

However, the two examples they cited as doing this [6,7] do not do so. Indeed, the study by Sears and Chesson is a decomposition of mean plant performance into components due to the environment, that due to competition, as well as the covariation between them. This is in no sense a 'binary' approach and is indeed a fully quantitative alternative.

One of the major problems with the concept of importance as it is frequently used is that the notion of 'important' is highly dependent on the particular question asked. In many cases the question asked may indeed be a binary one. For example, competition leading to density-dependence may explain only a small fraction of the variation in fitness; if, however, this results in density-dependent population regulation, the outcome is the difference between an equilibrium and a population that grows without bound or declines to extinction, i.e. a binary outcome. The literature on population and evolutionary dynamics contains many examples where the prediction of theory is a condition, not a measure.

In the plant ecology literature the difference between 'importance' and 'intensity' of competition is made, in part, because this is said to allow distinction between the theories of Grime and Tilman [8,9]. Close examination of the literature reveals that this is a non-quantitatively derived distinction made by Grace [8,9], and not in the primary papers by Grime or Tilman. Indeed this is acknowledged by Grace [8]. The basis for the distinction is therefore without theoretical justification. Plant community ecology has been dominated by this debate for over 20 years, with alarming

lack of progress. We believe this is in part a consequence of the reliance on metrics derived from heuristics, rather than close consideration of theory, and similar arguments to the one we outline above will very likely apply to other indices. We strongly recommend that other areas of ecology do not go down the same route.

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Letters Response

Conceptualizing importance: response to Freckleton and Rees

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Freckleton and Rees (hereafter F&R) [1] make three major critical points on our recent paper in *TREE* [2]: (i) we highlight C_{imp} , which is a flawed index of competition; (ii) we incorrectly dismiss previous measures of competition as 'binary tests'; (iii) the question of 'importance' of competition depends on the context in which it is being examined, and the measure used should be driven by the question asked.

We disagree. Our main focus is on the general concept of importance, and there is no 'special reference' to C_{imp} . It is used here just as a case of an index that has gained some popularity, but shares space with other ways of quantifying the importance of competition. In addition we have previously addressed the majority of critical arguments concerning the use of C_{imp} [3]. Only a very

few new comments have been added by F&R, which we address below.

(i) F&R base their criticism on the assumption 'that plants subject to competition are much smaller than those grown alone'. This is not true along the full length of a productivity gradient – plants subject to competition can be comparable in size with those grown alone at less productive sites, e.g. on poor soils [4] or in alpine environments [5,6]. C_{imp} is designed precisely to track this trend along the gradient.

Besides, 'where conditions are so poor that plants cannot grow' means that plants cannot take up resources, no pre-emption is possible and thus competition intensity equals zero. Non-existent processes cannot have any importance, and consequently C_{imp} equals zero. Finally, our citing of Freckleton *et al.* (2009) refers only to the mathematical link between the C_{imp} and population growth model derived by

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them, not to their interpretation. C_{imp} and similar indices measure the net outcome of multiple effects (whether positive and negative) and precisely for this reason are useful and informative on productivity gradients.

(ii) We do not dismiss these measures. As F&R write, 'In many cases the question asked may indeed be a binary one'. Obviously, these are the areas of application of the 'other', population dynamics measures designed to assess whether competition will lead to exclusion. Accordingly, we respect the work of Sears and Chesson [7] as a mathematically elegant analysis of the consequences of competition between two populations. We did not dismiss it, but show it as one of the ways to deal with the importance of competition. However, this approach, although successful where it was used, does not help us to understand changes in importance along spatial (productivity) gradients. It does not rival other approaches reviewed in our paper (including C_{imp}), but rather complements them. In addition, our discussion of the possible measures used (Box 1 in [2]) recognizes the possibility of multiple approaches to the measurement of importance.

(iii) We propose extension of the formalized importance concept precisely to account for these sorts of contexts. Ecological effects can be quantified in various ways and indices continue to be frequently used. What we advocate is the enrichment of our approaches to conceptualize and measure ecological effects by having in mind the fact that multiple effects and interactions operate simultaneously.

The distinctions between the theories of Tilman and Grime are evident without using the formalized concept of importance but it certainly helps to reconcile these two theories. Further, the formalized concept of importance as advanced in our *TREE* article [2] is based on the work of Welden and Slauson [8], not the work of Grace [9,10].

Finally, although we see no reason to refrain from using 'heuristic indices', we point out that our paper in *TREE* is not written to support any special type of quantitative tool. Instead, we strongly recommend conceptualizing and measuring ecological effects in any appropriate way but taking into account the context of simultaneously operating multiple effects and interactions.

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Book Review

A practical guide to merging behavior and conservation

A Primer of Conservation Behavior by Daniel T. Blumstein and Esteban Fernández-Juricic, Sinauer Press, 2010. US\$34.95, pbk (224 pages), ISBN 978 0 87893 401 0.

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Like Emperor Nero fiddling while Rome burns, behavioral ecologists have been accused of focusing predominantly on theoretical concerns without contributing substantially to scientific endeavors addressing the current biodiversity crisis [1]. Conservation behavior, the application of behavioral knowledge to conservation and management, seeks to bridge the gap between the basic and applied scientific communities. Over the past decade,

however, the number of research studies focusing on conservation behavior has increased at a disappointingly slow rate [2]. The recently published *A Primer of Conservation Behavior* is the first attempt at a practical guide to integrating behavioral theory into conservation biology and wildlife management. As such, it has the potential to inspire a new generation of scientists to participate in this emerging field.

The authors are well-known leaders in conservation behavior and have had central roles in the development of this interdisciplinary topic. The book is organized into 12 chapters primarily based on subthemes of behavioral ecology and animal behavior (e.g. foraging theory, mate choice,

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