

## Comment on the article “On testing temporal niche differentiation in carabid beetles” by M. Loreau\*

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The article I read at the 27th Phylogenetic Symposium on “Competition and Niche Theory” in 1984 at the University of Bielefeld (Den Boer 1985) was meant as a warning against the common tendency to assume that phenomena, which are connected with the co-occurrences of species, are dominated in some way by interspecific competition. However, effective interspecific competition cannot be simply inferred from differences in size, in feeding habits, in timing of breeding seasons, etc, between co-occurring species. One will have to perform sophisticated experiments to actually show that the presence of species A significantly puts species B at a disadvantage (see e.g. Connell 1975; Birch 1979). Phenomena that can only indirectly be related to possible competition, such as differences in breeding season, may have diverse other explanations. The paper criticized by Loreau was a trial to show that these phenomena usually can be considered very well as the kind of common differences that can be expected to exist between different species (see also Den Boer 1980). Hence, I did not claim that interspecific competition should be rejected as a factor explaining community structure, as is suggested by Loreau, but I concluded that there are no compelling reasons to accept interspecific competition as such a factor.

The model I used to demonstrate that the overlap in breeding seasons among co-occurring carabid species does not show remarkable features was based at the same reasoning as the permutation test introduced by Reddingius & Den Boer (1989): as a special case of a Mann-Whitney test the mean overlap among a number of carabid species that coexist at the same site is compared with 100 or 200 expected values of mean overlap that are derived from that number of samples (of the same size) of the breeding seasons of arbitrarily chosen, non-coexisting carabid species abundantly occurring in our area. As the significant parts of reproductive cycles of the 68 carabid species in this sample space can be ranked as a continuous sequence from a very early start (in March) until a late one (in September–October) with a step-size of not more than one or two weeks (see Den Boer 1985: Fig. 5), among randomly chosen species very high overlap values may occur, which should effectively contrast with the low values that might be expected for co-occurring species under the competition hypothesis. Especially if co-occurring species as a rule would

indeed minimize the amount of overlap, dissociation of the species from their sites and thus from potential competitors, as applied in this test, would work well, whether the exact timing of the breeding seasons of most species is already affected by interspecific competition, or not, thus contradicting the suggestions of Loreau.

To estimate the power of this test we should be able to dispose of sound estimates of the amount of overlap under the competition hypothesis, so that the chance of a type II error (wrongly accepting the null hypothesis) can reliably be established. As far as I know, reliable estimates for a competition hypothesis are not available. Therefore, I invite Loreau to convince me that there is such a theoretically acceptable overlap value that should be taken as the base for an alternative hypothesis. The ad hoc value of 50%, used by Loreau, is unacceptable for that, of course, because it is even higher than the mean overlap in a number of “null assemblages” of each size; see Den Boer, 1985: Table 1). Therefore, his discussions on the power of my test, as far as connected with that value, do not contribute to removal of the controversy. A value of zero overlap might have been more appropriate, I suppose; the more so, because it would have given my test the maximally possible power. But, of course, competition need not merely result in situations that extreme. Thus, for the time being we have no base to judge the power of my test.

The formula (1) for mean overlap, used throughout the paper of Loreau, is not “strictly equivalent” with mine when applied to real breeding seasons of existing carabid species. In my formula the mean amount of overlap is weighed against the mean length of the reproduction periods in the species pairs concerned, whereas Loreau weighted against the number of species pairs. Allowing for the lengths of reproduction periods was necessary because significant breeding seasons of our carabid species vary between 8 and 29 weeks, and such differences highly influence the overlap values. Therefore, the derivations of Loreau from his formula cannot be applied to my estimates of expected overlap under the null hypothesis, let alone that his considerations on the power of my test would apply. This is clearly illustrated by the fact that in the overlap formulas (6) and (7) number of species ( $n$ ) and number of sites ( $m$ ) are the only variables, by which the problem in question, the timing of breeding seasons, has been worked out completely. By selecting such special cases we cannot make science.

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I also refute the claim of Loreau that my test would not allow  $P$  to lie below the critical level of 0.05: mean overlap would significantly deviate from the expected value under the null hypothesis (between brackets for forest species only), if it is below 22% (25%) for 6 co-occurring species, <28% (31%) for 9 species, <29% (33%) for 12 co-occurring species, <31% (35%) for 15 species, and <32% for 18 co-occurring species. Such values are not unreasonable if species would indeed significantly avoid each other in time. For instance, a value lower than 25% could be reached if the 6 species of dry forest *Pterostichus oblongopunctatus*, *Notiophilus rufipes*, *Abax ater*, *Amara brunnea*, *Carabus problematicus* and *Leistus rufomarginatus* would coexist: mean overlap would be 23%, which corresponds with a  $P$ -value of 0.015 (3/201).

In the alternative test of Loreau as a rough measure of the “quantitative importance” of a species is used the total 4-year catch of that species in pitfalls,  $N$  (see Loreau 1986). However, summed pitfall-catches of different carabid species over one or more years are not quantitatively comparable (Den Boer 1986a), because there are differences in catch efficiency (Luff 1975), and important differences in activity patterns, in area of activity, etc. between species. For instance, the individual area of activity of carabid beetles highly depends on body size, varying between 0.02 ha for small beetles to more than 200 ha for big ones (e.g. *Carabus problematicus*: Den Boer 1970). Also, many forest species are usually active on tree trunks (e.g. *Agonum assimile*, *Carabus problematicus*), others pass the majority of the breeding season underground (e.g. females of *Abax ater*), or outside the forests (e.g. *Asaphidion flavipes*), etc., by which these are significantly underrepresented in pitfall catches in the forest. Moreover, a big carabid beetle, such as *Carabus problematicus* (25 mm), must have a many times greater “quantitative importance”, especially in competition, than a co-occurring small carabid beetle, such as *Notiophilus biguttatus* (5 mm). Therefore, including  $N$  as the “quantitative importance” of the species into the alternative hypothesis is a catastrophic methodological error that takes away any value for the present discussion.

Finally, I want to make a general remark on possible competition between carabid species. Nearly all carabid beetles are highly polyphagous, usually rather indiscriminately feeding on all kinds of arthropods, sometimes even taking snails and worms, and often consuming plant materials too (Hengeveld 1980). Moreover, the foraging behaviour of carabid beetles is simple, rigid, and far from “optimal” (Den Boer 1986b), making them ineffective competitors. Therefore, before modelling special biological effects from

sampling data, one should closely study the relevant behaviour of the animals concerned, or at least take into account data from literature on that (foraging) behaviour.

Summarizing, in spite of the paper of Loreau my model (Den Boer 1985) still tells us that the degree of overlap of coexisting carabid species does not show features that deviate from common differences between arbitrarily taken carabid species. Whether or not interspecific competition plays some part in the structuring of communities is beyond the present discussion, and asks for a different kind of – especially experimental – investigations.

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