

## Reply to Foster et al.: Using a forest to measure trees: Determining which vital rates are responding to climate change

In response to our paper (1) showing a recent increase in forest-biomass growth in an eastern United States forest, Foster et al. (2) emphasize the importance of considering biomass loss caused by mortality when inferring biomass rate changes and modeling uncertainty in these analyses. Although decreases in biomass loss caused by mortality could lead to an observed increase in biomass, we believe that growth and not mortality is the critical driver of this documented biomass rate. Fig. 1 shows that, although changes in both net primary productivity (NPP) and mortality could combine to create the observed mean increase in stand growth in ref. 1, mortality is an unlikely contributor for three primary reasons.

First, changes in rates of biomass accumulation were observed across all stand ages, regardless of species composition; the many mechanisms that drive tree mortality are unlikely to combine to create such a broad decrease. Mortality in forests is caused by many exogenous mechanisms, such as storms and pathogens (2), as well as endogenous mechanisms, such as competition for light and nutrients (thinning) and death of large trees (gap-phase dynamics) that change over succession. Growth, however, is a single mechanism common to all stands.

Second, mortality is a highly nonlinear process, and stand mortality loss is near an optimum ( $\sim 0.98$  survival rate). A decrease in mortality from 0.021 to 0.011 as posited by ref. 2 corresponds to a halving of the loss of biomass from forest stands. This would mark an extreme change in tree longevity and successional turnover. Furthermore, any decrease in mean mortality would lead to a decrease in variance around that mean, which is not represented in ref. 2. (3). Climate change is thought to in-

crease variance of environmental conditions, which subsequently would increase mean mortality, leading to lower annual biomass accumulation (3). The observed trends of increased CO<sub>2</sub>, mean annual temperatures, and growing season as documented in ref. 1, however, should lead to a systematic increase in NPP.

Third, uncertainty in NPP rates is easy to posit, because nutrient availability, species composition, stand age, etc. can all lead to changes in growth. Uncertainty in mortality, however, is difficult to quantify and is dependent on stochastic events that span broad spatial and temporal scales. Variance in mortality is best captured in the observed variance in rates (1) and not in positing a distributional form across stand ages. Fig. 2 shows how uncertainty in stand states does not greatly influence uncertainty in stand rates, which are insensitive to a wide range of parameter values. Growth is the likely mechanism driving recent biomass change in these forest stands, because it is the parsimonious explanation, has documented causes, and describes the full scope of the observed changes. Further work on these changes and any extrapolation of this pattern to other systems, however, certainly needs to take into account balances of mortality and growth, sources of uncertainty in each measurement, and effects of sampling from plots of various sizes over various time intervals.

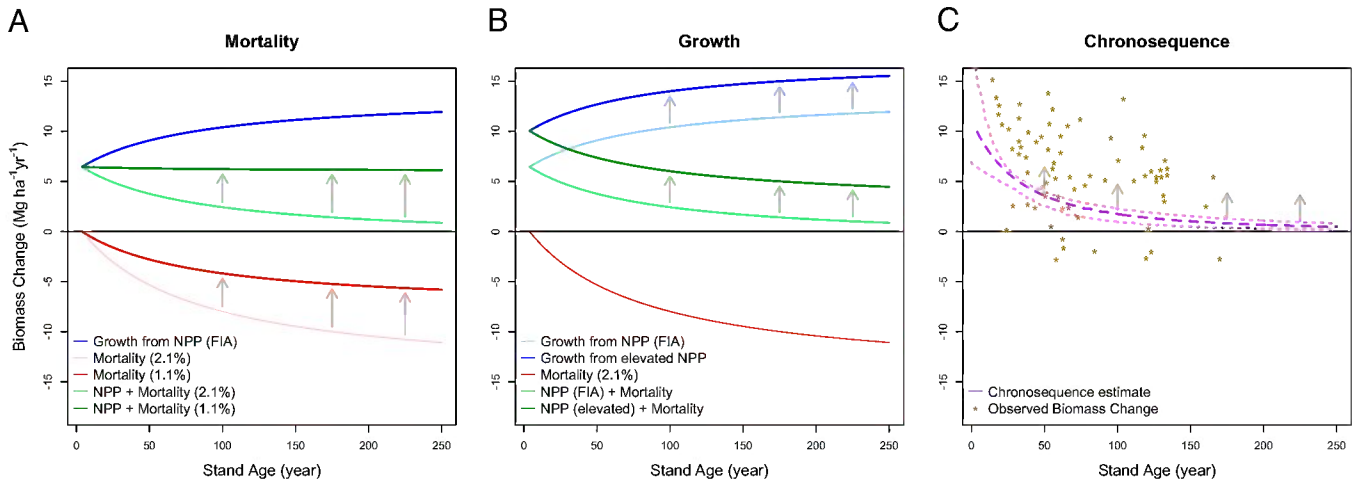
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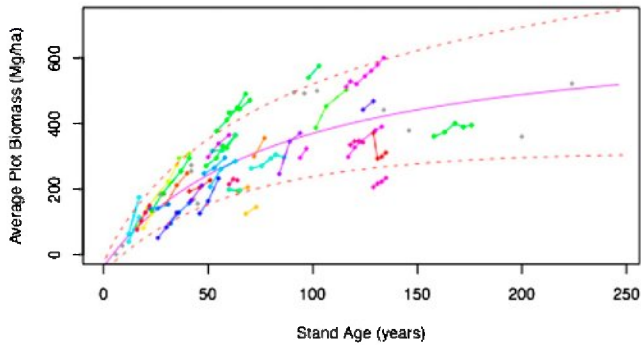
Author contributions: S.M.M. and G.G.P. designed research; S.M.M. performed research; S.M.M. analyzed data; and S.M.M., G.G.P., and D.R.M. wrote the paper.

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**Fig. 1.** Examining vital rates affecting biomass change. (A) Projected net annual biomass change with a 1% decrease in mean mortality rate as proposed in ref. 2. (B) Change with an increase in NPP of  $3.6 \text{ Mg}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$  as estimated from census-interval weighted mean difference in ref. 1. (C) Net annual biomass change estimated from the chronosequence-derived rate from ref. 1 with 95% confidence envelope and the observed rate changes from census data (gold stars). Arrows in A and B show simulated increases in vital rates and growth rate responses. In C, arrows show how an increase in the chronosequence rate would match the observed rates. In young stands, a mortality rate of 0 cannot explain the high observed biomass rates. Lines in A and B were created using data from ref. 2.



**Fig. 2.** Plot biomass against stand age with census intervals shown and a confidence interval including two times the standard deviation of the data adjusted for age (methods in ref. 1). Clark et al. (4) correctly argue that inferences about differences in median values of the Monod fit need to incorporate uncertainty in the data. McMahon et al. (1) model uncertainty in the slope of the median line, and the slope is not sensitive to varying values of  $b_1$  and  $\theta$ .