Paper* volume 1066 series and the *Treatise on Invertebrate Paleontology*. Ordered numeric states (e.g., body volume, mobility, and distance from seafloor) were rescaled as five discrete, equidistant bins (seven for body volume) so that they ranged from 0 to 1. See Supplementary Appendix 1 for list of characters and states and an example of how life-habit (functional-trait) inferences were coded using the Ohio state fossil, the trilobite *Isotelus maximus*.

Of the 237 taxa in the species pool (Supplementary Appendix 3), 101 were identified to (and coded at) species level and 136 were coded at genus level, with just 7 of these taxa having uncoded (unreliably inferred) states. The relative completeness of this coding is important, as sensitivity analyses have demonstrated that missing data (traits or species) can lead to inaccurate functional diversity measurements (Pakeman 2014); this impact is also mitigated here by having replicate samples and the use of a model-selection routine that explicitly incorporates variation among simulation trials. Indeterminate taxa (e.g., trepostome bryozoan indet. or *Platystrophia* sp.) that occurred within individual samples (but were excluded from the aggregate 237-taxon species pool unless their occurrence was the sole member of that taxon, see below) were coded for a particular state only when all other members of that taxon within the Kope-Waynesville species pool unanimously shared that common state; otherwise, the state was listed as NA (missing). Although there are differences in taxa and functional traits between the Kope Formation and Waynesville Formation species pools (especially resulting from the Richmondian Invasion; Holland and Patzkowsky 2007, 2009), a single aggregate pool is used here for simplicity. Use of formation-specific species-pool models does not alter the current results.

Eight ecological disparity and functional diversity statistics were calculated for the 218 Kope and Waynesville samples and for section-, member-, and formation-level aggregates of these samples. The routine used to produce temporal and geographical aggregates only retained indeterminate taxa if no other members of the same taxon were found in the aggregate; this logic also applied to genus-level occurrences, excluding them when a named species of the genus was present. This left 135 unique taxa (representing 83 unique life habits) in the Kope Formation aggregate and 174 unique taxa (93 unique life habits) in the Waynesville Formation aggregate. Eight samples were excluded from model-fitting protocols because they had fewer than four life habits, the minimum needed to calculate the functional diversity statistics.

Simulations, Constraints, and Model Selection

Two criteria must be met when considering candidate models for these samples (Burnham

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and Anderson 2002; Johnson and Omland 2004). The first concerns adequacy: Do the models predict values of similar magnitude to those found in the samples? The second concerns model selection: Among adequate alternative candidates, which model best represents the empirical samples? "Best" in this context can be defined in multiple ways, such as model simplicity, maximum likelihood, or chi-squared or Kolmogorov-Smirnoff statistics (Burnham and Anderson 2002), but classification trees trained (and validated) on simulated data sets are used here because of the nonindependent, multidimensional nature of the model statistics.

Five seed species were used in the simulations, as this approximated (the 12th percentile) the sample size of the smallest samples, and this value allows calculation of all functional diversity statistics and provides powerful model discrimination using classification trees. Adequate models were obtained by implementing simulations iteratively and altering constraints of the ecospace framework to produce models with statistics similar to those found in empirical samples and aggregates (Fig. 3). Note that simulations proceeded in identical manner in each simulation; only constraints delimiting the nature of the theoretically possible ecospace were modified. As discussed below, the alterations needed to achieve realistic statistics are themselves informative as to the types of constraints that may exist in defining the realized Kope/Waynesville ecospace.

The simulations used when building the models in Figure 2B used an ecospace framework that allowed at most "two presences" for each binary character ('constraint = 2'; see "Theoretical Ecospace Framework" section). These models all fail the first test of adequacy. Except for *H*, *FEve*, and *FDiv*, the model simulations predict disparity and functional diversity statistics much larger than the values found in the actual Kope and Waynesville samples (compare with points in Fig. 3A). It is unwise to select the best model out of a group in which all perform poorly. The inadequacy is attributable to the relatively unconstrained framework, which allows for 930 billion unique life habits to occur in simulations, many of which are unlikely or impossible to occur in nature (such as animals that feed using any two foraging combinations among ambient, filter, attachment, mass, and raptorial habits). The highly multidimensional nature of this framework provides so many opportunities for unrealistic life habits that empirical samples are bound to be depauperate by comparison.

Simulations in Figure 3A further constrain the framework so that life habits can inhabit only a single binary character state ('constraint = 1'; e.g., only infaunal or epifaunal are allowed but not semi-infaunal). This additional constraint diminishes all statistics by a negligible amount, but the overall dynamics are largely unchanged, with the largest differences occurring in the partitioning simulations. Empirical samples continue to have statistics substantially below those predicted by these models, implying that even this more constrained framework—allowing only 1.13 billion unique life habits—is too permissive to represent life habits that actually occur in nature. For example, it "permits" animals the size of humans to crawl between grains of sediment, a logically impossible life habit. However, many of the life habits created by this framework are biologically possible, even if they require some creativity to envision an organism inhabiting such a life habit. As an example, the framework could happen upon a "buried" microscopic, fluid-feeding carnivore that feeds facultatively attached to its prey on hard substrates while living far above the seafloor. Although seemingly implausible, this is a typical life habit for a number of parasites (cf. Huntley and Scarponi 2012). The exposure of such unlikely (or at least rarely fossilized) life habits (see Novack-Gottshall 2007 for others) is not a flaw or bias in the simulations or analyses and can reveal important constraints that structure actual biotas (Raup 1966; Seilacher 1970; Thomas and Reif 1993).

The generally unchanged dynamics in Figures 3A and 2B, despite their ability to represent orders-of-magnitude different numbers of life habits, also demonstrate that the inclusion of large numbers of potentially illogical or biologically unreasonable life habits has little effect on resulting dynamics. The imposed "single-presence" constraint is also biologically

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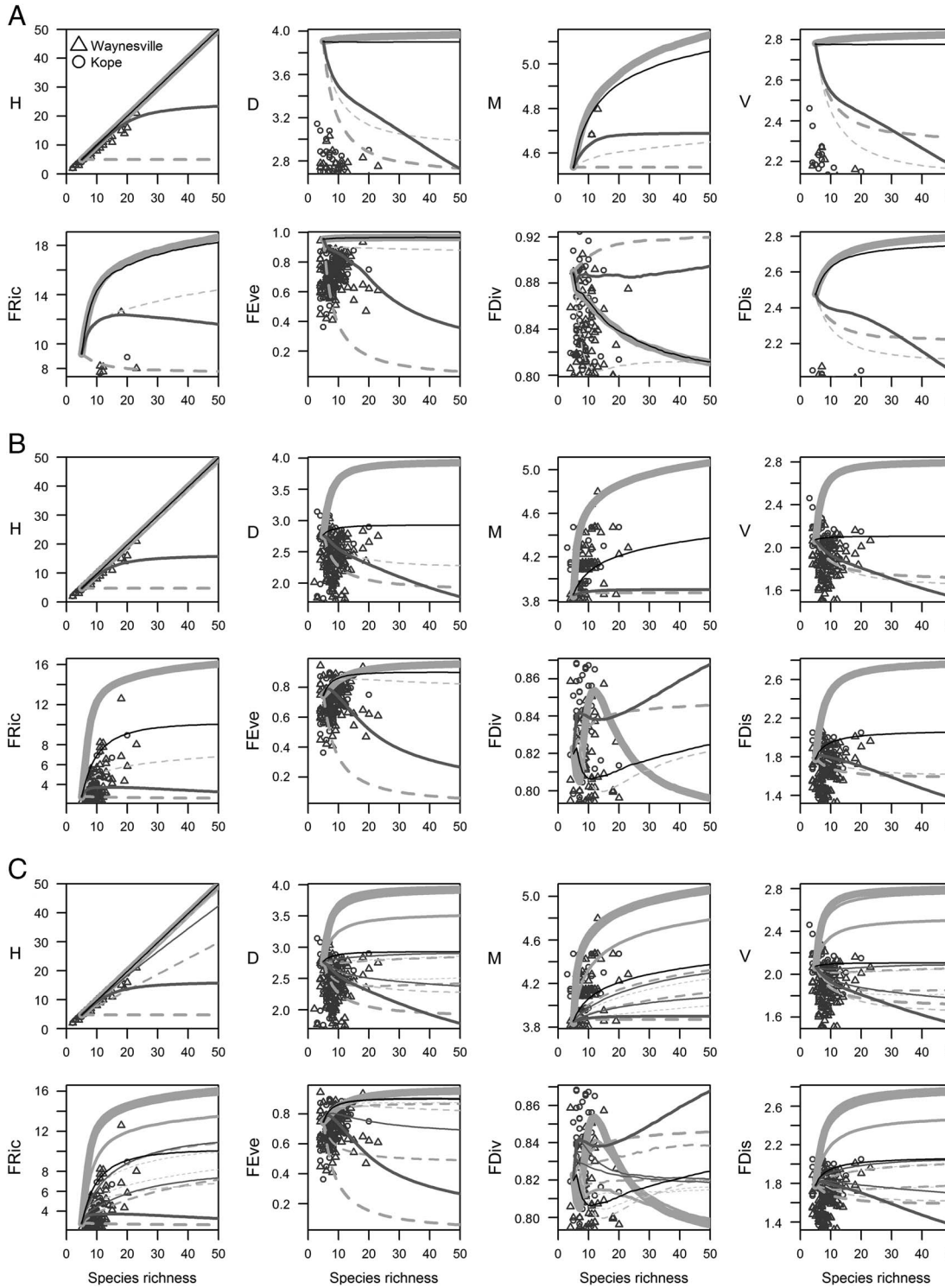
unrealistic, as 52% of the Kope/Waynesville taxa are coded using "two-presence" characters (e.g., corals reproduce both sexually and asexually; semi-infaunal bivalves are common; and many crinoids, brachiopods, and bryozoans are known to attach to lithic and biotic substrates). Different



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kinds of constraints must be imposed to allow the models to approximate actual Ordovician samples.

The next simulations relax the "one-presence" constraint to allow for "two-presence" characters but use the Kope/Waynesville aggregate pool to weight the inhabitation of character states. For example, because 87% of the pool taxa are coded as epifaunal, 9% as infaunal, and 4% as semi-infaunal, simulated life habits within the neutral model (and seed species for all models) will mimic these proportions, on average. Similarly, because no taxa are coded as simultaneously autotrophic and carnivorous, that combination is removed as a possible character state across all simulations, as are other such nonoccurring ones. Imposing such empirical weighting still allows for 57 billion unique life habits and allows the ecospace framework to mimic important features of the empirical species pool, albeit indirectly. For example, although the simulation rules do not specify actual predator:prey or producer:consumer trophic-group ratios (Van Valkenburgh 1988; Dunne et al. 2008; Mitchell et al. 2012; Hatton et al. 2015), size-diet relationships (Van Valkenburgh and Molnar 2002; Codron et al. 2013), or other regulating factors, the weighting allows the simulation to indirectly mirror these empirical ecological rules. As a result of this weighting, most of the simulated life habits also correspond to biologically reasonable life habits commonly inhabited by animals, living or extinct. Neutral simulations yield life habits differing by approximately four states (out of 37 in the framework) from ones actually occurring in the Late Ordovician species pool (after allowing the simulation to proceed through completion at 50 species per sample). The dynamically restricted models produce life habits differing by <1 state from actual Ordovician life habits for redundancy (with 95% rule following) and strict partitioning simulations and ~2 states for the relaxed partitioning simulations. The expansion model, as intended, explores the most disparate (and slightly unreasonable) life habits, but still produces life habits that differ by ~10 states from actual Ordovician life habits. Thus, the life habits produced by the simulations, when weighted by empirical species pools, are biologically quite reasonable approximations of reality. (It should be emphasized, however, that the model-selection method only considers the disparity structure of each assemblage and not the identity of simulated life habits.) Further analysis of the nature of these constraints is beyond the scope of this study, but it seems reasonable that the implementation of empirical weighting is a practical solution to restrict the theoretical ecospace to those approximate regions locally allowed by whatever combination of historical, biological (adaptational), and structural constraints shaped the species pool (Raup 1966; Seilacher 1970; Thomas and Reif 1993).

FIGURE 3. Comparison of Late Ordovician samples to dynamics of different simulation implementations: A, 100% rule-following implementation with one-state constraint; B, 100% rule-following implementation with two-state constraint and empirical weighting of states; C, 100%, 90%, and 50% rule-following implementation with two-state constraint and empirical weighting. The legend and graphical interpretation is the same as Figure 2, and variability around the mean trend lines are of similar magnitude. Statistics for Late Ordovician (type Cincinnatian) Kope Formation and Waynesville Formation samples are represented by circles and triangles, respectively. A, Simulations were enacted at 100% rule following, and each life habit was constrained to have just one character state within a given life-habit character; for example, a taxon could be either sexual or asexual, but not both (hermaphroditic). The dynamics are similar to those for the two-state implementation in Figure 2B, although values are slightly diminished, especially for the partitioning models. In all cases, the empirical sample statistics lay well below the mean trend lines, implying a poor fit between these simulations and reality. B, The simulations included the two-state constraint, but were modified so that the combined Kope and Waynesville species pool was used to weight how seed species were chosen (i.e., they were chosen at random from the species pool) and the inhabitation of character states of all successive species were weighted by their frequency of occurrence in the species pool. The fit between the empirical samples and the model dynamics is much improved (that is, there is substantially more overlap). C, Eight additional "weaker" simulations are added, in which the model rules are followed on average 90% and 50% of the time. The average trend lines for these weaker simulations are slightly thinner (but with the same shadings and line types) than the 100% implementations to make it easier to distinguish them (although the 90% expansion model trend mostly overlies the 100% implementation). A 0% simulation is always present, the neutral model, in which no model rules are followed. The empirical samples frequently overlie weaker versions of the models, and all models coalesce toward the neutral model as they become weaker and weaker.

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Implementing these weightings also result in simulations (Fig. 3B) that reflect adequately the statistics of empirical samples across all eight statistics, with dynamics substantially diminished compared with the unweighted simulations. Statistical dynamics are also quite altered, although the rank order of models remains generally unchanged: expansion (also the least altered, with asymptotic values negligibly diminished from prior unweighted implementations) has the largest disparity/diversity values, followed by neutral (now dynamically distinct from expansion) and the two partitioning implementations, with redundancy at the lowest values. The distinct model dynamics also result in improved performance for the classification tree, with 96% of the training data sets classified correctly (compared with 91% for the one- and two-constraint simulations), primarily resulting from improved ability to distinguish the expansion and neutral models (see Supplementary Appendix 2 for details).

Although the empirical samples adequately overlie model dynamics, they follow the mean trends only rarely, occurring more frequently in the region between the passive neutral model and the other active models. This could indicate that the best models to represent the samples are not 100% implementations of the models but instead weakened versions of the models. This is illustrated in Figure 3C, where eight additional "weaker" simulations are added, in which the model rules are followed on average 90% and 50% of the time. In other words, for the 50%-strength implementation, a computational "coin flip" was used in the assignment for each taxon's character states, whether to assign it at random (weighted by the species pool) or whether to use the model rules to assign it (but still only allowing states present in the species pool). The neutral model represents a 0% simulation, in which no active model rules are followed, and model dynamics coalesce toward the neutral model as they become weaker and weaker. Most empirical samples overlie the weakened model dynamics. Although many of the nine models share similar dynamics (more so, given the often overlapping variation around each mean trend line), the classification tree displays a remarkable ability to distinguish them, with 90% of training data sets classified correctly, and 73% correct when tested against independently created validation data sets.

The classification tree used below in model selection of samples is simpler, using just the 100% and 50% rule-following models in Figure 2C as training data sets; it classified 92% of training data sets and 78% of validation data sets correctly (Supplementary Appendix 2). Although the training data sets here represent just two strength levels (50% and 100%), validation samples produced at different strengths (75%, 90%, and 95%) indicate the simple "two-strength" classification tree is able to provide generalizable approximations for other model-strength implementations (Supplementary Appendix 2, Supplementary Fig. 9). Performance remains strong at sample sizes as low as six, the minimum sample size when the models could be classified (i.e., because five were seeded without any assembly rules). (It is reassuring that if the simulated assemblages with five or less species are submitted to model selection, they are overwhelmingly, and correctly, classified as representing neutral models.) More complicated trees (i.e., those trained on 75%-, 90%-, and 95%-strength models) are used to confirm the strength of models, especially for larger samples, where these more complex trees are better suited for distinguishing their less dissimilar dynamics.

The majority of Kope and Waynesville samples are classified (Fig. 4, Supplementary Appendix 4) as representing partitioning models (73% and 74%, respectively), with most classified as 100%-strength versions of the model (51% and 43%, respectively). Some samples are classified as weak (50%-strength) redundancy models (14% and 16%, respectively), and negligible numbers are classified as neutral or expansion models. A chi-squared test confirms that the model classifications are statistically indistinguishable between formations ($\chi^2 = 48$, df = 36, p-value = 0.087). Average model support (measured in terms of proportion of tree-classification votes cast) for the "best" model is 0.50, above the threshold of 0.20 at which support can be considered substantial and 0.40 at which it can be considered unambiguously strong (see Supplementary Fig. 9). Only one sample had winning support below this threshold, a small seven-taxon Waynesville sample deemed neutral

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with support of 0.18. The relatively low numbers of samples classified as weakened partitioning models (<5% of samples) also suggests that most Kope and Waynesville samples are best represented by strong (>75%, and likely >90%) partitioning models, based on sensitivity analyses in Supplementary Figure 9. This is confirmed using more complicated classification trees: when additional strength simulations are included (i.e., when adding 90% as in Fig. 3C or adding 75%, 90%, and 95% to the training data sets), most samples remain classified as strong (90%, 95%, and 100%) versions of strict partitioning, 100%-strength relaxed partitioning, and 75%- and 90%-weakened redundancy models (Supplementary Appendix 4). Classification trees and simulations that used separate species pools for each formation (i.e., creating a Kope tree trained only on Kope species pool simulations) also produced similar model classifications, as expected given that 42% of genera and 69% of life habits are identical in each separate pool.

Representative samples classified by the four driven models are illustrated in Figure 5 on two-dimensional nonmetric multidimensional scaling plots. As expected, samples classified as partitioning models demonstrate continuous gradations, either in a linear fashion for the strict partitioning version of the model or in a central cluster in the relaxed version. Samples classified as weakened redundancy demonstrate discrete clusters of life habits, often with multiple taxa sharing similar or identical life habits. At large sample sizes, both the partitioning and redundancy models yield many instances of taxa with nearly overlapping life habits, although those produced by partitioning tend to have more continuous gradients between these clusters (compare Figs. 1 and 5). Samples classified as expansion tend toward relatively large distances between life habits, often have the centroid empty, and encompass a broad range of the ecospace, even at small sample sizes.

If the model classifications indicate evidence for ecological structure within these generally autochthonous samples, then one might expect different models to emerge at larger temporal and spatial scales, where samples are aggregated into individual outcrops (sections) and stratigraphic members and formations (Patzkowsky and Holland 2003; Holland 2010; Tomašových and Kidwell 2010; Hautmann 2014). For example, if beta diversity is substantial, one might expect a preponderance of redundancy models, as samples with similar structure duplicate one another in aggregation. Alternatively, one might expect greater frequency of neutral models, as patterns at the larger scales increasingly reflect the regional species pool.

Such a transition is partially borne out here. The Kope and Waynesville stratigraphic sections have model classifications similar to those of their individual samples (Fig. 4), dominated by 100%-strength partitioning (albeit only the strict implementation) and the remainder largely weak redundancy. The sole section deemed neutral has the smallest sample size and lowest (but still substantial) model support of 0.34. These classifications are generally supported when using more complex classification trees, with all eight Kope sections best classified as 90–100% strict partitioning models, but a greater number of Waynesville sections classified as 50–90% redundancy models (Supplementary Appendix 4).

At the larger sample sizes of stratigraphic members and formations, it is possible to use more complex classification trees (i.e., adding 90%-strength training data sets or adding 75%-, 90%-, and 95%-strength implementations) to conduct model selection. This is especially worthwhile, because the dynamics of redundancy and both partitioning models are similar if even slightly weakened (i.e., 90–99%). This is evident by their overlapping dynamics in Figure 3C and when examining model classifications and confusion matrices on validation data sets (Supplementary Fig. 9, Supplementary Appendix 2). In particular, slightly weakened (90–95%) redundancy models are typically misclassified by the simple tree as strong strict partitioning models at sample sizes >30 (Supplementary Fig. 9), and moderately weak (75–90%) relaxed partitioning models are typically misclassified as strong relaxed partitioning and weak redundancy models (Supplementary Fig. 9). Note that these misclassifications tend to occur only at sample sizes >30, where the more asymptotic dynamics make it easier for the simple

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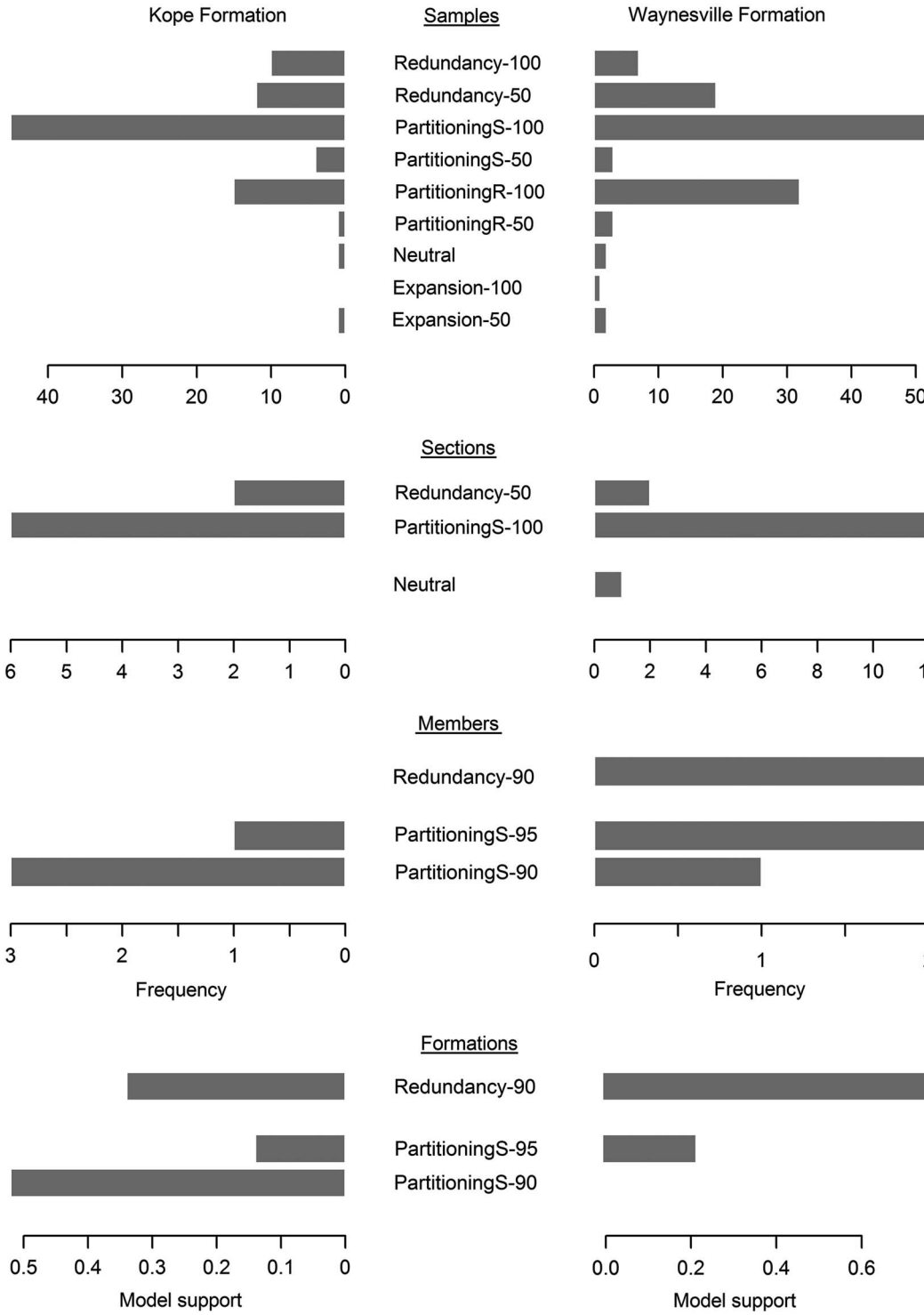
classification tree to reject implementations that are different from those in the training data set. One might argue that these classifications point to indistinguishable dynamics for these models, regardless of whether named "redundancy" or "partitioning." Yet the



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simple tree is able to correctly distinguish these models more than 33% of the time (Supplementary Fig. 9). In contrast, the more complex three-strength (50%, 75%, and 100%) and five-strength (50%, 75%, 90%, 95%, and 100%) trees classified 90% of training data sets correctly and displayed improved ability to distinguish all weakened implementations of each model.

When the five-strength tree is used, all four Kope members are classified as strong (90–95%) strict partitioning models, consistent with model classifications at smaller scales (Fig. 4). The Waynesville members have divided support, with three best classified as 90–95% strict partitioning and two as 90% redundant models (Supplementary Appendix 4). Classifications using the three-strength tree are identical, but with the 95% votes classified instead as 90%-strength implementations.

The entire Kope Formation species pool, using the five-strength tree (Fig. 4), is classified as 90% strict partitioning (0.52 support), with substantial support for a 90% redundancy model (0.34), whereas the Waynesville formation pool is classified as 90% redundancy (0.78 support) with the remainder for 95% strict partitioning. The three-strength tree provides similar classifications (Supplementary Appendix 4). This classification is intuitively evident when considering the ratio of unique life habits to taxa (H/S) in each formation: the Waynesville pool has substantially more true redundancy (81 of 174 taxa, or 47%, are functionally identical) compared with the Kope (with 52 of 135 taxa, or 37% functionally identical). The structure of each formation is visualized in Figure 5. Although they look quite similar (the most obvious difference being the presence of corals in the Waynesville, one of many new immigrants during the Richmondian Invasion; Holland and Patzkowsky 2007, 2009), the classification trees are sufficiently sensitive to their structural differences to classify them accordingly.

When comparing classifications across spatially and temporally mixed scales, the Kope Formation remains consistently classified by strong (>90%) strict partitioning models. There is no evidence of change in ecospace structure across scales. In contrast, the Waynesville is typically classified as representing partitioning models (both relaxed and strict versions) at the scale of samples, switching to greater support for ~90% redundant models at larger scales, especially when considering the entire formation species pool. The consistent lack of support for neutral and expansion models at any scale is evidence that the ecospace structure of these Late Ordovician samples is decidedly nonrandom and restricted. Even when weighted by the life-habit traits known to occur in the Late Ordovician regional species pool, the ecospace actually inhabited by this biota remains substantially constrained.

Although the simulations do not incorporate phylogenetic structure (newly added species are added solely on account of their functional traits), it is promising that model selection is not a simple artifact of which taxa are present within a sample (Fig. 5). If it were, one might expect that samples classified as redundancy or partitioning would be dominated by one or a few taxonomic groups, whereas samples classified as expansion might have greater taxonomic diversity. That is not the case here, where a wide range of major taxonomic groups is present at all scales and clusters of functionally similar species likewise tend to be taxonomically diverse. The same ecological structure reoccurs when taxonomically quite different biotas are analyzed.

FIGURE 4. Relative model support for Kope (left column) and Waynesville (right column) samples at scales of individual samples, aggregated stratigraphic sections, members, and entire formation species pool. Model support for samples and sections was calculated using a classification tree trained on the 100% and 50% simulations used in Figure 3C; model support for members and formations used the classification tree trained on 50%, 75%, 90%, 95%, and 100% simulations, which is a more powerful classifier at larger sample sizes. Models are only listed (middle column) when they have support in a particular scale. Support for all but the formation scale is the number of samples/sections/members that were classified for each model. Support for the formations (bottom row) is the proportion of votes for each model. The aggregate Kope Formation is overwhelmingly (0.52) classified as the 90% strict partitioning model, although there is also substantial support (0.34) for the 90% redundancy model. The aggregate Waynesville Formation has overwhelming support (0.78) for the 90% redundancy model, with less but substantial support (0.22) for the 95% strict partitioning model.

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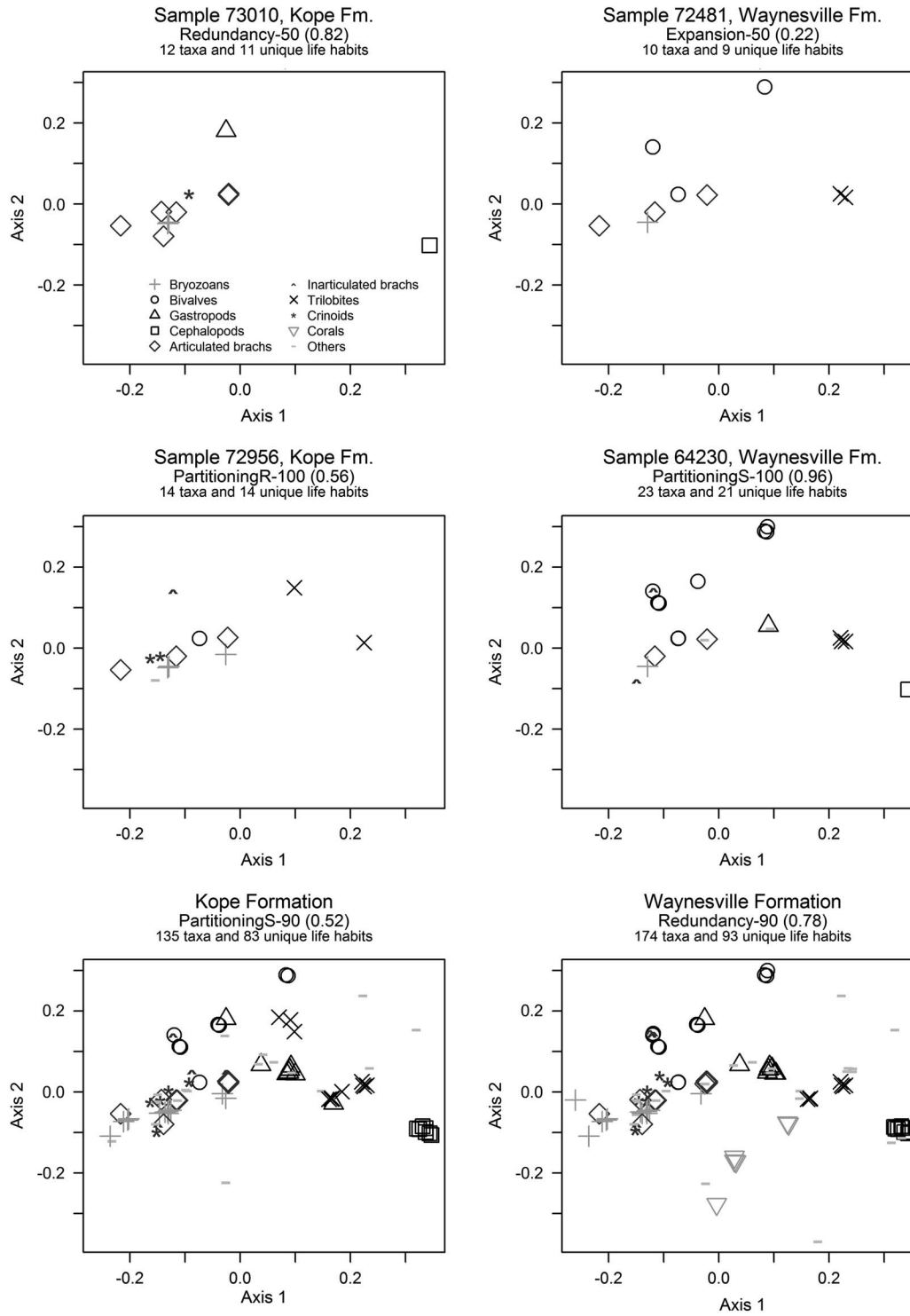
Ecological and evolutionary theory underlying these models (see companion article [Novack-Gottshall 2016]) allows speculation as to the nature of processes structuring these biotas. At the scale of individual samples, partitioning dynamics are consistent with



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ecological niche partitioning: coexisting taxa have similar (but not identical) life habits. Holland and Patzkowsky (2007; Patzkowsky and Holland 2007) demonstrated similar tight packing of species along onshore–offshore gradients in these intervals, even more so in the Waynesville samples. This partitioning could be manifested at the scale of local communities or through evolutionary processes at the regional scale, in which speciation produces multiple variants with slightly different specializations. Consideration of phylogenetic relatedness could offer a useful test of these claims (Gerhold et al. 2015), in particular whether newly evolving taxa within the regional species pool were more likely to have life habits different from those previously existing. Patzkowsky and Holland (2003) found no evidence for saturation within Cincinnatian samples, suggesting regional processes as the more important factor. This conclusion is tentatively supported here, especially for the Kope Formation, where the same model support across all scales could suggest a shared cause. Within the Waynesville sequence, Patzkowsky and Holland (2007) identified greater beta diversity, driven in large part by faunal incursions during the Richmondian Invasion. This could explain the redundancy dynamics found within the Waynesville Formation and its members, in which the accumulation of many different life habits within individual samples results in functional duplication when aggregated.

These results, however, do not rule out an important role for local processes. Although not illustrated here, individual Kope and Waynesville samples, even those classified by the same model, do not share the same life habits (or taxa). In other words, when plotted on a common ordination (such as for the partitioning samples in Fig. 5), taxonomic and functional composition varies substantially among samples. Model selection results simply suggest that most samples share a similar level of ecological disparity (Fig. 4), one best represented by the partitioning model. This consistency of structure suggests that local processes could still play an important role in regulating these communities. Among the many possible life habits available within the regional species pool, individual communities were preferentially composed of groups of generally similar but nonidentical life habits, although the particular life habits present in any setting could vary a great deal.

Relevance to Broader Phanerozoic Trends in Ecospace Utilization

The general correspondence between empirical samples and the dynamics of the model simulations suggests that the simulations provide reasonable null models for understanding how ecospace is structured in extant and fossil biotas, at many spatiotemporal scales. Support for the partitioning model, and to a lesser extent redundancy, indicates that these Late Ordovician biotas had relatively constrained ecospace structures. Broader discussion of this model support is warranted, especially within the context of how these results might generalize to understanding Phanerozoic-wide trends in ecospace utilization. In particular, one might want to know whether these results are consistent with an expansion in ecospace utilization in later Phanerozoic biotas, as has been widely claimed (Bambach 1983; Vermeij 1987, 2011, 2013; Knoll and Bambach 2000; Bush et al. 2007; Novack-Gottshall 2007; Bush and Bambach 2011). A conclusion cannot be made at this point, but speculation might be made based on the interactions of three factors: changes in the

FIGURE 5. Ordinations of four representative Kope and Waynesville samples best fit by various models, and the corresponding ordination of each formation species pool. Ordinations were conducted as two-dimensional nonmetric multidimensional scaling on a common Kope/Waynesville species pool to allow comparison across graphs. Text above each graph notes which model was best fit (i.e., had the most votes in the classification tree) for each sample, as well as the relative support for that "vote-winning" model. Also listed are the Paleobiology Database sample collection number, its taxonomic richness and number of unique life habits (*H*), and symbols representing major taxonomic groups. Note that jittering (moving overlapping points by tiny amounts) was not used in this figure; points that overlap incompletely represent distinct life habits. Aside from at the formation scale, there is relatively little absolute redundancy among life habits.

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species pool used (which changes allowable ecospace traits and resulting simulation dynamics), measures of functional diversity/disparity in later biotas, and changes in taxonomic richness.

The most important of these factors is the species pool one chooses to use (cf. Cornell 1999; de Bello 2012). The analyses above used a narrowly defined one, the aggregate pool of species known from a single habitat in one small (tristate) region during a short (~8 Myr) time interval. Analyses using a Kope-only versus Waynesville-only pool had negligible effect, but future analyses should test the sensitivity of simulation dynamics to more distinct species pools. Use of a much larger pool would allow for a greater range of life habits in the framework, which could increase dynamical values in simulations (although this remains to be determined). The effect of this change might be to increase classification-tree support for the partitioning and redundancy models, and especially so if using a Paleozoic-wide or Phanerozoic-wide species pool, given the greater range of epifaunal and infaunal tiering (Ausich and Bottjer 1982; Bottjer and Ausich 1986) and body sizes (Novack-Gottshall 2008a; Heim et al. 2015; Zhang et al. 2015) evolved by later biotas. Because the analyses above rescaled these ordered numeric characters, incorporating broader ranges would depress the empirical disparity statistics calculated here to some extent. However, the effect of this is likely minor, as post-Ordovician ranges would only add a single bin (given the logarithmic binning scale used in the framework) and the largest, most deeply infaunal, and tallest tiering animals were likely proportionally minor components of these biotas (which diminishes their effect for these extreme character states because of the empirical weighting used). It remains to be determined what pool is best suited to such analyses given the major evolutionary changes throughout the Phanerozoic, but the use of more inclusive pools would likely demonstrate that these Ordovician samples are even more functionally restricted (i.e., less ecologically disparate) compared with later Phanerozoic samples.

Species richness also increased during the Phanerozoic, both globally (Sepkoski 1981; Alroy et al. 2008) and within individual assemblages (Bambach 1977; Powell and Kowalewski 2002; Bush and Bambach 2004; Kowalewski et al. 2006). The effect of this increase, by itself, is also likely to be limited here, because the dynamics tend to reach asymptotic values at moderate (>20) species richness values, which means that simply increasing sample sizes, all things equal, will yield negligible changes to statistical values. The greater effect will be related to how these larger biotas utilize ecospace. Novack-Gottshall (2007) demonstrated that extant marine biotas had greater ecological disparity (measured as D, after accounting for differences in sample sizes) than early–middle Paleozoic ones, despite an insignificantly greater number of life habits. Increasing values for statistics D and H through time could provide greater support for the expansion model for such biotas, although it remains uncertain whether this increase would be attenuated by using a larger species pool. It is worth reiterating that one would expect these statistics to increase with increasing species richness, even if ecospace was occupied by a passive process (i.e., that expected by the neutral model). The discussion above includes many subjective hypotheticals, and so this author is unwilling to make a wager on the outcome. Without conducting formal simulations and statistical analyses, it simply remains too early to predict whether the Phanerozoic trend would be better supported by the driven expansion model, the passive neutral one, or perhaps another. It seems a worthwhile goal to conduct such analyses.

Conclusions

Despite documentation of synoptic paleoecological trends across the Phanerozoic and speculation about their causes, we lack in many—perhaps most—cases specific quantitative claims on ecospace inhabitation that can be tested analytically. The models and analytical methods proposed here, none of which are entirely novel, offer potentially fruitful avenues for such tests, whether applied to individual assemblages or to the entire biosphere throughout the Geozoic.

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In particular, the analyses presented here, and in the accompanying article, lead to the following conclusions.

1. Simulations of the redundancy, partitioning, expansion, and neutral models demonstrate dynamical consistency in functional diversity/disparity statistics across different data structures (ecospace frameworks), number and type of functional traits (characters), and implementations of the simulations. However, ecospace frameworks with greater numbers of functional traits, use of ordered factors, and modest numbers of seed species tend to be statistically more powerful for differentiating the models, especially the dynamically similar neutral and expansion models and the often similar partitioning and redundancy models. The ecospace package provides R functions to conduct simulations for any ecospace framework and to calculate a wide range of functional diversity/disparity statistics.
2. Classification trees are a powerful method for rigorously classifying these models in a multimodel inference framework (Breiman et al. 1993; Cutler et al. 2007), with relative support allocated to candidate models according to proportion of votes from the classification tree. Classification trees are successful in identifying models correctly, even when the statistical dynamics are similar and when tested with foreign data sets unlike those used to train the tree. The trees are also able to identify which statistics are most valuable. This method identifies number of unique life habits (functional-trait combinations, *H*) as the most important statistical discriminant, followed by functional evenness (*FEve*) and functional dispersion (*FDis*). However, because all metrics retain useful information on ecospace structure and tree algorithms perform well using a large number of predictive variables, it is recommended that analyses of ecological disparity/functional diversity use all statistics when conducting model-selection analyses.
3. Comparison of stochastic simulation dynamics to those of Ordovician empirical samples demonstrates that actual fossil assemblages are substantially constrained in their inhabitation of life habits compared with what is possible in the theoretical ecospace framework. Although the identities of constraints are not analyzed here specifically, they likely reflect a combination of logically impossible trait combinations, maladaptive strategies, inherent covariation among functional traits, ecologically meaningful restrictions to the regional species pool, and other factors. Incorporating constraints into the ecospace framework (such as limiting allowed life-habit combinations and weighting functional traits by those occurring in the empirical species pool) causes simulation dynamics to converge on more realistic values, allowing simple approximations for many of these constraints. However, doing so still demonstrates that these Late Ordovician biotas had substantially constrained ecospace structures.
4. Empirical application of the classification trees demonstrates that Late Ordovician (type Cincinnatian) samples from the Kope and Waynesville formations are primarily best fit by partitioning models. When larger stratigraphic and temporal aggregates are analyzed, the entire Kope Formation pool remains best fit by the partitioning model, but the aggregate Waynesville pool is better fit by the redundancy model. This structural transition in the Waynesville Formation can be biologically interpreted by greater beta diversity in this unit, likely related to faunal incursions caused by the Richmondian Invasion. However, the consistency of support for the partitioning model at small scales suggests an important role for local processes.
5. Most hypotheses regarding patterns in ecospace utilization across the Phanerozoic are superficially consistent with multiple models of ecological diversification, despite being caused by distinct processes. Most documented trends are equally consistent with passive processes. Statistical tests that consider alternative stochastic models must be conducted before we can confidently claim that ecological patterns across the Geozoic history of life had driven causes.

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Similar concerns are shared with ongoing research in community ecology and functional ecology.

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