

Putting 'red alerts' in an ecological and evolutionary context

Sir,

In a recent issue of *BioEssays* ("Plants on red alert: do insects pay attention?"), Schaefer and Rolshausen⁽¹⁾ review two hypotheses on the evolution of leaf colours and propose a different and, according to them, new hypothesis that they call "Defence Indication". We would like to point out (i) that there are some significant misunderstandings in their review and (ii) that the new hypothesis that they propose is not really new.

Schaefer and Rolshausen⁽¹⁾ start by stating that according to the Coevolution Theory^(2–4) leaf colour indicates plant fitness. In fact, the Coevolution Theory predicts a correlation between leaf colour and the *level of defensive commitment* of the tree—which may or may be not correlated with the fitness. This is a misunderstanding that we have already noted elsewhere⁽⁴⁾ but it is repeated again here. If the signal is costly then it is likely that leaf colour (and defences) are also correlated with tree vigour,⁽²⁾ but this is not necessary.^(3,4)

Schaefer and Rolshausen⁽¹⁾ go on suggesting something that they believe is new: "we hypothesize that insects avoid plants which are coloured by anthocyanins, because this colouration indicates the presence of defensive compounds". This statement is presented as a novel idea and against the Coevolution Theory, but in fact it is the key component of the Coevolution Theory.^(2–4) We can't see how, by any means, it can be presented as an argument against it.

According to Schaefer and Rolshausen,⁽¹⁾ however, autumn colours evolve simply because they are adaptations against physical damage and not because (as the Coevolution Theory suggests) they are warning signals towards insects. But then Schaefer and Rolshausen's "new" hypothesis is little more than the idea that leaf colours protect against physical damage (the Screening Theory) put forward in the late 19th century⁽⁵⁾ and revived recently by physiological studies.^(6,7)

They do acknowledge that insects may avoid bright trees and so avoid well-defended trees,⁽⁸⁾ but they say that this has no influence on plant evolution (whereas according to the Coevolution Theory, choosy insects are the driving force of colour intensification in signalling species, and the Screening Theory makes no specific prediction about insect preference). Of course this makes sense only if insects have no impact on the tree's fitness. However, there is a whole literature of evidence suggesting that insects are important pests for trees.

Schaefer and Rolshausen⁽¹⁾ also confuse the distinction between short-term (physiological—immediate cause) and long-term (evolutionary—adaptive value) explanations of

autumn colours when they write that "if abruptly falling temperature in autumn decreases the number of aphids migrating to their hosts, the Coevolution Theory does not expect an increase in leaf colouration". This is misleading. Trees "decide" to change their leaf colour when autumn approaches according to sunlight and temperature, certainly not by detecting aphids arriving, as Schaefer and Rolshausen⁽¹⁾ seem to imply. But this is by no means in contrast with the Coevolution Theory, as insect life cycles depend on temperature and daylight as well: if autumn colours are late because of the temperature, then so typically will aphid migration.

The Coevolution Theory has been misinterpreted in Schaefer and Rolshausen's review.⁽¹⁾ Moreover, their "Defence Indication" hypothesis⁽¹⁾ is not a new adaptive explanation of autumn colours, but is the Screening Theory^(6,7) with a more specific prediction about cue-reading by insects. We have previously made clear that not all species of trees are likely to be engaged in a signalling interaction with their insect pests⁽⁴⁾ and, for some species of tree, there may well only be cue-reading by insects. The relative importance of the Coevolution Theory and of the Screening Theory is open to empirical test, however even if multiple selective pressures contribute to the evolution of autumn colours, mixing up the two theories does not help in our understanding of the subject.

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