Invited reply

Problems detecting density-dependent diversification on phylogenies: reply to Bokma

1. INTRODUCTION

Time-calibrated molecular phylogenies of extant taxa can provide a useful window into the tempo and mode of species diversification. One of the most interesting results to emerge from this research is the widely observed tendency for the rates of species diversification to decline through time during evolutionary radiations (McPeck 2008; Phillimore & Price 2008). These temporal declines in diversification are predicted by ‘niche-filling’ models of diversification, whereby the probability of speciation or lineage persistence is the highest when the number of occupied niches is the lowest (Nee *et al.* 1992; Phillimore & Price 2008), a possibility that has garnered wide interest because of its implied links between ecological and evolutionary processes. Under the niche-filling scenario, the rates of diversification through time should be density dependent, i.e. the probability of speciation and/or extinction should vary inversely with the number of closely related species within the same broadly circumscribed biogeographic region.

In a recent paper, we explored the tempo of species diversification through time in North American wood warblers (Rabosky & Lovette 2008a). Our research was motivated by a simple question: are patterns of lineage accumulation through time in wood warblers more consistent with density-dependent speciation than with other processes that can cause real or apparent temporal declines in the rate of lineage accumulation? To distinguish between density-dependent diversification and alternative processes that could generate real or apparent temporal declines in the rate of diversification, we contrasted the fit of density-dependent and time-varying speciation models to an ultrametric molecular phylogeny for North American wood warblers. We found that a model of density-dependent speciation fits the data much better than a model where speciation rates decline linearly through time. Importantly, our results also showed that incomplete taxon sampling, with or without linear declines in the speciation rate, could not generate a pattern of speciation through time consistent with the wood warbler data. As we stated in our conclusions, our results are certainly not the only possible explanation for the observed patterns, but they provide robust evidence against two alternative explanations for them.

2. THE PROBLEM OF EXTINCTION?

Bokma (2008) commented on our paper and questioned our conclusions. The central criticism he raised relates to a difficulty that has also been recognized, explicitly or

implicitly, by virtually all researchers who use molecular phylogenies to reconstruct the rates of species diversification (e.g. Nee *et al.* 1994). This problem is that a molecular phylogeny based only on extant taxa does not provide information about species that have gone extinct. Bokma suggests that our conclusions are problematic because we modelled the speciation rate (λ) as a function of the number of species present at some point in time t in the reconstructed phylogeny (N_t), rather than as a function of the true (unknown) number of species (n_t). He argues that the number of species in the reconstructed phylogeny is probably a poor predictor of true species diversity when extinction is present.

There is always merit in making models conform better to biological reality, but in this case there are reasons to believe that our conclusions are unaffected by extinction. We neglected extinction in part because high background extinction rates will reduce the signature of temporal declines in the speciation rate that we observed in the wood warbler tree (Rabosky & Lovette 2008b). Because extinction causes an apparent excess of recently diverged lineages in a lineage-through-time (LTT) plot, it is difficult to see the signature of an ‘early burst’ of diversification in a reconstructed phylogeny if extinction rates have been high. To illustrate this phenomenon, we generated the expected LTT plots for diversification processes undergoing an identical 20-fold exponential decline in the net rate of diversification ($\lambda - \mu$) under five different relative extinction ratios (ϵ), where the relative extinction ratio is simply the ratio of extinction to speciation (figure 1). The concave-down curve generated under $\epsilon = 0$ shows a classic temporal decline in diversification (solid line). However, as the magnitude of ϵ increases towards $\epsilon = 0.99$, the signature of early, rapid speciation becomes more difficult to detect. Between $\epsilon = 0.75$ and $\epsilon = 0.99$, it becomes very difficult to detect a temporal decline in the rate of diversification, despite the severe 20-fold decline in $(\lambda - \mu)$ used to generate the curve. Thus, the pronounced decline in the rate of lineage accumulation through time in wood warblers may constitute evidence for the low rates of background extinction. We provided direct evidence for this interpretation in a related study in which we estimated extinction rates in this same group of wood warblers under a model of exponentially declining speciation rates with non-zero extinction; as expected, extinction rates were estimated as approximately zero (Rabosky & Lovette 2008b: fig. 3; table 2).

Even if we assume that wood warbler extinction rates were moderate or high, it is still true that the number of lineages in a reconstructed phylogeny is a reasonable predictor of the true species richness. Figure 2 shows the

The accompanying comment can be viewed on page 993 or at <http://dx.doi.org/doi:10.1098/rspb.2008.1249>.

Figure 1. Expected LTT curves for clades growing under identical 20-fold declines in the net diversification rate but with different relative extinction ratios. When the relative extinction rate is high, the signal of early, rapid diversification is reduced or even eliminated from the LTT plot. Curves are theoretical expectations from Nee *et al.* (1994) (eqn (30)). Dashed line is expected LTT plot under constant-rate pure birth process ($\epsilon = 0$). For each value of ϵ , we found parameters that would result in (i) an identical decline in the net diversification rate, and (ii) a total of surviving 80 lineages after $t = 1.0$ time units. Values of ϵ are 0, 0.25, 0.50, 0.75 and 0.99 (left to right). The net diversification rate was modelled as $r(t) = \lambda_0 e^{-\epsilon t} (1 - \epsilon)$.

correlation between N_t and n_t for the phylogenies of the same size as the wood warbler tree simulated under a range of ϵ -values. The correlation remains high for even moderate levels of background extinction, suggesting that in these cases it is acceptable to use N_t as a proxy for n_t . Even when we consider only the earliest diverging subset of lineages (figure 2b), the correlation between N_t and n_t remains high across a range of relative extinction rates.

Regardless, it is clear that when extinction rates are high, it should be difficult to detect a signal of density-dependent diversification, because extinction will (i) reduce the signature of early, rapid lineage accumulation, and (ii) weaken the correlation between N_t and n_t . There is no evidence that extinction can create the spurious impression of density-dependent diversification when such density dependence has not occurred. Yet, our results clearly favour a density-dependent diversification scenario over the alternatives we considered. Comparisons of fitted models and simulation results seem to reject the possibility that these patterns result from a linear change in the speciation rate through time, incomplete taxon sampling or some combination thereof.

3. PARAMETER ESTIMATES

Bokma is correct in pointing out that confidence limits on λ may decrease if μ is not included in the model. However, if μ has in fact been low—as the evidence summarized above suggests—then this is likely to be a trivial change. We disagree that there is anything ‘artificial’ about this: confidence intervals on parameters estimated under any model may change as parameters are added to the model. For example, the birth–death model used in our study (and many others) assumes that speciation and extinction rates do not vary among lineages across a phylogenetic

Figure 2. (a) Spearman correlations between the number of lineages in the LTT plot (N_t) and the true number of lineages in existence, including those that failed to survive to the present (n_t), as a function of the relative extinction ratio ϵ . For each ϵ , 1000 phylogenies of $n = 25$ species were simulated under a constant-rate birth–death model; shown are the medians and 2.5 and 97.5% quantiles of the distribution of correlation coefficients. (b) Correlation between N_t and n_t , considering only the initial 13 lineages in the LTT plot. Although the correlation is weaker during the early history of the phylogeny, N_t is still a reasonable predictor of n_t across a wide range of ϵ .

tree; relaxing this (unrealistic) assumption would almost certainly change confidence limits.

4. CONCLUDING REMARKS

In summary, we do not claim that density dependence is the only possible explanation for these results. A number of alternative explanations for the widespread phenomenon of ‘explosive early’ diversification should be investigated, including the possible role of among-lineage variation in diversification rates and the extent to which inadequate models of molecular evolution might contribute to the pattern. However, while we agree with many of Bokma’s points, we feel that the evidence in favour of density-dependent speciation cannot be dismissed out of hand merely because our underlying models seem simplistic. Indeed, given the potential effects of extinction on lineage accumulation curves, it is all the more remarkable that both simulations and modelling results favour the density-dependent diversification scenario over the alternatives we consider. As Bokma notes, the palaeontological literature overwhelmingly suggests that extinction rates have been high relative to speciation rates (e.g. Stanley 1979; Alroy 1996). Why, then, do so many species-level radiations appear to show evidence for low extinction? As we suggested in a previous paper (Rabosky & Lovette 2008b), this might reflect non-random extinction, in which case fossil-derived estimates of extinction might not apply to the phylogenies of extant taxa. It is also possible that the perception of low

extinction stems from a failure of the birth–death model to adequately capture the major features of the diversification process. For example, McPeck (2008) has shown that the effects of extinction on the patterns of lineage accumulation through time can vary dramatically if extinction is modelled as a function of population size. Such ecologically explicit models of speciation and extinction may potentially refine and even challenge our understanding of diversification in wood warblers and other taxa.

Daniel L. Rabosky^{1,2,*} and Irby J. Lovette^{1,2}

¹*Department of Ecology and Evolutionary Biology,
Cornell University, Ithaca, NY 14853, USA*

²*Cornell Laboratory of Ornithology,
159 Sapsucker Woods Road, Ithaca, NY 14850, USA*

*Author for correspondence (dlr32@cornell.edu).

REFERENCES

- Alroy, J. 1996 Constant extinction, constrained diversification, and uncoordinated stasis in North American mammals. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **127**, 285–311. (doi:10.1016/S0031-0182(96)00100-9)
- Bokma, F. 2008 Problems detecting density-dependent diversification on phylogenies. *Proc. R. Soc. B* **993**–994. (doi:10.1098/rspb.2008.1249)
- McPeck, M. A. 2008 The ecological dynamics of clade diversification and community assembly. *Am. Nat.* **172**, E270–E284. (doi:10.1086/593137)
- Nee, S., Mooers, A. & Harvey, P. H. 1992 Tempo and mode of evolution revealed from molecular phylogenies. *Proc. Natl Acad. Sci. USA* **89**, 8322–8326. (doi:10.1073/pnas.89.17.8322)
- Nee, S., May, R. M. & Harvey, P. H. 1994 The reconstructed evolutionary process. *Phil. Trans. R. Soc. B* **344**, 305–311. (doi:10.1098/rstb.1994.0068)
- Phillimore, A. B. & Price, T. D. 2008 Density-dependent cladogenesis in birds. *PLOS Biol.* **6**, e71. (doi:10.1371/journal.pbio.0060071)
- Rabosky, D. L. & Lovette, I. J. 2008a Density-dependent diversification in North American wood warblers. *Proc. R. Soc. B* **275**, 2363–2371. (doi:10.1098/rspb.2008.0630)
- Rabosky, D. L. & Lovette, I. J. 2008b Explosive evolutionary radiations: increasing extinction or decreasing speciation through time? *Evolution* **62**, 1866–1875. (doi:10.1111/j.1558-5646.2008.00409.x)
- Stanley, S. M. 1979 *Macroevolution: pattern and process*. San Francisco, CA: Freeman.