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On trade-offs, elasticities and the comparative method: a reply to Shea, Rees & Wood

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Shea, Rees & Wood (1994) apply null models and an analytical argument to test our suggestion (Silvertown *et al.* 1993) that correlations among elasticities reflect evolutionary trade-offs between plant life history variables. We welcome such scrutiny and accept their analytical proof that trade-offs between matrix elements do not necessarily alter the elasticities of the elements and therefore trade-offs cannot be detected in this way. Clearly, our original suggestion was simplistic, but we mantain that the relationships between elasticities are worth further investigation.

Shea *et al.* (1994) found complex, curvilinear relationships between elasticities derived from artificially constructed matrices. We argue that these patterns were dependent upon two assumptions of the null models; allowing λ to vary and using an exponential function in the trade-off between reproduction & survival. While it is true that λ varied between species in our original dataset, the ideal model designed to test the relationship between elasticities at equilibrium should constrain $\lambda = 1$.

In order to test whether Shea, Rees & Wood's results were a consequence of the exponential function in their model and of not constraining λ to a fixed value, we repeated their exercise using the smallest figures of their Appendix I with further decreases in some of the elements to yield $\lambda = 1$. We then simulated a trade-off between fecundity (f) and survival in the last category following their stated rules ($a_{15} = 0.6f$; $a_{25} = 0.4f$) and found that keeping λ constant required the linear functions $a_{15} = 3.14 - 4.209a_{55}$ and $a_{25} = 1.711 - 2.293a_{55}$. Similarly, elasticity analysis on matrices determined in this way showed that the relationships between composite elasticities $E1-E6$ were all linear, not curvilinear or 'complex' as in Shea *et al.*'s model. The reason for this linear behaviour is that, in a linear matrix model, a decrease in the probability of survival of reproductive individuals must be compensated by a proportional increase in their fecundity. This shows that the patterns Shea *et al.* found were model-dependent and that they were a consequence of their unrealistic assumption of an exponential trade-off function which changes λ systematically from a low value when survival is low but fecundity is high, to a high value when the reverse is true.

When we simulated trade-offs between elements in different columns of the projection matrix (e.g. early vs. late survival) complex patterns of the kind found by Shea *et al.* were obtained. This reflects the interdependence of matrix elements. The point we wish to draw from this is that, although in their simplest form elasticities cannot be interpreted in terms of trade-offs, disentangling direct from indirect effects may still allow the use of elasticities to draw conclusions on possible trade-offs. Indeed, P. van Tienderen (unpublished manuscript) has explicitly derived formulas to separate the direct from the indirect effects in what he terms 'integrated elasticities' and 'integrated sensitivities'. The integrated elasticity (and the integrated sensitivity) of a matrix element is calculated using a linear combination of the slope relating that particular element to each other element, weighted by their respective elasticities (or sensitivities). Determining the relationships among matrix elements involves measuring trade-offs. According to this view, sensitivities and elasticities still have a role to play in the interpretation of trade-offs among life cycle components.

Acknowledgements

References

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