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Population variance and stability: a response to Horwood

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Horwood raises some interesting points concerning the less-than-perfect relationship between deterministic stability and the dynamics of stochastic models. His discussion, however, concerns an issue that was only of secondary interest in my paper (Taylor 1992), and even then his results, in my opinion, are not greatly at odds with mine.

My principal question was whether, for at least some models, deterministic stability analysis is useful: whether it gives qualitative guidance as to the dynamics of the models even in stochastic environments. By far the most important use of stability analysis is simply the delineation of conditions under which systems are or are not stable. Since Horwood's analyses work only for stable systems, they simply cannot address the fundamental issue I examined, of whether this deterministic distinction is valid; indeed, they presuppose that it is.

The issue Horwood does address is whether, in deterministically stable systems, there is a correspondence between greater stability and lower variability. In Horwood's first model (equation 1), this correlation was found, while in the second (equation 5), the opposite was found: variability was proportional to stability. But in this latter model the 'noise' term is multiplied by the return time: rather than being found in an 'all else equal' comparison, a correlation between stability and variability is arbitrarily imposed.

Horwood mentions in passing the suggestion by Roughgarden (1975; also May 1976; Turelli 1977) that a less-stable system might average out fluctuations in carrying capacity, and therefore vary less than a more-stable system which would track the carrying capacity more closely. This effect apparently was present in my simulations: the minimum variability in the single-species model occurred not in the most stable system ($\lambda = 0$) but instead with moderately undercompensating systems (λ near 0.5; see my Fig. 8 and accompanying text). However, as stability decreased further (λ approached 1) this effect disappeared: variability increased, contrary to Roughgarden's result. Furthermore, the magnitude of the effect was negligible: differences in variability among systems with λ in the range 0–0.5 were so much less than the differences between them and unstable systems that in most of the figures in Taylor (1992) little if any difference is seen in the range

from $\lambda = -0.5$ to $\lambda = 0.5$. Finally, it should be noted that this result pertains only to systems with exponential damping; with damped oscillations stability and the population variance are negatively related (Roughgarden 1975), as in my simulations.

Horwood's last example, an age-structured fisheries model, also shows a partial discrepancy between variability and stability. Using the coefficient of variation as the more appropriate measure of variability, Horwood's Fig. 1 shows that the CV increases monotonically with fishing intensity, F , but stability is greatest at intermediate F . Therefore, stability and variability are inversely related when F is large, but positively related when F is small. The changes in both variability and stability in this range of F , however, are relatively modest compared to those at large F , so again we are dealing with relatively small discrepancies in details superimposed on a general concordance between stability analysis and stochastic dynamics. We also are given too little explanation of these results, in the original papers (Horwood & Shepherd 1981; Horwood 1983) as well as in Horwood (1993), to determine whether this is an instance of a general phenomenon or simply a peculiarity of this model.

Finally, I agree that my conclusions 'cannot be taken as [complete] generalities.' The word 'some' is in the title of my paper (Taylor 1992) precisely to make this clear. Indeed a counter-example more compelling than any of Horwood's comes from a body of theory of considerable interest to me: in predator–prey metapopulation models, stability analysis is of essentially no value (Reeve 1988). I do believe, however, that good qualitative correspondence between deterministic stability analysis and stochastic dynamics would be found in most if not all simple one- or two-species discrete-time models such as I studied. Given the importance of such models in general ecological theory (as distinct from more system- or purpose-specific models such as Horwood's fisheries model), confirmation of the validity of deterministic analysis of these models may be of limited generality but certainly is not of trivial significance.

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