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The role of soil community in plant population dynamics: is allelopathy a key component?

In his recent *TREE* news & comment, Watkinson[1] drew attention to the role of soil microorganisms in plant population dynamics. In particular, he reported on the dynamical framework for the inter-relations between the composition of plant and soil communities, proposed last year by Bever *et al.*[2] It is worth adding allelopathic interactions to this picture.

Allelopathy has been defined by Rice[3] as 'any direct or indirect harmful or beneficial effect by one plant (including microorganisms) on another through production of chemical compounds that escape into the environment'. If we apply this definition to Bever *et al.*'s framework for the feedback interaction between the soil community and two plant species, at least two further aspects come into play.

The first concerns the potential mechanisms for positive and negative feedbacks. We can hypothesize direct interactions, such as mycorrhizal systems, for positive feedback (the fungal symbiont allows plant species to explore more soil resources, thus augmenting the autotrophic community) and pathogens for negative feedback. But we can also hypothesize indirect interaction: the plant produces allelochemicals that are metabolized by soil microorganisms[4], leading to the release of compounds into the soil that might affect (positively or negatively) the plant species[5].

The second concerns the feedback model proposed by Bever *et al.*[2] The authors did not depict any direct or indirect interaction between the two plant species in their model. Nevertheless, one could add connections between them because of the potential occurrence of direct allelopathic interactions among plant species.

I agree with Watkinson's conclusion that 'the soil community is something that plant population biologists can no longer ignore' (if indeed they do), but they should not ignore allelopathy either.

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Reply from A.R. Watkinson

Pellisier is quite right to draw our attention to allelopathy as a potential component in the interaction between plants and microorganisms in the soil. But readers familiar with John Harper's strong views on the subject[1,2] will not be surprised to know that I, having been a student of his, am also rather sceptical about it. Unfortunately, Rice's definition quoted above is not at all helpful in defining allelopathy so broadly as any harmful or beneficial effect, direct or indirect, produced by a chemical that just happens to have escaped into the environment. That means that carbohydrate exudate from the root or the chemical compounds from a damaged piece of root are potential allelopathic agents. Most people would not accept that as allelopathy and indeed it is not what is studied.

Others restrict the definition of allelopathy to a form of interference competition by means of chemical compounds produced by one species that reduce the performance of other species[3]. Whether this interaction is direct or indirect is – I believe – critical, especially when one considers how allelochemicals may have evolved; I suspect that the direct interaction is relatively rare. Unfortunately it is impossible to say how rare or common a phenomenon it is, as many of the criticisms made by Harper[2] and others[4] of the methodologies involved in demonstrating allelopathy, and in particular the use of leachates, still apply. I would not dispute that chemical compounds (carbohydrates, proteins, phenols) from the roots of plants may have an impact on the microbial community and thus potentially on other plants as outlined in my original article. But are simple carbohydrates allelochemicals?

A computer literature survey (BIDS) of references to allelopathy in the past 10 years revealed that the subject barely merits a mention in the mainstream ecological literature: e.g. *American Naturalist* (0), *Journal of Ecology* (1), *Oikos* (1), *Ecology* (6), *Oecologia* (10). While agronomists, weed scientists and foresters clearly have more time for the concept, most of the 455 references to allelopathy are in the specialist *Journal of Chemical Ecology* (109) and *Phytochemistry* (23). There remain few attempts to relate the results of laboratory experiments to field situations.

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Reply from J. Bever, K.M. Westover and J. Antonovics

Watkinson[1] and Pellissier provide valuable perspectives on our model of the impact of the soil community on plant population dynamics[2]. The routes for such feedback can indeed be quite complex. In our work within a grassland in North Carolina, USA, we found that the accumulation of host-specific pathogens from the genus *Pythium* plays an important role in generating the negative feedbacks on plant growth that are common within the system[3,4]. However, we have also found evidence that host-specific shifts in the composition of the community of mycorrhizal fungi[5] and of the community of rhizosphere bacteria[6] can also contribute to the observed negative feedbacks. It seems quite possible that these soil organisms are responding to differences in host secondary chemicals – both those within the root and those released into the soil – as suggested by Pellissier.

Pellissier also observes that we hadn't included direct interactions between the two plant species in our model. While such effects were not explicitly included in our simple model, in analyzing the influence of soil community changes we implicitly assumed that the plants directly compete and that their competitive ability was equivalent. As Pellissier points out, explicit inclusion of the wide range of potential direct effects between the plants may alter the outcome of our model. We are in the midst of evaluating these possibilities.

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Quantifying brain–behavior relations in cetaceans and primates

In their recent *TREE* review, Connor *et al.*[1] provide an excellent and thought-provoking comparison of behavioral ecological patterns between toothed whales (odontocetes) and terrestrial mammals, particularly primates. The authors end their review with a provocative call for efforts to quantify the relationship between behavioral ecology and brain size among odontocetes in a similar manner to Dunbar's analyses for primates[2,3]. Nevertheless, in doing so they leave the reader with the impression that these quantitative studies have not yet been attempted. There are two studies that do exemplify the very approach Connor *et al.* advocate. These studies provide quantitative support for the 'combination of convergence and novelty'[1] suggested by observational and qualitative comparisons of brain and behavior between odontocetes and primates.

First, there is a significant positive correlation between pod size and encephalization quotient (a measure of relative brain size taking into account brain–body allometry) among 21 odontocete species from all six odontocete families[4]. Therefore, the relationship between one measure of sociality (i.e. social group size and brain size) appears to be similar in primates and odontocetes.

Second, although there is a positive correlation between encephalization level and gestation length among primates[5], in an analysis using the same encephalization values for the 21 odontocete species already mentioned, there is no significant relationship between encephalization and gestation length among odontocetes[6]. Rather, body size accounts for more of the variation in gestation length than encephalization among odontocetes. Therefore, there is quantitative evidence for differences in brain and life history relationships across primates and odontocetes.

My point here is not to criticize Connor *et al.* but to strengthen and extend their emphasis on quantitative analyses of odontocete behavioral ecology by showing that these kinds of studies are already underway. It is, of course, important to continue to further these studies while moving towards formulating and testing hypotheses about the evolution of cetacean brain–behavioral relationships and its implications for general mammalian evolution.

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Reply from R.C. Connor *et al.*

Marino correctly points out that we overlooked her work relating brain and group size in odontocetes. This is an important subject, and worthy of study. However, there are problems with her analysis that prevent us from embracing her finding of a 'significant positive correlation between pod size and encephalization quotient among 21 odontocete species' as being equivalent to Dunbar's conclusions for primates[1].

The hypothesis in question holds that the size of the brain (or, more specifically, the neocortex) places a limit on the number of social relationships that an individual can handle simultaneously[1]. Individuals in Dunbar's primate 'groups' have their primary social relationships with each other and not individuals of other groups. Thus his 'group size' is very closely related to the mean number of social relationships of an individual. In contrast, the 'pod size' reported most often for odontocetes, and apparently used by Marino, is simply the number of individuals that are usually observed together at a given point in time. This may be very different from the number of social relationships of an individual for several reasons.

First, coastal bottlenose dolphins (*Tursiops* sp.), and probably many other cetaceans, live in fission–fusion societies in which the typical number of individuals found together (<10) does not reflect the size of the social network (>100) (Refs 2,3). If small-brained odontocetes such as *Inia*, *Platanista* and *Pontoporia* live in similar fission–fusion societies, then available 'pod size' data will significantly underestimate the number of social relationships individuals maintain.

Second, large groups of large-brained pelagic delphinids (e.g. *Lagenorhynchus*) might reflect nonsocial assemblages of smaller social units attracted to food sources or minimizing predation risk. Until these species are studied we simply do not know.

We conclude that while the number of social relationships maintained by individuals in a few large-brained, well studied odontocetes clearly rival or exceed nonhuman primates, a correlation between the number of social relationships individuals maintain and brain size among odontocetes has not been established.

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