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Global Ordovician faunal transitions in the marine benthos: proximate causes

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Abstract.—During the Ordovician Radiation, domination of benthic marine communities shifted away from trilobites, toward articulate brachiopods, and, to a lesser degree, toward bivalves and gastropods. In this paper, we identify the patterns in origination and extinction probabilities that gave rise to these transitions. Using methods adapted from capture-mark-recapture (CMR) population studies, we estimate origination, extinction, and sampling probabilities jointly to avoid confounding patterns in turnover rates with temporal variation in the quality of the fossil record. Not surprisingly, higher extinction probabilities in trilobites relative to articulate brachiopods, bivalves, and gastropods were partly responsible for relative decreases in trilobite diversity. However, articulate brachiopods also had higher origination probabilities than trilobites, indicating that relative increases in articulate brachiopod diversity would have occurred even in the absence of between-class differences in extinction probabilities. This contrasts with inferences based on earlier Phanerozoic-scale, long-term averages of turnover probabilities, and it indicates that a major cause of this faunal transition has been overlooked.

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Introduction

The Ordovician Radiation was a pivotal interval in the history of marine biodiversity. Global diversity increased dramatically at many taxonomic levels. At the family and genus levels, the fossil record records a threefold to four-fold increase during the period, an increase that was more rapid and extensive than at any other time in the history of marine life (Sepkoski 1979, 1981, 1986, 1993, 1997). This occurred within an equally dynamic geophysical context. Major increases in tectonic activity occurred, particularly in the Middle to Late Ordovician (Khain and Seslavinsky 1996). Associated with increased mountain-building and volcanic activity were increases in productivity and in the supply of siliciclastic sediment to benthic habitats (Miller and Mao 1995; Miller 1997b; Veizer et al. 1999), two factors proposed to promote diversification (Miller and Mao 1995; Vermeij 1995).

In addition to the global increase in marine biodiversity, major faunal transitions occurred during the Ordovician. Marine communities shifted from the trilobite-dominated state that prevailed during the Cambrian Period and toward a state dominated primarily by articulate brachiopods and associated taxa that persisted through the end of the Paleozoic (Sepkoski 1981). In addition, many members of the Modern Fauna, particularly bivalve and gastropod higher taxa, first appeared during this period (Babin 1993, 1995). In some regions, these classes dominated benthic communities (Babin 1993, 1995). In these respects, the Ordovician faunal transitions set the stage for marine community structure patterns that persisted for the rest of the Paleozoic.

Trilobites, articulate brachiopods, and bivalve and gastropod mollusks have the strongest statistical affinities with Sepkoski's Cambrian, Paleozoic, and Modern Faunas, respectively (Sepkoski 1981). Therefore, the extent to which the dynamics of the Ordovician faunal transitions are consistent with Sepkoski's Phanerozoic-scale calibration of the coupled logistic model is particularly salient to the search for regularities in the kinetics of diversification. Recent research on these faunal transitions has emphasized calibration of diversity patterns in several ways, including

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sample-standardized estimates of taxonomic diversity (Miller and Foote 1996; Miller 1997a,b), geographical decomposition of taxonomic diversity patterns (Miller 1997a,b; Miller and Mao 1998), and calibration of morphological diversification (Foote 1993, 1995). In this paper, we take these qualitative transitions at face value—increased articulate brachiopod, bivalve, and gastropod diversities relative to trilobites—and we seek to identify their causes.

There are two components to changes in relative diversity: per-taxon origination patterns and per-taxon extinction patterns. Conceptually, then, there are two levels of causation for the Ordovician faunal transitions. Proximately, differences in either or both of these components of relative faunal change caused the transitions. Ultimately, however, these differences themselves have biological or physical causes. Those causes may be intrinsic to higher taxa; that is, they may be characteristics of taxa themselves that confer higher or lower turnover rates, relative to other taxa (Sepkoski 1979). Alternatively, they may be environmental, if changes in turnover rates are due to environmental change (Miller and Mao 1995). More likely, however, they arise from an interaction between the two, as characteristics intrinsic to higher taxa cause them to respond differently to environmental change. Here, we will focus on the proximate causes of the Ordovician transitions: identifying the patterns in origination and extinction that gave rise to shifts in relative diversity. Upcoming work will address ultimate causes, i.e., the environmental factors that caused those patterns in origination and extinction (Connolly and Miller 2002).

Previous work has emphasized differences among taxa in turnover probabilities (or per-taxon rates, their deterministic analogues) over Phanerozoic timescales as important proximate causes of long-term, global faunal transitions. For instance, Sepkoski (1998) estimated long-term average per-genus origination rates for several marine invertebrate classes. He found higher origination rates in trilobites, intermediate origination rates in articulate brachiopods, and low origination rates in bivalves and gastropods. Earlier estimates of per-family extinction rates have indicated a similar rank ordering (Sepkoski 1979, 1984; Gilinsky 1994). If these differences prevailed during the Ordovician, then a decrease in trilobite diversity relative to articulate brachiopods, gastropods, and bivalves should be attributable to higher trilobite extinction probabilities. Conversely, increased articulate brachiopod diversity relative to bivalves and gastropods would result from higher origination probabilities in the former group.

In this paper, we estimate differences in genus origination and extinction probabilities through the Ordovician for trilobites, articulate brachiopods, bivalves, and gastropods, as well as their associated uncertainties. Maximum likelihood methods, adapted from capture-mark-recapture (CMR) population theory, are used to jointly estimate per-genus sampling, origination, and extinction probabilities (Connolly and Miller 2001). This joint estimation avoids confounding temporal change in turnover with temporal change in preservation or sampling rates. We fit multiple alternative models of the sampling process and quantitatively compare their performance. This affords greater precision and reduced bias in estimated origination, extinction, and sampling probabilities. It also allows us to assess alternative causes of variation in sampling probabilities.

This approach yields some results that are consistent with established views on the proximate causes of transitions among Cambrian, Paleozoic, and Modern Faunas. Others, however, differ strikingly. Previously published, Phanerozoic-scale analyses have found higher origination probabilities in trilobites relative to articulate brachiopods (Gilinsky and Good 1991; Sepkoski 1998), and the long-term transition from trilobites to articulate brachiopods has been attributed to lower extinction probabilities among brachiopods. However, our results indicate that, during the Ordovician, when much of this transition occurred, origination probabilities were *higher* in articulate brachiopods than in trilobites, indicating that a major cause of this transition has been overlooked.

TABLE 1. Temporal binning protocol. Note that ages are approximate, based on those of Harland et al. (1990), updated in accordance with more recent subseries boundary ages (Tucker and McKerrow 1995; Bowring and Erwin 1998).

Interval	Interval duration (Myr)	Series/Subseries	Time between midpoints (Myr)
1	7	Tremadocian	8
2	9	Lower Arenigian	8
3	7	Upper Arenigian Lower Llanvirnian	8
4	9	Upper Llanvirnian Llandeilian	8
5	7	Lower Caradocian Middle Caradocian	8
6	8	Upper Caradocian Ashgillian	—

Data

The data consist of occurrences of trilobite, articulate brachiopod, bivalve, and gastropod genera collected in discrete samples from different locations in Ordovician strata. These data have been compiled from the literature by A. I. Miller and coworkers for ongoing studies of Ordovician macroevolutionary dynamics (Miller and Foote 1996; Miller 1997a,b,c, 1998; Miller and Mao 1998; Connolly and Miller 2001 [this volume]). In addition, we combined adjacent subseries in an unconventional manner to minimize percentage variation in interval durations, as described elsewhere (Connolly and Miller 2001). The result was a binning protocol consisting of six intervals whose durations were approximately 7–9 Myr, according to current estimates (Table 1). The duration between adjacent interval midpoints was approximately 8 Myr in each case.

We also wished to minimize the extent to which the portion of the globe that was sampled varied from interval to interval. Under the binning protocol described above, one paleocontinent, Australia, was represented by sampling locations in some, but not all, intervals. Therefore, we excluded Australian sampling locations from our analyses (Connolly and Miller 2001).

Modeling Approach

This investigation utilizes an analytical approach based on CMR population models, which we have described in detail elsewhere (Connolly and Miller 2001). What follows is a brief outline of the procedure, along with a description of the specific models utilized in this particular study.

The approach involved the following steps:

1. Identify a general model that includes probabilities of sampling, origination, and extinction.
2. Formulate a set of additional models in which sampling probability is constrained to be a function of quantities suspected of being good predictors of this probability (e.g., number of habitat types sampled in an interval).
3. Analyze the Ordovician database using each of these models. Obtain maximum likelihood estimates of turnover and sampling probabilities for trilobites, articulate brachiopods, bivalves, and gastropods.
4. Assess the goodness-of-fit of the general model using bootstrap simulations, and the relative fit of the additional models using Akaike's Information Criterion (AIC).
5. Utilize each model's parameter estimates, along with information about the relative plausibility of the alternative models, to obtain robust estimates of origination, extinction, and sampling probabilities.
6. Estimate differences in these parameter values between taxonomic classes.

General Model

Our modeling framework was originally developed by Pradel (1996) for CMR population studies, recently reformulated for application to the fossil record (Connolly and Miller 2001). In this formulation, i indicates interval number, and it increases toward the Recent. Thus, interval i is younger than interval $i - 1$ and older than interval $i + 1$. p_i is the probability that a genus extant during i was preserved, sampled, and ultimately recorded in the database (hereafter "sampling probability"). ϕ_i is the probability that a genus extant during i survived to $i + 1$. $1 - \phi_i$, then, is the probability of genus extinction between i and $i + 1$. γ_i is the probability that a genus extant during i was already extant during $i - 1$. Thus, $1 - \gamma_i$ is a per-genus origination rate: the probability that a genus extant during i originated between $i - 1$ and i (and survived until i). We follow Nichols and Pollock (1983) and interpret sampling during i as if it occurred at the interval's midpoint. Previous work indicates that this is a reasonable approximation for purposes of estimating trends in origination and extinction (Hargrove and Borland 1994; Connolly and Miller 2001).

In practice, the parameters actually estimated were logistic transformations of the sampling and turnover probabilities:

$$\text{logit}(p) = \ln\left(\frac{p}{1 - p}\right). \tag{1}$$

Utilization of this transformation constrains the sampling and turnover probabilities to remain between zero and one (Connolly and Miller 2001).

Because we wished to estimate differences among taxa in turnover probabilities, we analyzed each of the four classes (trilobites, articulate brachiopods, bivalves, and gastropods) separately.

Alternative Models

The model described above is known as a fully time-varying model, because the parameters are not constrained to vary among intervals in any predetermined fashion (e.g., we did not assume that they were constant over time). Indeed, we did not wish to constrain origination and extinction probabilities, because we wished to detect temporal variation in those probabilities, whatever pattern that variation took. However, we did explore constraints on sampling probabilities. Because constrained models have fewer parameters than the fully time-varying model, they offer increased precision in estimates of origination, extinction, and sampling probabilities (Connolly and Miller 2001).

We considered four alternative constraints on variation in sampling probability among intervals:

Number of Lists.—The number of samples (faunal lists) varies among intervals (Fig. 1A). In models with this constraint, sampling probability for interval i was assumed to be a function of the number of faunal lists from which data for interval i were compiled. Note that sampling locations varied in extent from individual beds to entire locales. (The largest locales were regional composites of reasonably uniform lithology/depositional setting at the formational scale, although few faunal lists came from sampling locations this broad.)

Environmental Zones.—Each sampling location in the database is identified according to both the paleocontinent and the bathymetric setting (intertidal to shelf slope) from which it comes. The number of bathymetric settings (utilizing a 1–6 onshore-offshore scheme [see, e.g., Sepkoski and Miller 1985]) represented by samples from each paleocontinent, summed over all paleocontinents, provides an estimate of the geographical and ecological breadth of sampling. (For instance, three sampled types of bathymetric settings on one paleocontinent + four types of bathymetric settings on another paleocontinent = seven total environmental zones sampled on the two paleocontinents.) These counts are plotted in Figure 1B. These models constrain sampling probability for interval i to be a function of the number of environmental zones sampled in interval i.

Orogeny.—When using raw diversity trajectories to infer the relationship between orogenic activity and diversification, a potential problem involves the effect of increasing orogenic activity on fossil preservation. If increased orogenic activity caused more regions to experience high sedimentation regimes, then rates of preservation, and thus probabilities of sampling, might have increased (Miller 1997b). We examine this possibility by modeling sampling probability as a function of orogenic index, an estimate of global orogenic activity based on the number, geographical extent, and persistence of centers of orogeny

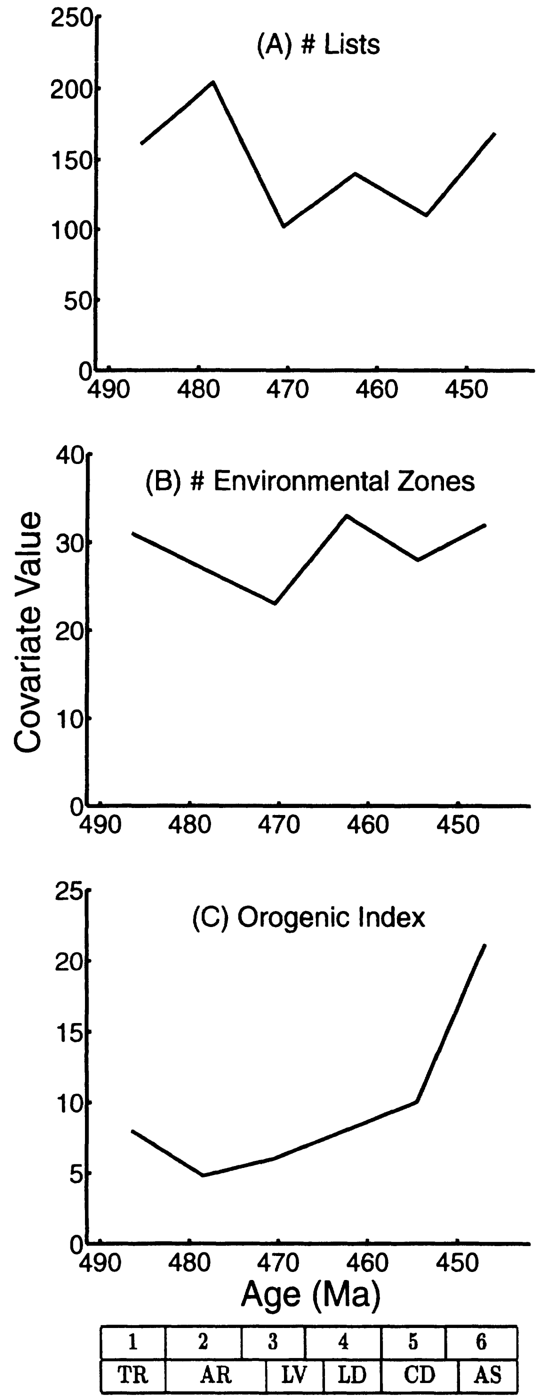

FIGURE 1. Covariate values through time, plotted at interval midpoints. (A) Number of samples or faunal lists. (B) Number of environmental zones. (C) orogenic index. Interval boundaries from Table 1, along with conventional series boundaries, are indicated below the horizontal axis label.

(Khain and Seslavinsky 1996). Figure 1C plots orogenic index through the Ordovician.

Constant Sampling.—This model constrains all p_i to be equal. When testing the robustness of analyses of macroevolutionary patterns to incomplete sampling, workers frequently assume that sampling probabilities are constant over time (e.g., Strauss and Sadler 1989; Marshall 1990; Kirchner and Weil 2000). Comparing this model to the alternatives will indicate whether this is a good approximation for the Ordovician taxa analyzed here.

In each of the above models, sampling probability is constrained according to the function

$$\mathrm{logit}(p_i) = \alpha_0 + \alpha_1 x_i \qquad (2)$$

(cf. Connolly and Miller 2001). For the number-of-lists, environmental-zones, and orogeny models, x_i is the number of faunal lists, number of environmental zones, or orogenic index, respectively. For the constant-sampling model, α_1 is assumed to be zero, i.e., $\mathrm{logit}(p_i) = \alpha_0$ for all i. Thus, we explored five alternative characterizations of variation in sampling probability among intervals: (1) fully time-varying, (2) no variation, and variation as a function of (3) number of lists, (4) number of environmental zones, and (5) orogenic index.

Sampling probabilities may vary among genera, as well as among intervals. Until recently, all Jolly-Seber-type models assumed no such variation; this is why considerable attention has been devoted to the robustness of parameter estimates to violation of this assumption (see Pollock et al. 1990, Connolly and Miller 2001, and Williams et al. 2001 for reviews). Now, however, this assumption can be relaxed by characterizing sampling probability as follows:

$$\mathrm{logit}(p_{ij}) = F_i + \beta z_j \qquad (3)$$

(Smith et al. 1994). p_{ij} is the probability of sampling genus j during interval i. F_i indicates how sampling probability varies among intervals. It can take on a different value for each i (a fully time-varying model), it can remain constant over time, or it can be constrained to vary in response to a covariate, such as orogenic index. βz_j indicates how sampling probability varies among genera within an inter-

TABLE 2. Candidate models, indicating the manner in which sampling probability was assumed to vary among intervals and among genera. See Modeling Approach for further details.

Notation	Variation among	
	Intervals	Genera
$p(t)$	Fully time-varying	None
$p(t, NOcc)$	Fully time-varying	No. of occurrences
$p(L)$	No. of lists	None
$p(L, NOcc)$	No. of lists	No. of occurrences
$p(E)$	No. of environmental zones	None
$p(E, NOcc)$	No. of environmental zones	No. of occurrences
$p(O)$	Orogenic index	None
$p(O, NOcc)$	Orogenic index	No. of occurrences
$p(.)$	Constant	None
$p(., NOcc)$	Constant	No. of occurrences

val. z_j is a covariate specific to individual genera, generally termed an "individual covariate" (Smith et al. 1994), that is believed to be a good predictor of among-genus variation in sampling probability. Examples might include body size, range size, or mean within-community abundance. Thus, rather than having the same value for all genera in an interval, sampling probability for each genus j is a function of z_j, with intercept F_i and slope β.

In this way, among-genus variation can be modeled if a good predictor variable z_j can be identified. It is reasonable to suspect that more abundant or geographically widespread genera will have higher sampling probabilities than rarer or more geographically restricted genera. That is, a relatively abundant or widespread genus should have a relatively high probability of appearing in at least one sample from an interval. Moreover, such genera should also appear with greater frequency (i.e., in samples from more locations) within intervals, when they do appear. For each genus, we can calculate this latter quantity for each interval in which a genus appears, then take the average of those values across all intervals. For instance, if a genus occurs in five samples from interval 2, ten samples from interval 4, and seven samples from interval 5, its average number of occurrences is $22/3 = 7.3$. Note that variation among genera in this quantity is statistically independent of the number of intervals in which those genera appear. This ensures that any relationship between p and number of occurrences is not a statistical artifact.

To determine whether average number of occurrences was a good predictor of among-genus variation in sampling probability, we fit one group of models in which we assumed no variation among genera in sampling probability, and a second group in which sampling probability varied among genera according to equation (3), where z_j was average number of occurrences, normalized to have a mean of zero and a standard deviation of one. These two alternative characterizations of among-genus variation were combined with the five alternative characterizations of among-interval variation, yielding a total of ten possible combinations of among-interval and among-genus sampling probability (Table 2).

Model Selection and Model Averaging

Each of the ten alternative models was fit to each of the four taxonomic classes using the maximum likelihood estimation algorithm implemented in Program MARK (White 2000). We utilized Program MARK's bootstrap goodness-of-fit test to assess the goodness-of-fit of the fully time-varying model. When significant lack of fit was detected, we estimated the severity of this lack of fit by calculating a variance inflation factor, $\hat{c}$, and adjusting parameter estimates and model-selection criteria accordingly. To be conservative, we considered lack of fit to be significant whenever $p < 0.10$. See Connolly and Miller 2001 for a description of goodness-of-fit testing and discussion of the meaning and calculation of the variance inflation factor.

As described previously (Connolly and Miller 2001), we used Akaike's Information Criterion (AIC), adjusted for sample size or lack of model fit where necessary, to rank alternative models. For each model, we calculated Δ, the difference in AIC between that model and the estimated best model in the model set. Δ, in turn, was used to calculate model weight, w_k, which is an estimate of the probability that model k is actually the best model in the model set (Burnham and Anderson 1998). Burnham and Anderson (1998) utilize the term "confidence set" to refer to the subset of models likely to contain the true best model with some degree of confidence. When presenting results, we will adopt this terminology and occasionally refer to a 95% confidence set of models.

Model-averaging was used to obtain interval-by-interval estimates of origination, extinction, and sampling probabilities that are robust to uncertainty about which model is best (Connolly and Miller 2001). In addition to these interval-by-interval estimates, we estimated overall average values of parameters for the Ordovician as a whole in the following manner. Consider the ϕ_i and γ_i for a particular taxonomic class as themselves drawn from probability distributions. The means of these distributions, $\bar{\phi}$ and $\bar{\gamma}$, can be estimated as the averages of the $\hat{\phi}_i$ and $\hat{\gamma}_i$ ("^" denotes an estimate; e.g., $\hat{\phi}$ is an estimate of the value of ϕ). The variance of $\hat{\bar{\phi}}$ and $\hat{\bar{\gamma}}$ can be estimated from the variances of and covariances among the $\hat{\phi}_i$ and $\hat{\gamma}_i$ (see Pitman 1993).

Results and Discussion

Goodness-of-Fit

For trilobites, articulate brachiopods, and gastropods, no significant lack of fit in the fully time-varying model was detected ($p > 0.1$ in each case). For bivalves, however, bootstrap goodness-of-fit tests did identify significant deviation from model assumptions ($p < 0.05$); the estimated variance inflation factor, $\hat{c}$, was 1.3, indicating that lack of fit was relatively mild (Eberhard 1978; Anderson and Burnham 1994).

The number-of-occurrences models were formulated specifically to account for variation in sampling probabilities among genera, one possible cause of lack of model fit. It is possible that much of the lack of fit detected for bivalves is not present in those models, particularly given that model weights indicated that those types of models fit the data much better than the models without this genus-specific covariate (see below). Unfortunately, goodness-of-fit tests for individual covariate models such as these do not yet exist, so we could not identify the extent to which lack of fit may have been reduced in these models. Therefore, we took the more conservative approach and used $\hat{c} = 1.3$ to adjust model weights, as well as estimated variances and covariances, for bivalves.

TABLE 3. Model selection: trilobites. In all models, extinction and origination were fully time-varying. Δ indicates the difference in AIC$_c$ between each model and the estimated best model, and w is the model weight.

Model	Δ	w
$p(., NOcc)$	0.0	0.46
$p(E, NOcc)$	1.84	0.18
$p(O, NOcc)$	1.84	0.18
$p(L, NOcc)$	2.05	0.17
$p(t, NOcc)$	8.06	0.01
$p(O)$	82.9	0.00
$p(.)$	84.20	0.00
$p(t)$	84.72	0.00
$p(E)$	85.45	0.00
$p(L)$	86.25	0.00

Model Selection

Trilobites.—Model rankings are presented in Table 3. The models in which sampling probabilities were functions of average number of occurrences were substantially better than the models in which sampling probabilities did not vary among genera. Combined, model weights of the former group exceeded 0.99999. The best model was model $p(., NOcc)$, which corresponds to constant sampling probabilities over time, but variation among genera according to number of occurrences. However, there was substantial uncertainty ($w_{.,NOcc} = 0.46$—meaning that there is a 46% probability that this *estimated* best model is *actually* the best model in the model set). The 95% confidence set of models included three additional models: $p(E, NOcc)$—the environmental-zone, number-of-occurrences model; $p(O, NOcc)$—the orogenic index, number-of-occurrences model; and $p(L, NOcc)$—the number-of-lists, number-of-occurrences model. Each of these

TABLE 4. Model selection: articulate brachiopods. In all models, extinction and origination were fully time-varying.

Model	Δ	w
$p(E, NOcc)$	0.0	0.66
$p(t, NOcc)$	3.20	0.13
$p(., NOcc)$	4.04	0.09
$p(L, NOcc)$	4.67	0.06
$p(O, NOcc)$	5.19	0.05
$p(t)$	42.79	0.00
$p(E)$	43.79	0.00
$p(.)$	47.18	0.00
$p(L)$	49.14	0.00
$p(O)$	49.15	0.00

TABLE 5. Model selection: bivalves. $\phi(TR)$ and $\gamma(TR)$ denote trends through time. $\phi(.)$ and $\gamma(.)$ denote constant extinction and origination, respectively. $p(t)$ denotes the general model, in which extinction and origination are fully time-varying.

Model	Δ	w
$\phi(.)\ p(t, NOcc)\ \gamma(.)$	0.0	0.50
$\phi(TR)\ p(t, NOcc)\ \gamma(.)$	1.55	0.23
$\phi(.)\ p(t, NOcc)\ \gamma(TR)$	2.00	0.18
$\phi(TR)\ p(t, NOcc)\ \gamma(TR)$	3.50	0.09
$\phi(.)\ p(L, NOcc)\ \gamma(TR)$	11.06	0.00
$\phi(TR)\ p(L, NOcc)\ \gamma(TR)$	12.93	0.00
$\phi(.)\ p(L, NOcc)\ \gamma(.)$	13.91	0.00
$\phi(TR)\ p(L, NOcc)\ \gamma(.)$	14.67	0.00
$p(t)$	24.60	0.00

had modest levels of support ($0.15 < w < 0.20$ in each case).

Articulate Brachiopods.—Model rankings are presented in Table 4. As for trilobites, models including number of occurrences as a genus-specific covariate were substantially better than those without it (combined $w > 0.99999$). The best model was model $p(E, NOcc)$—the environmental-zone, number-of-occurrences model, but, again, there was model-selection uncertainty ($w_{E,NOcc} = 0.66$). The 95% confidence set of models includes all five models that incorporate among-genus variation in sampling probabilities according to average number of occurrences (Table 4).

Bivalves.—Several origination and extinction probabilities were inestimable in all of the bivalve models. This indicates that there are too many parameters, given the number of observations of genera in the database. (In principle, this could be caused by origination or extinction probabilities that were actually zero for one or more intervals. However, we consider this possibility unlikely, given the 7–9-Myr duration of the sampling intervals.) This affects the validity of model averaging, as fixed parameters are assumed to have zero variance. Because estimation of origination and extinction probabilities and their associated uncertainties is the principal objective of this study, we fit several reduced-parameter models to the bivalve data.

The initial analysis indicated that model $p(t, NOcc)$—the fully time-varying, number-of-occurrences model—had strong support ($w = 0.86$). This model had more than an order of magnitude more support than the second-best model, $p(L, NOcc)$—the number-of-lists, number-of-occurrences model ($w = 0.08$). All other models had less than 5% support (i.e., $w < 0.05$). Therefore, we used $p(t, NOcc)$ and $p(L, NOcc)$ as our alternative constraints on sampling probability for the reduced-parameter analysis. To each of these we coupled two different constraints on origination and extinction probabilities: they could be constant, or they could change linearly, over time. Model rankings for this reduced-parameter set are presented in Table 5. Since goodness-of-fit tests are appropriate to the fully time-varying model, $p(t)$, it is included for comparison. Constant seniority and survival are denoted by $\gamma(.)$ and $\phi(.)$, respectively. Temporal trend models are denoted by $\gamma(TR)$ for seniority and $\phi(TR)$ for survival.

All of the reduced-parameter models were substantially better than the fully time-varying model, $p(t)$, which assumes no among-genus variation in sampling probability (combined $w > 0.99999$). Again, there was substantial model-selection uncertainty. The best model, $\{\phi(.)\ p(t, NOcc)\ \gamma(.)\}$ (survival and seniority constant; sampling probability varying over time and according to number of occurrences), had only modest support ($w = 0.50$). The 95% confidence set consisted entirely of the four models with $p(t, NOcc)$—sampling probability fully time-varying, and variation among genera by number of occurrences.

Gastropods.—Similar problems with inestimable parameters occurred for gastropods. Again, we fit a reduced-parameter model set,

TABLE 6. Model selection: gastropods. $\phi(TR)$ and $\gamma(TR)$ denote trends through time. $\phi(.)$ and $\gamma(.)$ denote constant extinction and origination, respectively. $p(t)$ denotes the general model, in which extinction and origination are fully time-varying.

Model	Δ	w
$\phi(.)$ $(p(t, NOcc)$ $\gamma(TR)$	0.0	0.51
$\phi(TR)$ $p(t, NOcc)$ $\gamma(TR)$	1.48	0.24
$\phi(.)$ $p(t, NOcc)$ $\gamma(.)$	2.68	0.13
$\phi(TR)$ $p(t, NOcc)$ $\gamma(.)$	4.46	0.05
$\phi(TR)$ $p(L, NOcc)$ $\gamma(TR)$	6.59	0.02
$\phi(.)$ $p(L, NOcc)$ $\gamma(.)$	7.21	0.01
$\phi(.)$ $p(L, NOcc)$ $\gamma(TR)$	7.25	0.01
$\phi(TR)$ $p(L, NOcc)$ $\gamma(.)$	7.64	0.01
$p(t)$	40.62	0.00

using the constraints on origination and extinction described previously for bivalves. In this case, however, the original model set indicated a greater degree of model-selection uncertainty, with the best model having only modest support ($w < 0.4$ for all models). Models including number of occurrences were strongly supported (combined $w > 0.99999$). Therefore, the constraints on sampling probability that included number of occurrences were combined with the set of alternative constraints on origination and extinction in the second model set. Again, the model whose goodness-of-fit was evaluated, $p(t)$, is included for comparison.

Table 6 presents the results of this analysis. Only the models with sampling constraints $p(t, NOcc)$ and $p(L, NOcc)$ had levels of support >0.01, so, to preserve space, only those results are presented. The best model, $\{\phi(.)\ p(t, NOcc)\ \gamma(TR)\}$ (survival constant; sampling probability fully time-varying and varying among genera according to number of occurrences; seniority exhibiting a trend over time), had only modest support ($w = 0.51$). As with bivalves, however, the 95% confidence set consisted entirely of the models with fully time-varying sampling probability and among-genus variation according to average number of occurrences, $p(t, NOcc)$.

Origination and Extinction Patterns

In the discussion below, we use the terms "early," "mid," and "late" Ordovician to refer to intervals 1–2, 3–4, and 5–6, respectively. Note that these differ somewhat from conventional Early, Middle, and Late Ordovician subseries classifications (Table 1).

Estimated turnover probabilities varied substantially over time for both trilobites and articulate brachiopods, less so for gastropods, and very little for bivalves (Figs. 2, 3). Trilobite estimates suggest a decrease in both origination and extinction through the Ordovician (Figs. 2A, 3A). By contrast, articulate brachiopod origination probabilities are markedly higher in the mid Ordovician than at any other time (Fig. 2B). Estimated extinction probabilities are also highest in the mid Ordovician (Fig. 3B), suggesting a major pulse of brachiopod turnover in the mid Ordovician that did not occur in the other classes. Interestingly, this pulse in turnover coincides with a shift in substrate affinities in this class (Miller and Connolly 2001) and a temporary dip in their raw genus diversity trajectory (Patzkowsky 1995; Sepkoski 1995). It also includes one of Boucot's ecologic-evolutionary unit (EEU) boundaries (Boucot 1983). For bivalves, both origination and extinction estimates are relatively constant; the slight increases over time are small, relative to their associated uncertainties (Figs. 2C, 3C). Gastropod origination estimates decrease through the Ordovician (Fig. 2D), but extinction probabilities exhibit very little change (Fig. 3D).

For bivalves and gastropods, the reduced-parameter models from which these estimates are taken included only constant, monotonically increasing, or monotonically decreasing origination or extinction patterns. Thus, more complex patterns, such as a pulse in turnover akin to that observed for brachiopods, would go undetected.

If one takes these estimates at face value, there appears to be strong support for positively correlated per-taxon origination and extinction through time. This would be consistent with earlier claims to this effect (Gilinsky and Good 1991), but at a finer scale of resolution. However, while the estimates associated with each interval are individually the most likely parameter values, there are statistical covariances among origination and extinction probabilities, as these probabilities are estimated jointly. Thus, a perfect rank correlation between origination and extinction

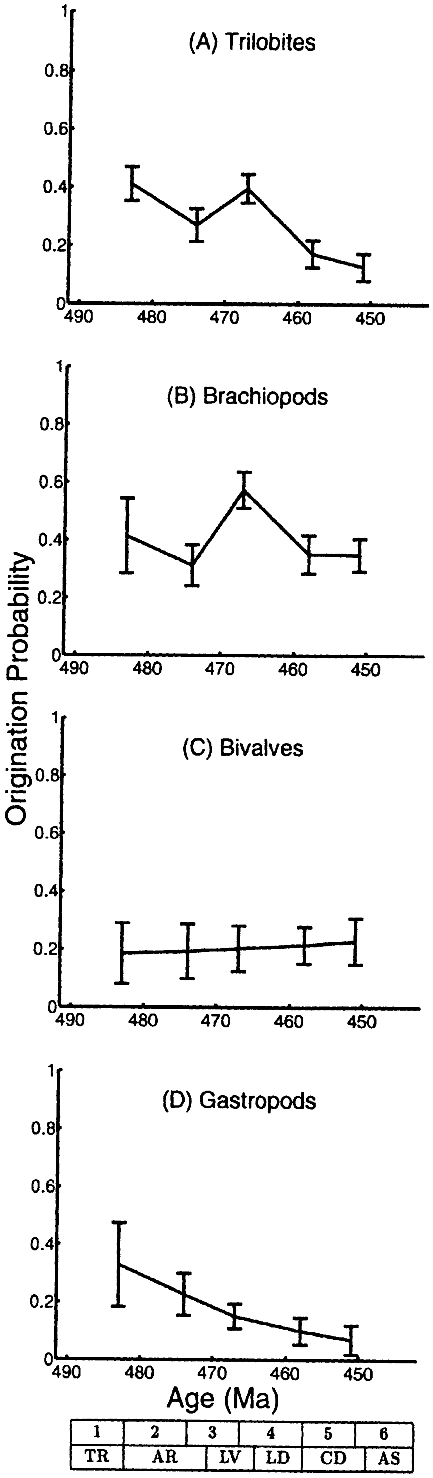

FIGURE 2. Model-averaged estimates of the probability of genus origination between interval midpoints (i.e., per ≈ 8 Myr) for trilobites (A), articulate brachiopods (B), bivalves (C), and gastropods (D). Estimates are plotted at interval boundaries. Standard errors were estimated from sampling variance estimates produced by Program MARK (White 2000) using the normal approximation (Pitman 1993). The binning protocol is shown as in Figure 1.

estimates does not necessarily indicate a statistically "significant" correlation between the parameter values themselves. This is because correlated *estimates* of origination and extinction can arise because of true biological correlation, statistical correlation (i.e., apparent correlation arising from effects of incomplete sampling), or both. In the present case, inspection of the variance-covariance matrices suggests that, in general, the statistical covariance of ϕ_i and γ_j is strongest when $i = j$. Further, this covariance decreases as the amount of time separating j and i increases. Correlated estimates of origination and extinction (in general, not just in the present study) do not necessarily imply that origination and extinction probabilities are themselves correlated. We advise against making such inferences without at least a cursory inspection of statistical covariances. One way to circumvent this problem is to fit a model in which origination and extinction are explicitly constrained to be correlated, then to compare the relative fit of such a model with alternatives in which such a constraint is not applied. See Connolly and Miller 2001 for an illustration of this approach.

Differences among Taxa

Interval-by-interval estimates of differences between classes in origination and extinction probabilities vary considerably over the course of the Ordovician (Figs. 4, 5). However, despite this variation, differences in overall (Ordovician-scale) average probabilities of origination and extinction were detected (Fig. 6). In the following discussion, estimates for each pairwise comparison are addressed separately.

Articulate Brachiopods versus Trilobites.— Overall, origination probabilities are higher in articulate brachiopods than in trilobites, whereas extinction probabilities are lower (Fig. 6). The magnitude of the estimated difference is actually greater for origination (0.13, greater than zero with >95% confidence) than

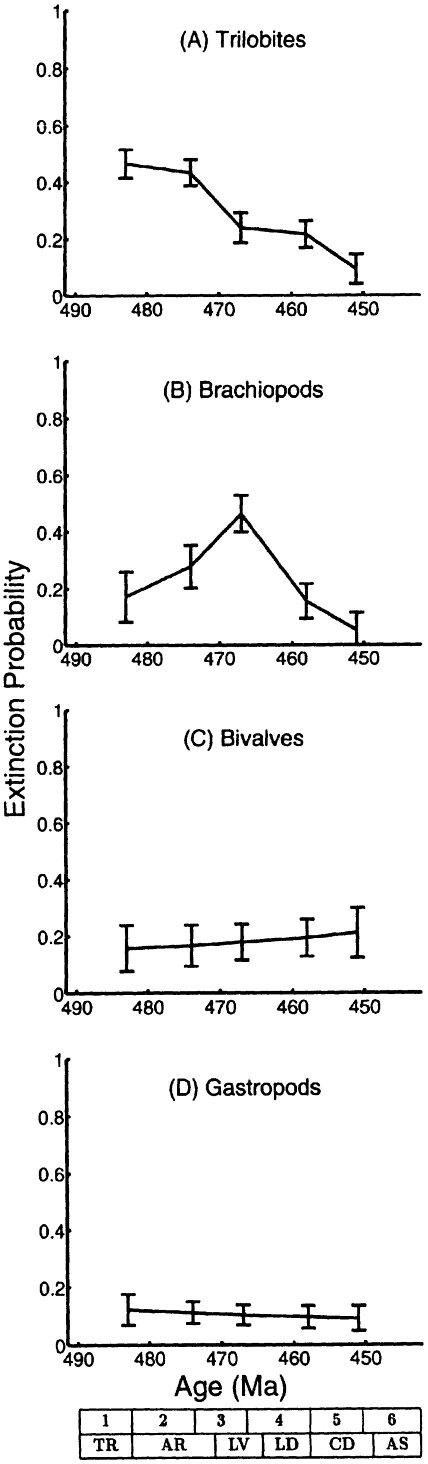

FIGURE 3. Model-averaged estimates of the probability of genus extinction between interval midpoints (i.e., per ≈ 8 Myr) for trilobites (A), articulate brachiopods (B), bivalves (C), and gastropods (D). Standard errors were estimated as described in Figure 2. The binning protocol is shown below the horizontal axis label as in Figure 1.

for extinction (−0.07, not significantly different from zero). Previous interpretations of the Ordovician faunal transitions have emphasized higher turnover (both origination and extinction) in trilobites and other elements of the Cambrian fauna (Sepkoski 1979, 1991, 1998). This study does not support that conclusion; rather, it suggests that higher per-taxon origination in brachiopods contributed to the transition, and that it may have been more important than lower extinction in brachiopods. Averaged over the entire Phanerozoic, brachiopod origination probabilities may indeed be lower than trilobite origination probabilities (Sepkoski 1979, 1998). However, during a key period, one during which major shifts in relative diversities of these groups occurred (Sepkoski 1991; Miller 1997a; Miller and Mao 1998), this was clearly not the case.

Interval-by-interval patterns suggest that the overall differences in origination probabilities were due to differences that emerged, or became more pronounced, in the mid and late Ordovician (Fig. 4A). A pulse of brachiopod origination in the mid Ordovician, coupled with decreasing trilobite origination over time (Fig. 2A,B), seems to be the most likely explanation for this pattern. By contrast, estimated differences in extinction rates are greatest in the early Ordovician (Fig. 5A). Brachiopod extinction is actually estimated to have exceeded that of trilobites in the mid Ordovician, with little difference apparent in the late Ordovician. Relatively high brachiopod extinction in the mid Ordovician, coupled with decreasing trilobite extinction, are implicated here (Fig. 3A,B). These estimates suggest that the trilobite-to-brachiopod Ordovician faunal transition was produced by comparatively lower brachiopod extinction probabilities in the early Ordovician and comparatively higher brachiopod origination probabilities in the mid and late Ordovician.

Bivalves versus Trilobites.—In contrast to the comparison of articulate brachiopods with trilobites, overall differences between bivalve and trilobite turnover are consistent with earlier proposals (Sepkoski 1984, 1998; Gilinsky and Good 1991). Estimated mean origination and extinction probabilities are lower in bivalves than in trilobites, but uncertainties are

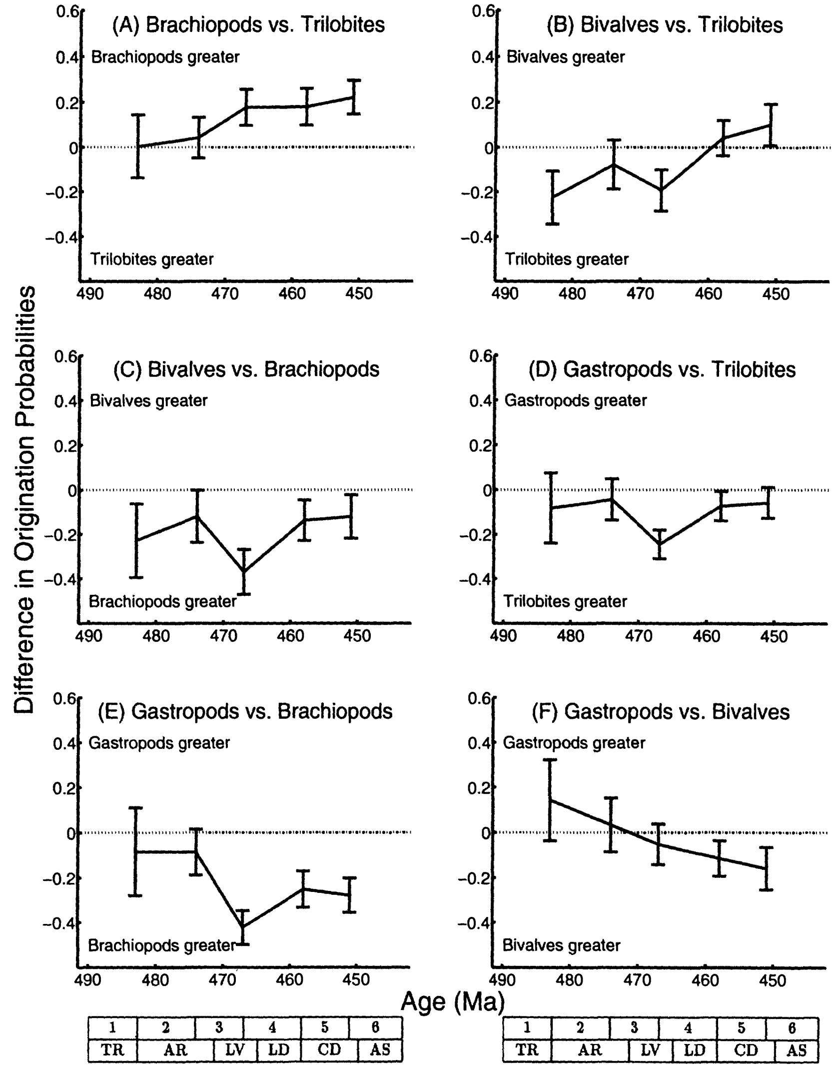

FIGURE 4. Model-averaged estimates of between-class differences in genus origination probabilities over time obtained from the estimates plotted in Figure 2. Differences are calculated by subtracting the origination probability of the second class named from the origination probability of the first. Standard errors of these estimates were calculated from the variances of the corresponding origination estimates. The binning protocol is shown below the horizontal axis label as in Figure 1.

large owing to low precision of bivalve turnover estimates, and neither quantity differs from zero with >95% confidence. This is a consequence of the comparatively small number of bivalve genera in the database (Table 5), coupled with significant lack of model fit in bivalves.

Interestingly, interval-by-interval comparisons suggest that these overall differences were present only in the early Ordovician (Figs. 4B, 5B). This pattern is especially pronounced in extinction probabilities, which are markedly lower for bivalves through the lower Arenigian (interval 2). By the late Ordovician, however, those differences are largely eliminated and possibly even reversed. Given the minimal change in the estimates of bivalve turnover probability (Figs. 2C, 3C), these patterns are largely driven by trends in trilobite turnover estimates (Figs. 2A, 3A).

Bivalves versus Articulate Brachiopods.—Estimated mean origination and extinction probabilities were lower for bivalves than for brachiopods (Fig. 6). As with bivalve-trilobite differences, this is consistent with previous Phanerozoic-scale estimates. However, the ex-

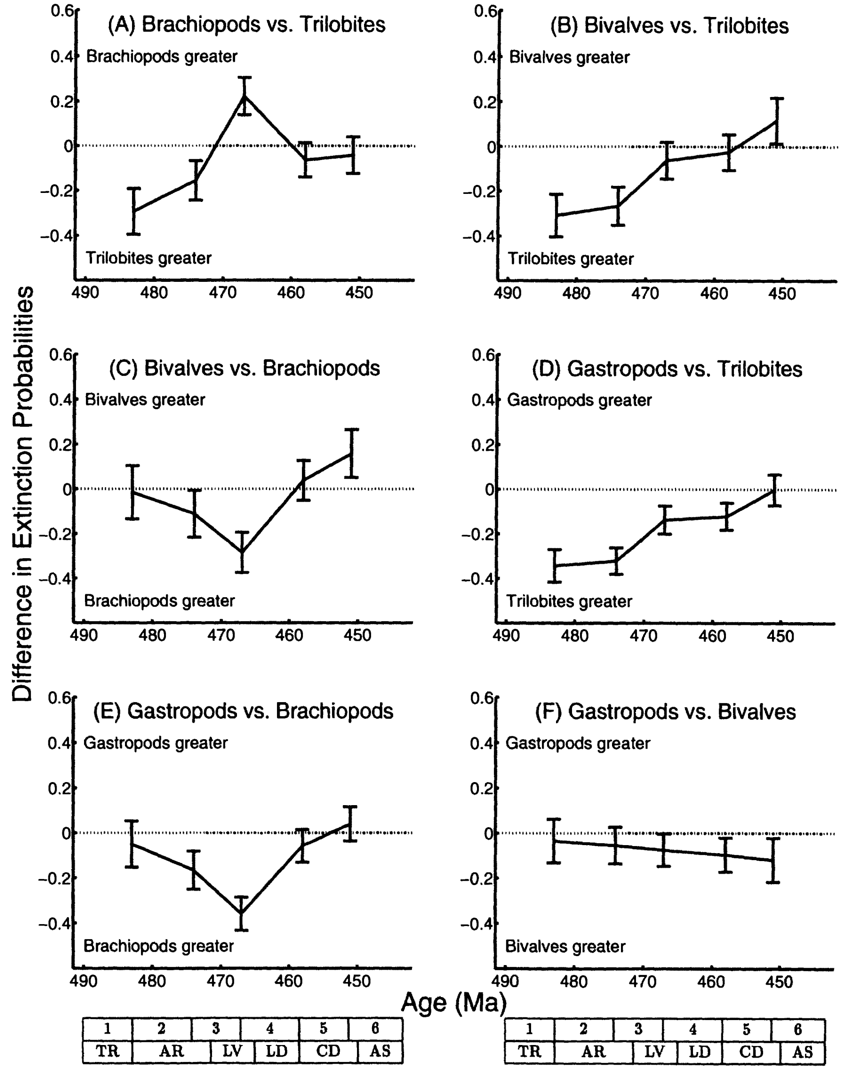

FIGURE 5. Model-averaged estimates of between-class differences in genus extinction probabilities over time obtained from the estimates plotted in Figure 3. Differences and their associated standard errors were calculated as described in Figure 4. The binning protocol is shown below the horizontal axis label as in Figure 1.

tinction difference is small (−0.04, with the standard error including zero difference), relative to the origination difference (−0.2, less than zero with >95% confidence). The origination difference appears to hold consistently throughout the period (Fig. 4C). This supports an increase in brachiopod diversity, relative to bivalves, driven by higher origination probabilities in brachiopods. This is consistent with earlier proposals (e.g., Sepkoski 1998).

Gastropods versus Trilobites.—For the Ordovician as a whole, differences in average origination and extinction probabilities are similar to those of the bivalve-trilobite comparison, although precision is greater. Origination and extinction probabilities were lower for gastropods than for trilobites, and this difference was greater for extinction (−0.18, less than zero with >95% confidence) than for origination (−0.10, not significantly different from zero), consistent with a relative increase in gastropod diversity. Interval-by-interval differences indicated little overall change in the origination differences over time (Fig. 4D), but estimated extinction differences were quite large early in the Ordovician (intervals 1–2;

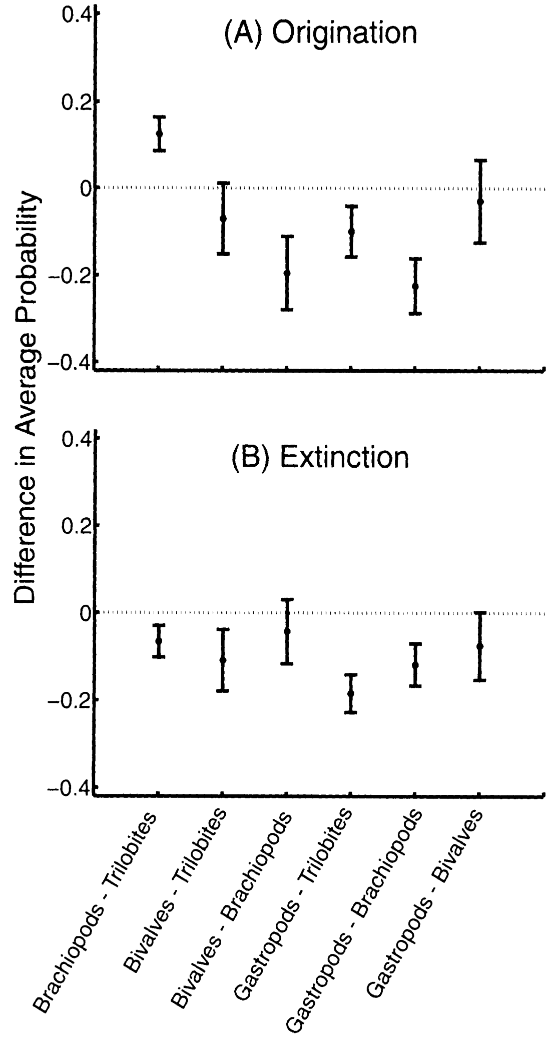

FIGURE 6. Model-averaged estimates of between-class differences in origination (A) and extinction (B) probabilities for the Ordovician as a whole. For each class, mean origination or extinction probability was estimated as the average of the interval-by-interval estimates. The estimated variance of this quantity was calculated from the variances and covariances of the interval-by-interval estimates using standard methods (Pitman 1993). Between-class differences and their associated standard errors were estimated as described in Figure 4. Differences for each pair of classes are indicated along the horizontal axis. For instance, "Brachiopods-Trilobites" in A indicates the difference between articulate brachiopod origination and trilobite origination.

Tremadocian and lower Arenigian) and nonexistent late in the Ordovician (interval 6; upper Caradocian and Ashgillian) (Fig. 5D).

Gastropods versus Articulate Brachiopods.— Overall differences between gastropods and brachiopods mirror those of bivalves and brachiopods. Origination and extinction probabilities are lower for gastropods, with the origination difference being larger than the extinction difference (Fig. 6). Estimated interval-by-interval differences suggest that the difference in origination probabilities was highest in the mid to late Ordovician (Fig. 4E)—a consequence of the pulse in brachiopod origination in the mid Ordovician and the decreasing trend in estimated gastropod origination (Fig. 2B,D). Estimated extinction differences are greatest in the mid Ordovician (Fig. 5E), associated with the pulse of brachiopod extinction (Fig. 3B). This supports an increase in the relative diversity of articulates, driven by higher origination in that group, particularly in the mid to late Ordovician.

Gastropods versus Bivalves.—Estimated differences in mean origination and extinction probabilities for the Ordovician as a whole suggest lower gastropod extinction and origination (Fig. 6). However, estimated differences are small (−0.08 for extinction and −0.03 for origination) and uncertainties are relatively large, with neither estimate differing significantly from zero. We are even more reluctant to draw inferences about temporal patterns in these differences, given our need to apply reduced-parameter models for bivalves and gastropods.

Factors Affecting Sampling Probabilities

Model-averaged estimates of sampling probabilities are presented in Figure 7. The alternative models in each model set were mathematical representations of alternative hypotheses about the causes of variation in sampling probabilities. Therefore, the relative fit of these models indicates their relative ability to explain the variation present in the data.

The most striking and consistent result of model selection was the substantially better fit obtained when average number of occurrences was used to model differences among genera in sampling probabilities (Tables 3–6). This supports our initial reasoning—that average number of occurrences would be a good surrogate for distribution and abundance and thus sampling probability. What is surprising, however, is that this remarkable improvement in model fit occurred despite the lack of significant heterogeneity of genus sampling

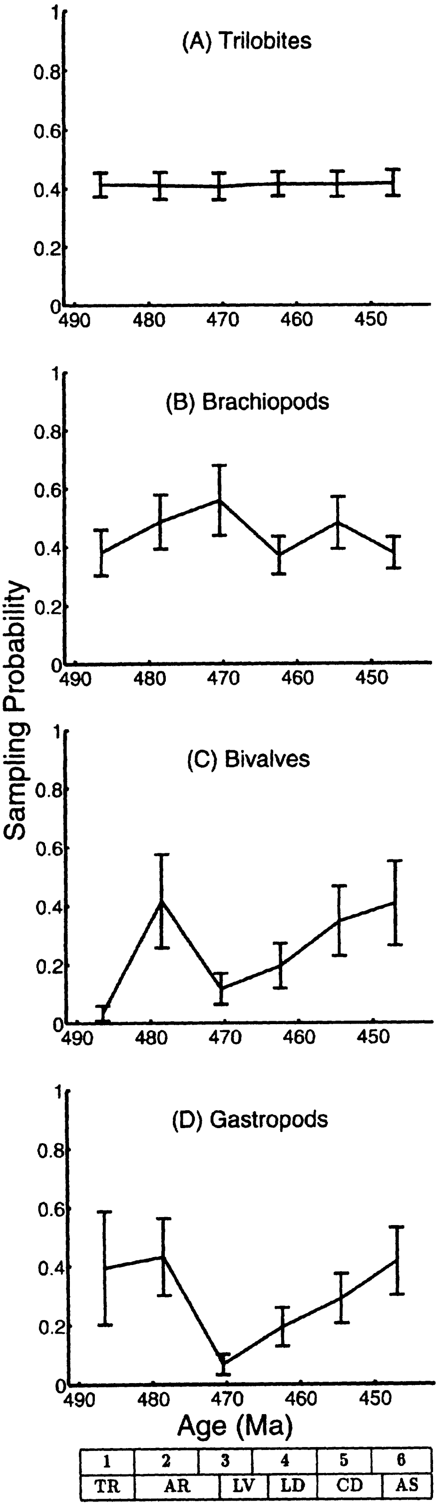

FIGURE 7. Model-averaged estimates of the combined probability of genus preservation and subsequent sampling per interval for trilobites (A), articulate brachiopods (B), bivalves (C), and gastropods (D), plotted at interval midpoints. Standard errors were estimated as described in Figure 2. The binning protocol is shown below the horizontal axis label as in Figure 1.

probabilities within trilobites, articulate brachiopods, or gastropods. Our interpretation of this is that the degree of heterogeneity was small enough within these classes that goodness-of-fit tests were not powerful enough to detect it. However, the strong support for a relationship between average number of occurrences and sampling probability for all classes suggests that some heterogeneity was present, and that it was explained, at least partially, by average number of occurrences.

By contrast, the among-interval covariate models (number of lists, environmental zones, and orogenic index) did not perform especially well. For trilobites, this was probably due to lack of variation in sampling probabilities over time. Model rankings suggest this conclusion, as the constant sampling model was the best model (Table 3). Moreover, model-averaged estimates of sampling probability indicated less than 1% variation among intervals with relatively high precision (standard errors <0.05 for all intervals; Figure 7). On the other hand, for bivalves and gastropods, the 95% confidence set included only models with fully time-varying sampling probabilities, *p*(*t*, *NOcc*) (Tables 5, 6), indicating that variation in sampling probabilities was present, but poorly characterized by the covariates we chose. This variation was quite large (Fig. 7C,D).

It would seem at first that the number of environmental zones explained variation in articulate brachiopod sampling reasonably well (Table 4). However, we suspect that the relationship between environmental zones and sampling probability was spurious in this case because it is in the wrong direction. That is, the slope of this relationship is negative, and thus sampling of fewer environmental zones predicts higher sampling probabilities, contrary to expectation. The second-best model is the fully time-varying model *p*(*t*, *NOcc*), also indicating variation in sampling probabilities that is not well characterized by the covariates we explored (Fig. 7B).

Conclusions

These results underscore the importance of jointly estimating sampling and turnover when exploring macroevolutionary patterns in the fossil record (Nichols and Pollock 1983; Conroy and Nichols 1984; Nichols et al. 1986). The robustness of macroevolutionary analyses is not necessarily confirmed by simulations in which sampling probabilities are assumed to remain constant or to follow simple trends. Variation in sampling probabilities can be substantial and non-monotonic, and can fall in the midst of key transitions in the history of life (Fig. 7). When sampling and turnover are jointly modeled, however, this variation is both detectable and separable from variation in turnover.

The relative fit of the alternative models is instructive. Although average number of occurrences seems to explain variation in sampling probabilities among genera, our constraints on among-interval variation—number of lists, environmental zones, and orogenic index—did not explain variation among intervals particularly well. This finding, coupled with the presence of substantial variation in sampling probabilities among intervals for all classes but trilobites (Fig. 7), suggests that sample quality varies over time and that the data are sufficiently well resolved to detect that variation, but that we do not have a good causal model for this variation.

This analysis identified likely proximate causes of global-scale Ordovician faunal transitions. In some respects, our results are consistent with prior, Phanerozoic-scale analyses that assume complete sampling. For instance, lower origination and extinction probabilities in bivalves and gastropods relative to trilobites and articulate brachiopods match earlier findings to this effect (Sepkoski 1979, 1991, 1998; Gilinsky and Good 1991). However, one finding in particular contrasts markedly with previous work: a major proximate cause of the transition from trilobites to articulate brachiopods was not intrinsically higher turnover in trilobites, but rather a combination of higher origination and lower extinction probabilities in brachiopods. Interval-by-interval trends in estimated origination probabilities suggest that this was due to decreasing origination probabilities in trilobites that were not reflected in articulate brachiopods, coupled with a mid-Ordovician pulse of brachiopod origination.

Finally, our ability to detect interval-by-interval variation in origination and extinction probabilities suggests that this approach can be used to examine how well changes in these probabilities over time are explained by changes in putative environmental causes of the Ordovician faunal transitions. Do existing hypothesized causes (e.g., diversity-dependence, orogenic activity) provide good explanations for the Ordovician faunal transitions? It is these problems to which we will turn in future work.

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