

Global Ordovician faunal transitions in the marine benthos: ultimate causes

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Abstract.—During the Ordovician Radiation, domination of benthic marine communities shifted away from trilobites, toward articulated brachiopods, and, to a lesser degree, toward bivalves and gastropods. Here, models are formulated that mathematically represent alternative hypothesized causes of this transition. These include models in which per-genus origination or extinction probabilities were constrained to be (1) constant, (2) diversity-dependent, (3) productivity-dependent, or (4) jointly dependent on productivity and diversity. Using a method adapted from capture-mark-recapture (CMR) population studies, we estimate origination, extinction, and sampling probabilities jointly in order to avoid confounding patterns in turnover probabilities with temporal variation in the quality of the fossil record. Using Akaike's Information Criterion (AIC), we assessed the fit of the alternative causal models relative to one another, and relative to a noncausal "phenomenological" alternative that placed no constraints on the pattern of temporal variation in origination or extinction. There were differences among taxa in the relative fit of these models, suggesting that the effects of productivity and diversity varied among higher taxa. In the aggregate, however, there was strong support for diversity-dependent origination. For extinction, poor fit of the alternative causal models suggests that we lack a good explanation for extinction patterns. These analyses support the hypothesis that diversity-dependent origination, particularly in trilobites, contributed to the Ordovician faunal transitions. By contrast, the effects of increased productivity, if indeed they were large enough to influence global diversification patterns, did not proceed in the hypothesized manner.

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Introduction

The Ordovician Radiation was characterized by major changes in benthic marine communities, including shifts in the relative diversities of several key higher taxa. Recently, we examined differences among taxa and over time in origination and extinction probabilities (i.e., the discrete, stochastic analogs of per-taxon origination and extinction rates), which we termed *proximate* causes of the faunal transitions (Connolly and Miller 2001b). We considered such causes to be proximate because patterns in turnover probabilities must themselves have causes. The characterization of these more fundamental causes is the focus of this paper.

Multiple explanations have been offered for Ordovician faunal transitions in particular, as well as the longer-term transition from Cambrian to Paleozoic to Modern faunas in general (represented here by trilobites, articulated brachiopods, and bivalve and gastropod mollusks,

respectively). These include (1) differential diversity-dependence in per-taxon diversification rates among higher taxa; (2) among-class differences in macroevolutionary responses to global, geophysically driven increases in productivity; and (3) simple exponential diversification at different class-specific rates. Each of these hypotheses can be offered as explanations, for example, for relative decreases in the genus diversity of trilobites. However, they lead to different expectations about how per-taxon origination or extinction probabilities changed through the Ordovician, thereby providing a means for testing between them. The mechanisms' predicted effects on per-taxon origination and extinction are described below and summarized in Table 1.

Diversity-Dependence

Under diversity-dependence, origination probabilities decrease and/or extinction probabilities increase as diversity increases. Differ-

TABLE 1. Predicted response of origination or extinction to increasing diversity or productivity.

Mechanism	Response of	
	Origination	Extinction
Diversity	Negative	Positive
Productivity	Positive	Negative

ences in the sensitivity of origination or extinction to increasing diversity among higher taxa could thus explain faunal transitions, as increasing diversity slows the diversification of some groups more than others. This hypothesis is epitomized by the coupled logistic model of diversification (Sepkoski 1979). In this model, higher taxa differ in their initial diversification rates (i.e., their per-taxon rates of diversification when diversity is very low), and they differ in the rate at which this diversification rate declines as diversity increases. These differences are assumed to be intrinsic to higher taxa; that is, they are taxon-specific *constants*. This model has been proposed as an explanation for broad-scale faunal transitions throughout the Phanerozoic in general, as well as for those of the Ordovician Radiation in particular (Sepkoski 1979, 1984; Miller and Sepkoski 1988). The higher taxa whose patterns are studied here are particularly appropriate to this broad-scale hypothesis, because they are the classes whose diversity dynamics best represent those of the Cambrian, Paleozoic, and Modern Faunas (Sepkoski 1981). Specifically, origination or extinction probabilities of trilobites should be more sensitive to changes in diversity than those of articulated brachiopods, which, in turn, should be more sensitive than those of bivalves and gastropods (Table 2).

Productivity-Dependence

Alternatively, Ordovician faunal transitions have been attributed to geophysical change associated with the marked increases in tectonism that occurred during this period. In particular, global increases in rates of nutrient supply associated with orogenic activity and submarine vulcanism, and concomitant increases in productivity, have been hypothesized to promote population expansion, thus decreasing extinction probabilities and increasing opportunities for origination as new habitats become productive enough to support founder populations (Miller and Mao 1995; Vermeij 1995). This mechanism could explain the faunal transitions, provided that effects were more dramatic for higher taxa whose relative diversity increased. For instance, trilobites might be less sensitive to changes in productivity than higher taxa whose constituents have, on average, more energy-demanding life habits (Bambach 1993; Vermeij 1995).

It is worth note that other links between orogenic activity and faunal turnover have been proposed, including seafloor disruption and increases in the prevalence of siliciclastic habitats (Miller and Mao 1995). However, it is not clear whether or how these mechanisms would influence class-level transitions at the global scale, as their effects would have been more localized than those of increased nutrient supply. The global scope of the present analysis is best-suited to assessing large-scale, long-term links such as those hypothesized for productivity and diversification. Therefore, we restrict our investigation of geophysically mediated effects to this particular mechanism.

TABLE 2. Differences among taxa in strength of diversity-dependence under the coupled-logistic model. Initial diversification rate is the per-taxon rate of diversification when diversity is very low. Equilibrium diversity is the diversity at which originations tend to balance extinctions, such that diversity remains constant. Strength of diversity-dependence is simply the rate at which per-taxon diversification decreases as diversity increases. Thus, if initial diversification rate is high, and equilibrium diversity is low, then diversification must decrease sharply with increasing diversity (i.e., diversity-dependence must be strong).

Higher taxon	Initial diversification rate	Equilibrium diversity	Diversity-dependence
Trilobites	Highest	Lowest	Strongest
Articulated brachiopods	Intermediate	Intermediate	Intermediate
Bivalves/Gastropods	Lowest	Highest	Weakest

Exponential Diversification

Finally, a simpler explanation attributes the faunal transitions to exponential diversification, with different intrinsic diversification rates for different taxa. That is, origination and extinction probabilities are stochastically constant over time, rather than varying predictably with specific biotic or geophysical factors. Gould and Calloway (1980) and Benton (1995), among others, have advocated this model in different contexts. These arguments follow from conceptualizing patterns of clade waxing and waning as possible consequences of independent random walks. Formulated as an alternative explanation for the Ordovician faunal transitions, this line of reasoning predicts that modeling per-taxon origination and extinction probabilities as constants provides a better explanation for the faunal transitions than one treating those probabilities as explicit functions of diversity, productivity, or any other biotic or geophysical variable.

Joint Effects of Diversity and Productivity

The diversity-dependent and productivity-dependent mechanisms are not necessarily mutually exclusive. It is possible that the Ordovician faunal transitions were driven jointly by productivity and diversity-dependence. The effects of these two putative causes may have been sufficiently similar in magnitude that the faunal transitions would have looked quite different had one or the other mechanism played no role. If so, an adequate explanation of the faunal transitions might need to incorporate both mechanisms.

This study's principal objective was to assess the relative plausibility of these four alternative explanations for the Ordovician faunal transitions. Toward that end, we fit a set of alternative models of per-genus origination and extinction probabilities for trilobites, articulated brachiopods, bivalves, and gastropods that represent each of the alternative mechanisms described above. Comparison of the relative fit of these models identified diversity-dependent origination as a likely contributing factor in the Ordovician faunal transitions, primarily owing to its stronger effects on trilobites than articulated brachiopods or

TABLE 3. Temporal binning protocol. Note that ages are approximate.

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

bivalves. By contrast, there was only weak support for a productivity model, suggesting that any global-scale effects of increasing tectonic activity on origination during the Ordovician either did not proceed in the hypothesized manner or was too weak to detect in the data (and thus unlikely to have been the principal cause of the Ordovician faunal transitions). For extinction, none of the causal models performed well, suggesting that we presently lack a good explanation for extinction patterns during the Ordovician.

Modeling Approach

We analyzed occurrences of trilobite, articulated 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, 1998; Miller and Mao 1998; Connolly and Miller 2001a,b; Miller and Connolly 2001). They were binned stratigraphically to minimize percentage variation in interval durations (Table 3), and some samples were excluded to minimize changes among intervals in the geographical extent of sampling (see Connolly and Miller 2001a,b for details).

The study used an analytical approach based on capture-mark-recapture (CMR) population studies (Connolly and Miller 2001a,b), and it involved the following steps: (1) We formulated alternative models of genus origina-

tion and extinction that corresponded to the diversity-dependent, productivity-dependent, and joint productivity-diversity explanations described above. (2) We fit these alternative models to the Ordovician data, and we then determined whether the estimated effect of diversity or productivity on origination or extinction was in the direction predicted by the corresponding hypothesis. (3) For those models in which the estimated effect of diversity or productivity was consistent with the hypothesis, we compared the fit of these models relative to one another, and relative to models in which origination and extinction probabilities were constant through time (i.e., in keeping with the exponential diversification hypothesis). (4) We compared these models (hereafter collectively termed “causal models”) with phenomenological models in which extinction and origination probabilities were fully time-varying (i.e., not constrained to remain constant over time or to have relationships with particular causal variables), in order to assess how well the set of alternative models characterized origination and extinction patterns in general. (5) We conducted these analyses on each taxonomic class separately, in order to identify differences among higher taxa in the strength of evidence for the alternative causal mechanisms. In addition, we treated classes as separate groups in a single, synthetic analysis. This allowed us to assess the extent to which the alternative causal hypotheses explained the Ordovician faunal transitions as a whole.

The framework for each of the alternative models was originally developed by Pradel (1996) for CMR population studies, recently reformulated for application to the fossil record (Connolly and Miller 2001a). 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 the approach of 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 2001a).

Covariates

Within the modeling framework described above, it is possible to constrain probabilities of origination, extinction, or sampling to have particular relationships with one another across intervals. One advantage of such constraints is that they can be used to formulate models that conform to particular hypotheses about the causes of variation in origination, extinction, or sampling probabilities (Connolly and Miller 2001a,b). That is our principal objective here. To model origination and extinction as functions of productivity and diversity, however, we first require estimates of how these quantities varied through the Ordovician.

Productivity.—Increasing tectonic activity should lead to increases in nutrient supply to the marine biosphere, and thus concomitant increases in productivity (Miller and Mao 1995; Vermeij 1995). An estimate of this activity can be obtained from the Orogenic Index, which is based on the number, geographic extent, and persistence of centers of orogeny (Khain and Seslavinsky 1996). Similarly, $\delta^{13}\text{C}$ values through the Ordovician can serve as a proxy for productivity (but see caveats in Veizer et al. 1999). We obtained an estimate of Orogenic Index for each interval as described previously (Connolly and Miller 2001b). To obtain a productivity trajectory, we analyzed $\delta^{13}\text{C}$ values from Veizer et al. (1999). We fit first-order and second-order linear regressions to Ordovician $\delta^{13}\text{C}$ values by maximum likelihood methods, then obtained a $\delta^{13}\text{C}$ trajectory using model averaging (Burnham and Anderson 1998). Orogenic Index and $\delta^{13}\text{C}$ trajectories are plotted together in Figure 1A. It is particularly striking that the rank orders of

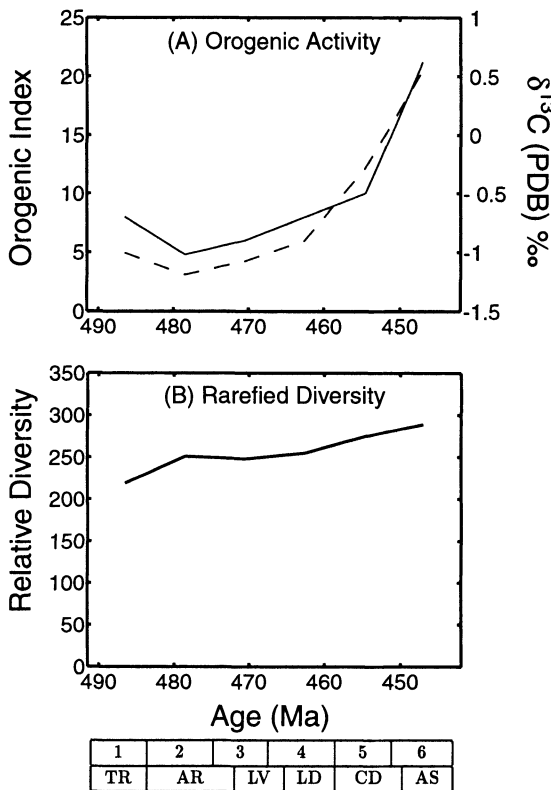


FIGURE 1. Trajectories of the quantities used as covariates in the productivity-dependent, diversity-dependent, and joint productivity-diversity models. A, Orogenic activity: Orogenic Index (solid line) and $\delta^{13}\text{C}$ (dashed line). Note that both share the same rank ordering among intervals. B, Rarefied diversity.

the two trajectories are identical. Therefore, we use these ranks as a proxy for productivity trends.

Diversity.—Diversity estimates can be made from the same data that are used to estimate turnover probabilities (Pollock et al. 1990). However, the extent to which a relationship between diversity and turnover is due to diversity-dependence versus statistical artifact can be unclear when this is done (Maurer 1989; Sepkoski 1991; Alroy 1998). To make diversity and turnover estimates less statistically dependent, we estimated diversity separately for each interval, using the subsamples (faunal lists) from which the interval's overall presence-absence data were compiled (see Pollock 1982 for a similar approach). Specifically, we rarefied the data, yielding estimates of sampled diversities after standardization to a common sample size (e.g., Raup 1975; Alroy

1996; Miller and Foote 1996). These estimates, plotted in Figure 1B, served as our proxy for diversity. Note that this trajectory, based on the binning protocol used in this study, does not show the mid-Ordovician plateau indicated by an earlier, series-level trajectory (Miller and Foote 1996), perhaps because culling of data required for the present study's binning scheme meant that fewer sampling locations could be used (Connolly and Miller 2001a). Because we were unsure which of these two trajectories most accurately reflects true changes in diversity through the Ordovician, we fit the entire model set twice, once using the trajectories shown in Figure 1B, and a second time assuming that diversity increased linearly through the mid Ordovician but remained constant thereafter.

Alternative Models

Our alternative models include the following:

Constant.—If diversification follows a simple exponential (continuous-time) or geometric (discrete-time) function, then both origination and extinction probability are constant over time (e.g., Benton 1995).

Diversity-Dependent.—In this model, origination and/or extinction probability is given by

$$\theta = \alpha_0 + \alpha_1 x, \quad (1)$$

where θ is a vector of origination or extinction probabilities and x is a vector of rarefied diversities. α_0 and α_1 are the parameters that are estimated, and θ is calculated from those estimates (see Connolly and Miller 2001a for details). α_0 represents the intercept—origination or extinction probability as diversity approaches zero—and α_1 indicates the slope—the strength of the effect of diversity on origination or extinction. Because origination and extinction probabilities correspond to transitions between intervals, rather than to intervals themselves (hence there are only five origination and extinction probabilities estimated), each x_i was actually an average of rarefied diversity from the intervals prior and subsequent to the relevant transition (Fig. 1B). For instance $1 - \phi_1$ is the probability of extinction between the first and second inter-

vals. Thus, the corresponding diversity covariate was the average of rarefied diversity estimates from those intervals.

Productivity-Dependent.—In this model, origination and/or extinction probability is a function of productivity according to equation (1), with \mathbf{x} as a vector of productivity ranks. As for the diversity covariates, productivity covariates were averages of productivity ranks from the intervals prior and subsequent to the relevant transition (Fig. 1A).

Joint Productivity-Diversity.—In this model, origination or extinction probability are functions of both productivity and diversity as follows:

$$\theta = \alpha_0 + \alpha_1 \mathbf{x}_1 + \alpha_2 \mathbf{x}_2, \quad (2)$$

where θ is a vector of origination or extinction probabilities, \mathbf{x}_1 and \mathbf{x}_2 are corresponding vectors of values of rarefied diversity and productivity rank, α_0 is an intercept term, and α_1 and α_2 indicate the strength of effects of diversity and productivity, respectively.

In multiple regression, the power to detect a significant effect is low when the independent variables are highly correlated, because very little additional variation can be explained when the second variable is added. The same principle applies here. Productivity rank and rarefied diversity are relatively highly correlated ($\rho = 0.85$). Thus, the power to detect joint effects in this analysis was somewhat low, and only particularly strong effects would have been detected.

Phenomenological.—In this model, origination or extinction is fully time-varying. We term this the phenomenological model here to emphasize that origination and extinction probabilities are not constrained according to a causal hypothesis, as the other models are. Rather, it corresponds to what we have termed the “fully time-varying” model in previous analyses (Connolly and Miller 2001a,b). Good fit of these models, relative to the causal models, indicates that the data are adequate to resolve among-interval variation in extinction or origination probabilities, but that the putative causal mechanisms represented by the other models fail to capture much of that variation (Connolly and Miller 2001b).

To ensure that meaningful parameter esti-

mates were obtained (i.e., no probabilities less than zero or greater than one), the logistic, or logit, transforms of sampling, origination, and extinction probabilities were estimated, rather than the probabilities themselves:

$$\text{logit}(p) = \log\left(\frac{p}{1-p}\right) \quad (3)$$

Any value of $\text{logit}(p)$ corresponds to $0 < p < 1$. Thus, θ in equations (1) and (2) actually corresponds to the logistic transforms of origination or extinction, rather than origination or extinction probabilities themselves (see Connolly and Miller 2001a for further discussion).

In all models, sampling probabilities were fully time-varying. That is, sampling probabilities for different intervals were not constrained to have specific relationships to one another. In addition, we modeled among-genus variation in sampling probabilities as a function of average number of occurrences at sampling locations *within* intervals, because previous analyses indicated that this offered markedly better fit than models in which sampling probability was assumed to exhibit no variation among genera (see Connolly and Miller 2001b for details).

Finally, because a causal factor may influence origination, but not extinction, or vice-versa, we compared alternative models separately for origination and extinction. We did this by modeling origination (extinction) probabilities as fully time-varying when we compared alternative extinction (origination) models. This approach allowed a more unequivocal assessment of the relative fit of particular alternative causal relationships (Williams et al. in press). Thus, for each taxonomic class, and for the aggregate analysis, two model sets were fit—one to compare alternative models of origination and another to compare alternative models of extinction.

Maximum likelihood estimates (MLEs) of the parameters for each of the five alternative models (constant, diversity-dependent, productivity-dependent, joint productivity-diversity, and phenomenological) were obtained by using the numerical estimation procedure implemented in Program MARK (White 2000), as described previously (Connolly and Miller 2001a).

Direction of Effects

For the diversity-dependent, productivity-dependent, and joint productivity-diversity models, we wanted to determine whether the estimated relationship between diversity or productivity and origination or extinction was in the direction predicted by the corresponding causal hypothesis. We did this by examining the MLE of the slope of the relationship between the covariate (diversity or productivity) and origination or extinction. When the MLE was in the predicted direction, we estimated the probability that the true relationship was in the predicted direction from the estimated standard errors of the MLEs.

Model Selection

Assessing Model Fit.—Previously, we described a protocol for comparing the fit of a set of alternative models for the same data set (Connolly and Miller 2001a). This process has two steps. The first involves assessing the goodness-of-fit of the fully time-varying model (what we call the “phenomenological” model). The second involves assessing the *relative* fit of the phenomenological model and the alternative causal models. Goodness-of-fit statistics for individual taxonomic classes have been calculated previously (Connolly and Miller 2001b), as have goodness-of-fit statistics when each class is treated as a separate group in a synthetic analysis (Connolly and Miller 2001a). Therefore, we use those statistics to calculate the variance inflation factor, \hat{c} , which is in turn used to adjust estimated uncertainties in MLEs and to modify model selection procedures (Lebreton et al. 1992; Anderson and Burnham 1994; see Connolly and Miller 2001a for a detailed summary).

The second step involves ranking models according to their relative fit. To do this, we calculate model weights from Akaike’s Information Criterion (AIC), adjusted for sample size (AIC_c) and according to goodness-of-fit test results (QAIC_c) where necessary. For each model, we calculated 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; Connolly and Miller 2001a).

Causal Model Evaluation.—To compare alternative causal hypotheses, we simply selected those covariate models (i.e., the diversity-dependent, productivity-dependent, and joint productivity-diversity models) whose effects were consistent in direction with the corresponding causal hypotheses, and we compared them to the constant and phenomenological models. We did this separately for each class, because it is possible that higher taxa differed in their responses to the alternative causal mechanisms.

Although w_k is an estimate of the probability that model k is the best model in the model set, it is important to note that there is not a direct correspondence between causal hypotheses and their corresponding models (because the causal hypotheses are direction-specific and the models were not). In practice, however, because model rankings include only those models whose estimated effects were in the predicted direction, covariate models included in rankings were only well supported when the estimated effects were in the predicted direction with high confidence, consistent with strong support for the causal reasoning underlying the model. Thus, model weights offer a reasonable means of identifying strongly supported causal hypotheses. See Franklin et al. 2000 for a similar use of model rankings.

Synthetic Analysis.—Examining each taxonomic class separately enabled us to identify class-specific differences in responses to causal variables. However, the causal models explored here have all been offered as explanations that span higher taxa, i.e., that apply to all of the classes investigated here. Thus, it was useful to determine how well origination and extinction patterns could be modeled both over time and across higher taxa, using the reasoning embodied in the alternative causal hypotheses. We did this by treating each class as a separate group in a single analysis (Connolly and Miller 2001a). For instance, we stipulated that each class exhibited diversity-dependence (although the strength of diversity-dependence may have differed among classes), and we fit this synthetic model to the combined trilobite, articulated brachiopod, bivalve, and gastropod data.

Before conducting this analysis, however, it was necessary to account for the direction-specific nature of the causal hypotheses. Simply modeling origination in all classes as diversity-dependent, for instance, would not have presented an accurate picture of the extent to which the diversity-dependent hypothesis was supported. This is because, for some taxonomic classes, the relationship was estimated to be positive, opposite that consistent with the model. Thus, when the estimated relationship was consistent with the causal hypothesis for a particular class, we modeled origination or extinction as a function of the relevant covariate for that class. When the estimated relationship was opposite that predicted, we used a constant origination or extinction model for that class. The constant origination or extinction model was used because it represents the limit as the effect of a covariate becomes very small. For instance, our class-by-class analysis indicated that the estimated effect of diversity on origination was consistent with the diversity-dependent hypothesis for trilobites, brachiopods, and gastropods, but not bivalves (see Results). Therefore, in the synthetic diversity-dependent model, diversity-dependent origination was assumed for the former three classes, but constant origination was assumed for the latter.

We applied the same logic for the synthetic joint productivity-diversity model. For example, our class-by-class analyses indicated that the joint effects hypothesis was consistent with origination patterns of trilobites, articulated brachiopods, and gastropods (see Results). Thus, in our synthetic joint productivity-diversity model, origination was a function of both productivity and diversity for these three classes. Joint effects were not supported for bivalves, however. There were two possible approaches here. One was to treat origination as constant; another was to treat it as productivity-dependent only (i.e., a joint model in which the effect of diversity on bivalve origination is zero). The results presented here use the latter, but were nearly identical when we used the former—model rankings were unaffected, and model weights of the alternative forms of the joint models differed by

<0.05 in both origination and extinction analyses.

Put simply, what we have done is assemble the most diversity-dependent model that the data support, the most productivity-dependent model that the data support, and a joint model that includes as many effects of both diversity and productivity that the data will support. We then compared these models with one another, with a simple constant origination or extinction model, and with a phenomenological model.

Results

Results of the “direction-of-effects” analysis are presented in Table 4, and model rankings are presented in Table 5. In discussing the direction-of-effects analysis, we adopt conventional terminology and use highly significant, significant, and marginally nonsignificant to refer to percent confidence levels of 99%, 95%, and 90%, respectively. However, we note that these confidence levels are not identical to $1 - p$ in a conventional one-sample t -test. Rather, they represent the probability that the estimated relationship was in the predicted direction.

Trilobites.—In the direction-of-effects analysis, the estimated relationship between origination and productivity in the productivity-dependent model was not in the predicted direction (Table 4). Therefore, as described earlier, we rejected this model, eliminating it from model rankings (Table 5). Those rankings provided strong support for diversity-dependent origination. The estimated best two models, diversity-dependent origination and joint productivity-diversity origination, both included an effect of diversity on origination (combined $w = 0.87$). This is consistent with the estimated effects of diversity on origination in the direction-of-effects analysis, which were significant or highly significant in both the diversity-dependent and joint productivity-diversity models (Table 4). Model rankings provided very little support for constant origination ($w = 0.02$).

The direction-of-effects analysis indicated that the relationships between diversity and extinction were not in the predicted direction for either the diversity-dependent or the joint

TABLE 4. Effects of diversity and productivity on origination and extinction. Table entries indicate whether the estimated relationship is in the direction predicted by the corresponding causal hypothesis, and, if so, the percent confidence that the "true" effect is in the correct direction. For the joint productivity-diversity models, the estimated effects of both productivity and diversity had to be in the predicted direction. Where this was the case, percent confidences are reported as XX%/YY%, where XX% and YY% indicate the percent confidence that the diversity effect and productivity effect, respectively, were in the predicted direction.

Class	Model	Origination		Extinction	
		Predicted direction?	% Confidence	Predicted direction?	% Confidence
Trilobites	Diversity-dependent	Yes	>99%	No	—
	Productivity-dependent	No	—	Yes	>99%
	Joint	Yes	95%/53%	No	—
Brachiopods	Diversity-dependent	Yes	73%	No	—
	Productivity-dependent	No	—	Yes	96%
	Joint	Yes	91%/87%	No	—
Bivalves	Diversity-dependent	No	—	Yes	90%
	Productivity-dependent	Yes	86%	No	—
	Joint	No	—	Yes	91%/87%
Gastropods	Diversity-dependent	Yes	99%	No	—
	Productivity-dependent	No	—	Yes	90%
	Joint	Yes	86%/63%	Yes	57%/87%

productivity-diversity models (Table 4). These models were rejected based on that initial analysis, and model rankings confined to the remaining models (Table 5). Rankings provided modest support for productivity-dependent extinction ($w = 0.68$), consistent with the fact that the estimated effect of productivity on extinction was highly significant under the productivity-dependent model. There was essentially no support for constant extinction ($w \approx 0$).

Articulated Brachiopods.—As with trilobites, the relationship between origination and productivity was not in the predicted direction for articulated brachiopods for the productiv-

ity-dependent model (Table 4), so it was eliminated from model rankings. Model rankings for the remaining models are presented in Table 5. There was modest support for constant origination ($w = 0.57$), and weak support for diversity-dependence and for joint effects of productivity and diversity ($w = 0.09$ and $w = 0.06$, respectively). The weak support for effects of diversity was reflected in our initial analyses, in which the estimated effect of diversity on origination was not significant under the diversity-dependent model, and marginally nonsignificant under the joint productivity-diversity model (Table 4). The estimated effect of productivity on origination under the

TABLE 5. Model weights. Covariate models were included in the ranking only if the maximum-likelihood estimate of the slope between the covariate and origination or extinction was in the direction consistent with the corresponding causal hypothesis (Table 4). In all models, sampling probability was fully time-varying, and among-genus variation was modeled as a function of average number of occurrences within intervals. For all origination models, extinction probability was fully time-varying. For all extinction models, origination probability was fully time-varying. The model weight of the best-supported model is reported in boldface.

Probability	Model	Trilobites	Articulateds	Bivalves	Gastropods	All
Origination	Productivity-dependent	—	—	0.15	—	0.01
	Diversity-dependent	0.64	0.09	—	0.74	0.84
	Joint Productivity-diversity	0.23	0.06	—	0.09	0.02
	Constant	0.02	0.57	0.60	0.15	0.01
	Phenomenological	0.11	0.28	0.25	0.02	0.13
Extinction	Productivity-dependent	0.68	0.00	—	0.40	0.01
	Diversity-dependent	—	—	0.31	—	0.00
	Joint Productivity-diversity	—	—	0.17	0.13	0.01
	Constant	0.00	0.00	0.45	0.45	0.00
	Phenomenological	0.32	1.00	0.07	0.02	0.98

joint productivity-diversity model was not significant either (Table 4).

Again, as for trilobites, the direction-of-effects analysis indicated that the relationships between diversity and extinction were not in the predicted direction for either the diversity-dependent or the joint productivity-diversity models (Table 4). Moreover, rankings of the remaining models indicated effectively no support for any of the causal models of extinction (Table 5). The phenomenological model was far better supported than the productivity-dependent or constant extinction models. Strong support for the phenomenological model indicated that the alternative causal hypotheses poorly characterized extinction patterns in articulated brachiopods. This finding is not surprising, given that previous estimates indicated a mid-Ordovician pulse in extinction probabilities (Connolly and Miller 2001b), a result that is not consistent with any of the causal models.

These model rankings illustrate the limitations associated with fitting only one model to data. Based only on the direction-of-effects analysis, one might have concluded that the statistically significant relationship between productivity and extinction indicated strong support for a productivity-dependent explanation of extinction patterns (Table 4). However, much better fit of the phenomenological model reveals that important temporal patterns present in the data are poorly characterized by the productivity-dependent model.

Bivalves.—On the basis of the direction-of-effects analysis (Table 4), the diversity-dependent and joint productivity-diversity origination models were eliminated from model rankings for bivalves. Rankings for the remaining models are presented in Table 5. There was modest support for constant origination ($w = 0.60$), and there was some support for productivity-dependent origination as well ($w = 0.15$). This modest to weak support for productivity-dependence is consistent with the estimated effect of productivity on origination, which was in the predicted direction but not statistically significant.

For extinction, the direction-of-effects analysis led to initial rejection of the productivity-dependent model (Table 4). In rankings for the

remaining models (Table 5), there was modest support for constant extinction ($w = 0.45$) and for diversity-dependent extinction ($w = 0.31$), whereas support for joint productivity-diversity effects on extinction was modest to weak ($w = 0.17$). Again, this is consistent with the results of our initial analyses. The estimated effect of diversity on extinction was marginally nonsignificant under the diversity-dependent model. Under the joint productivity-diversity model, the estimated effect of diversity on extinction was marginally nonsignificant and the estimated effect of productivity on extinction was nonsignificant.

Gastropods.—On the basis of the direction-of-effects analysis (Table 4), the productivity-dependent origination model was eliminated from model rankings for gastropods. Rankings for the remaining models are presented in Table 5. Diversity-dependent origination was most strongly supported ($w = 0.74$), but both the constant and joint productivity-diversity models also had non-negligible levels of support ($w = 0.15$ and $w = 0.09$, respectively). This was consistent with the estimated effect of diversity on origination, which was highly significant (Table 4). By contrast, the effects of diversity and productivity on origination in the joint productivity-diversity model were not statistically significant (Table 4).

For extinction, the direction-of-effects analysis led to elimination of the diversity-dependent model from model rankings (Table 4). In rankings for the remaining models (Table 5), the constant and productivity-dependent models received comparable levels of support ($w = 0.45$ and $w = 0.40$, respectively). The joint productivity-diversity model also had modest to weak support ($w = 0.13$). This was consistent with our initial analysis, in which the relationship between productivity and extinction under the productivity-dependent model was marginally nonsignificant, but effects under the joint productivity-diversity model were not significant (Table 4).

Synthetic Analysis.—Results of model selection from the analysis of all taxonomic classes together are presented in Table 5. For origination, the diversity-dependent model was by far the most strongly supported causal model ($w = 0.84$ vs. $w < 0.05$ for the other causal

models). It was also more strongly supported than the phenomenological model, suggesting that it parsimoniously characterized patterns in origination probabilities. For extinction, however, the most strongly supported model was the phenomenological model, relative to which the alternative causal models had essentially no support ($w \leq 0.01$). This strongly suggests that the alternative causal models poorly characterized patterns in extinction probabilities.

Robustness to Diversity Trajectory.—To examine the robustness of our results to the possibility that diversity reached a mid-Ordovician plateau (Miller and Foote 1996), we recalculated model rankings for diversity-dependent models under a diversity trajectory that increased through interval 3 (until approximately the Llanvirnian) and remained constant thereafter. There was little change in the results' implications for relative support for the alternative causal hypotheses under this analysis. For trilobites, diversity-dependent origination remained the best-supported model (see Table 5). For articulated brachiopods, support for diversity-dependent origination was virtually unchanged at $w \approx 0.05$ (see Table 5). For bivalves, support for diversity-dependent extinction was virtually unchanged $w \approx 0.30$ (see Table 5). For gastropods, however, diversity-dependent origination was much less well-supported, dropping to a level of support comparable to that of constant origination (see Table 5).

In light of this last result, which suggests that model rankings for gastropod origination patterns are sensitive to uncertainty in the diversity trajectory, we repeated our synthetic origination analyses using only trilobites, articulated brachiopods, and bivalves. The qualitative results were unchanged, with the diversity-dependent and phenomenological models having modest support, and the remaining causal models having weak support ($w = 0.54$ and $w = 0.27$ for the phenomenological and diversity-dependent models, respectively, and $w < 0.08$ for the remaining models).

Parameter Estimation.—Estimates of origination and extinction probabilities can be produced for any of the models fit here. Moreover,

entire model sets can be used to produce robust, model-averaged parameter estimates. Previously, we have done this for the higher taxa and time intervals investigated here, using models that put alternative constraints on preservation and sampling probabilities (Connolly and Miller 2001b). The same protocol can be applied here, and model-averaged estimates of origination and extinction produced from the alternative causal models fit in the present paper. These estimates are available upon request from the authors, or online at <http://homepages.uc.edu/~millerai/ultimate.htm>.

Discussion

The analyses presented above indicate that no single model best explains origination or extinction patterns for all classes. Moreover, in the aggregate, our alternative causal models of extinction poorly characterized temporal patterns in extinction probabilities (Table 5). By contrast, there was clearly strong support for incorporating diversity-dependent origination in a model of the Ordovician faunal transitions. From these analyses, we can assess the evidence for the alternative hypothesized causes of the Ordovician faunal transitions that motivated this study.

Origination.—Model rankings from the synthetic analysis strongly support a role for diversity-dependence in Ordovician origination patterns. In addition, with the exception of gastropods, class-by-class analyses indicate differences in the relative strength of evidence for diversity-dependence (strong for trilobites, weak for articulated brachiopods, and absent for bivalves) that are consistent with differences in the equilibrium diversities of the respective Evolutionary Faunas of which these taxonomic classes are members. Specifically, members of the Cambrian fauna, including trilobites, should exhibit the strongest level of diversity-dependence (Table 2) (Sepkoski 1979). Conversely, members of the Modern Fauna should be least sensitive to increases in diversity. Thus, when other factors are contributing to variation in origination or extinction probabilities, and those factors are not explicitly incorporated in the model being fit, diversity-dependent effects should be harder to detect in bivalves than in trilobites. Articulated

ed brachiopods, as members of the Paleozoic Fauna, should lie between the two.

Gastropods present a possible exception to this overall trend. However, we view results of the gastropod analyses with caution. Our re-ranking of the alternative models under the alternative diversity trajectory indicated that support for diversity-dependent origination in this group is sensitive to uncertainty in the diversity trajectory. In addition, there were some problems with inestimable parameter values for gastropods. As we have noted previously (Connolly and Miller 2001b), this can occur if the data are too sparse to support the number of parameters included in the models. As a result, the inferences suggested by gastropod model rankings are suspect.

In contrast to diversity-dependence, productivity-dependent origination received essentially no support in the synthetic analysis (Table 5). Indeed, our direction-of-effects analysis led to an initial rejection of productivity-dependent origination for all taxonomic classes except bivalves (Table 4). Productivity-dependent origination in bivalves is a plausible cause of increases in bivalve diversity, relative to trilobites, particularly in the Middle to Late Ordovician, when orogenic activity increased markedly. However, model rankings for bivalves indicate that support for the productivity-dependent model is rather weak, relative to constant or phenomenological origination models (Table 5).

A joint model in which origination decreases with increasing diversity but increases with increasing productivity is consistent with origination patterns in trilobites, articulated brachiopods, and gastropods; however, the estimated effects of diversity and productivity were never both statistically significant under these models (Table 4). Moreover, it is less well supported than the diversity-dependent model in all model rankings. We infer from this that the evidence for joint, additive effects of diversity and productivity on origination patterns is limited, with the caveat that the high correlation between rarefied diversity and productivity ranks, noted earlier, means that the power to detect joint effects, even if present, was probably low. A more powerful assessment of the potential for joint effects will probably require

a finer-scale analysis, in which origination patterns are modeled specifically for geographic regions in which the correlation between diversity and orogenic activity was lower.

Simple, constant origination (*sensu* Gould and Calloway 1980; Benton 1995) is not supported under the synthetic analysis, although it received modest support for all classes but trilobites (Table 5). Thus, the weak support for constant origination in the synthetic model is driven primarily by the strong support for diversity-dependent origination in trilobites and gastropods.

Extinction.—The synthetic extinction analysis strongly indicates that the set of alternative causal models, as a group, poorly characterized extinction patterns during the Ordovician. The phenomenological model was better than all of the alternative causal models with greater than 95% confidence in this analysis (Table 5).

In our analysis of origination patterns, differences among taxa in the performance of our covariate models were plausible, in light of the causal reasoning underlying them. Diversity-dependent origination was better supported for trilobites than other classes, consistent with their hypothesized low equilibrium diversity (Sepkoski 1979). Similarly, productivity-dependent origination was supported (albeit weakly) only for bivalves. Given that bivalve life histories tend to be more metabolically demanding than those of trilobites or brachiopods (Bambach 1993), and that they have strong siliciclastic affinities, unlike gastropods (Novack-Gottshall 1999), bivalves are the most likely candidates to exhibit strong responses to changes in tectonic activity.

In contrast to this, extinction patterns are inconsistent with the diversity-dependent hypothesis for trilobites, articulated brachiopods, and gastropods (Table 4). Extinction patterns are consistent with diversity-dependence only for bivalves, and even for this group, the significance of the relationship is only marginal (Table 4). Moreover, increases in bivalve extinction with increasing diversity would work against, rather than for, a faunal transition from trilobites to bivalves. Thus, even if real, diversity-dependent extinction is not a plausible cause of the Ordovician faunal transitions.

Conversely, productivity-dependent extinction is most strongly supported for trilobites (Table 5). Decreasing trilobite extinction with increasing orogenic activity would not contribute to decreasing relative diversity of trilobites; it would tend to have the opposite effect. Thus, even if real, it is not a plausible cause of the Ordovician faunal transitions.

The particularly strong support for the phenomenological model, relative to the causal models ($w \approx 1.0$), indicates that there was temporal variability in extinction probabilities, that this variability was statistically detectable, but that the causal models poorly characterized this variation. Some further insight can be gleaned from inspection of the model rankings for separate higher taxa (Table 5). Clearly, a major factor contributing to the synthetic rankings was the nearly complete lack of support for any causal models for articulated brachiopods and correspondingly overwhelming support for the phenomenological model. For the other taxa, however, there was always substantial model-selection uncertainty. In other words, there was no higher taxon for which one of the causal models was clearly the best model, and thus nothing to offset the overwhelming support for the phenomenological model for articulated brachiopods. Moreover, those taxa (bivalves and gastropods) for which there was only limited support for the phenomenological model had low sampled diversities. As a result, greater uncertainty in parameter estimates was associated with these taxa, so they had less effect on the results of the synthetic analysis, relative to trilobites and articulateds.

Caveats.—It is important to note that these results pertain to the sampling universe from which the data are drawn—global diversification of Ordovician trilobite, articulated brachiopod, bivalve, and gastropod genera. Explanations are scale-dependent, and the implications of this work with regard to both smaller- and larger-scale patterns should be evaluated with this in mind: Although the tectonism-diversification link modeled here—a global-scale, productivity-mediated change in tectonism with strong, global effects on origination and extinction—was not supported, the potential for more spatially variable, regional effects remain

a possibility. Work at regional scales over shorter time intervals than those explored here has identified major shifts in community structure and diversity associated with nearby tectonic uplift (Patzkowsky and Holland 1993, 1999). Moreover, articulated brachiopod genera show a marked transition (relative to trilobites) from carbonate to siliciclastic habitats in the Middle Ordovician (Miller and Connolly 2001). This transition coincides with an estimated pulse in articulated brachiopod turnover (Connolly and Miller 2001b). Such patterns suggest a link between orogenic activity and turnover, but a rigorous statistical assessment of such a link must await the formulation of a new conceptual (and thus mathematical) model of the relationship between orogenic activity and evolutionary turnover.

In addition, the fact that some models were good (or poor) models for Ordovician turnover dynamics does not necessarily imply that they will be equally good (or poor) at the Phanerozoic scale. If, for instance, diversity-dependent effects are transient at the Phanerozoic scale, dominating origination during the Ordovician but obscured by other factors during most other times, diversity-dependence may not provide a good model for Phanerozoic origination patterns as a whole. Nevertheless, the present results have important implications for Phanerozoic-scale diversity-dependent hypotheses. A major part of the transition from the Cambrian Fauna to the Paleozoic Fauna occurred during the Ordovician, so, had there been little support for diversity-dependence during this period, its adequacy as an explanation for the major faunal transitions of the Phanerozoic (*sensu* Sepkoski 1979, 1984) would have been undermined.

Conclusions

The evidence for diversity-dependent origination provided by the synthetic analysis supports the hypothesis that origination probabilities were damped by increasing diversity during the Ordovician Radiation (Table 5). Moreover, the fact that evidence for this effect was stronger for trilobites than for articulated brachiopods or bivalves is consistent with the hypothesis that differential diversity-dependence in origination contributed to decreases

in the relative diversity of trilobites during the Ordovician. Sensitivity of support for diversity-dependence in gastropods to uncertainty in the Ordovician diversity trajectory, however, makes an assessment of the strength of evidence for diversity-dependent origination in gastropods problematic. By contrast, support for productivity-mediated effects of increasing tectonism was weak (Table 5). This indicates that, if increasing tectonic activity influenced origination patterns during the Ordovician, it did so either weakly or in a manner different from that implied by a global, productivity-mediated effect. Constant origination is also a poor model for the Ordovician faunal transitions in the aggregate (Table 5), but model rankings for individual higher taxa suggest that this is primarily due to the fact that it poorly characterizes trilobite origination patterns (Table 5). Thus, constant origination, though it is never clearly the best-supported model, is a plausible cause of increases in articulated brachiopod diversity, relative to bivalve and gastropod mollusks.

In contrast to origination, overwhelming support for the phenomenological model in the synthetic analysis indicates that the alternative causal models do not characterize extinction patterns well. Other workers have also found origination patterns to be more tractable than extinction patterns (e.g., Gilinsky and Bambach 1987; Sepkoski 1991). One interpretation of this result is that the causes of extinction patterns are more variable over long timescales, so explanatory models incorporating just one or two factors, like those used here, poorly characterize the trends. Alternatively, the major factor(s) driving extinction patterns may simply have yet to be identified. Support for diversity-dependent origination, but not extinction, is particularly consistent with niche-incumbency mechanisms of diversity-dependence (Walker and Valentine 1984; Rosenzweig and McCord 1991; Alroy 1998).

Most previous approaches to evaluating the causes of diversification patterns have involved fitting a single model to fossil data, and evaluation of the effects of sampling have been ad hoc (e.g., Sepkoski 1979; Maurer 1989; Benton 1995; Alroy 1998). Such approaches have yielded important insights, but they have

limitations. For instance, a simple exponential diversification model may approximate Phanerozoic-scale fossil diversity dynamics, and this approximation may appear reasonable upon visual inspection (Benton 1995). However, is the explanation better or worse than a diversity-dependent model (i.e., does diversity-dependence explain enough additional variation to justify the extra parameter)? Is the good fit due to exponential diversification, or to long-term increases in the quality and completeness of the fossil record? To what extent is good fit of a diversity-dependent origination model a reflection of statistical covariances among origination and diversity estimates, rather than a real biological dependence? Prior approaches have allowed only provisional approaches to these questions.

By contrast, the analyses presented herein utilize a method by which alternative models of origination and extinction can be calibrated and quantitatively compared. They account for sampling effects through the simultaneous estimation of probabilities of preservation and sampling (Nichols and Pollock 1983; Nichols et al. 1986; Connolly and Miller 2001a,b). Given the growing emphasis on process-oriented explanations of long-term macroevolutionary patterns (e.g., Erwin 1993; Vermeij 1995; Miller and Mao 1998), and increasing recognition of the need to account for taphonomic effects in estimates of macroevolutionary rates (e.g., Alroy 1998; Foote 2000), we believe that this approach has an important place in the next generation of paleobiological models.

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