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Letter to Editor

Modelling the evolution of leaf colouration with binary assumptions is barking up the wrong tree

Four hypotheses on the evolution of non-green leaf colouration have recently attracted heated debate. The first, termed as the coevolution hypothesis, posits that red and yellow autumnal leaves evolved as warning signals to insects. The hypothesis is restricted to senescent leaves, and its fundamental assumption is that warning signals enable well-defended plants to reduce their herbivore load, whereas insects use the chromatic information to locate suitable hosts more efficiently (Archetti, 2000; Hamilton and Brown, 2001). In contrast, the photoprotection hypothesis holds that red and yellow leaf pigments function primarily to assist leaf physiology (Gould, 2004). By protecting chloroplasts from the photoinhibitory and photo-oxidative effects of strong light in combination with low temperatures, such pigments are believed to improve nutrient resorption from senescing foliage. Photoprotection is particularly important at that stage because the breakdown of cellular structures to transfer nutrients to perennial tissues is a tightly regulated and metabolically energetic process (Schaefer and Wilkinson, 2004).

A third hypothesis, termed the "defence indication hypothesis", acknowledges that plants can use the same defence mechanisms against a variety of both abiotic and biotic stress factors. According to that hypothesis, non-green foliar pigments evolved in response to abiotic stressors such as strong light. Because some pigments are end products of biosynthetic pathways that also produce many defensive compounds, these pigments indicate that the pathway is activated, and they therefore correlate to elevated defensive strength (Schaefer and Rolshausen, 2006). The hypothesis provides a functional explanation for why insects might react to leaf colouration, without herbivory being the selective pressure causing it. Thus, the defence indication hypothesis does not assume a coevolutionary signalling system. Finally, Lev-Yadun et al. (2004) proposed the hypothesis that non-green leaf colouration undermines the camouflage of herbivorous insects. This hypothesis, unlike the others, does not make predictions on the relationship between leaf colouration and the levels of defensive compounds, although it does predict a negative correlation between herbivore load and non-green leaf colouration.

Owing to the many correlated biochemical changes that occur during leaf senescence, careful experiments are needed to evaluate which of these hypotheses best explains autumnal leaf colouration (Ougham et al., 2005). Several studies have shown a negative correlation between leaf colouration and abundance of herbivorous insects (e.g., Hagen et al., 2003), which is compatible with the predictions of ~~the~~ several hypotheses above. However, the only published experimental study found no evidence that herbivorous insects react to colour cues (Schaefer and Rolshausen, 2007).

In contrast to the putative defensive functions of non-green leaf pigments, Holopainen and Peltonen (2002) suggested that aphids might in fact *prefer* to infest brightly coloured senescent foliage. Autumn leaves, the authors suggested, would turn red or yellow to protect chloroplasts from photo-oxidative stress, yet these same pigments would also inadvertently signal to insects that high levels of nitrogen are being transported in the phloem sap from the leaves to perennial tissue. Some theoretical support for this nutrient translocation hypothesis was provided by Archetti (2007a) using game theory modelling.

In a more recent letter, Archetti (2007b) proposed that a similar game theory model could distinguish among the coevolutionary, photoprotection and defence indication hypotheses. Using a binary model involving weakly or strongly defended plants (**d** versus **D**) that have either weak or strong colouration (**s** versus **S**), he concluded that the defence indication hypothesis is "wrong, or at least misleading". It was argued that if physiology, rather than herbivory, were the underlying driving force for pigmented leaves, then no tree would benefit by having only green leaves; the **ds** phenotype would be evolutionary unstable.

Archetti's (2007b) model is attractive because of its simplicity, but as Shipley (1997) has stated, "in mathematical models … the proof of the pudding is always in the eating, never in the making". We believe the pudding is inedible because the fundamental assumptions of the model are flawed. Neither plant defence nor photoprotection should be thought of as fixed binary traits (indeed, if they were, such models would be dispensable because plant strategies would be predictable!). On the contrary, plants use various defensive strategies including a vast assortment of secondary metabolites in defence (Bennett and Wallsgrove, 1994), and have evolved multifarious mechanisms for photoprotection (Niyogi, 2000). Moreover, the combinations of chlorophylls, carotenoids, and anthocyanins (or betalains) give rise to a broad spectrum of leaf colours (Davies, 2004). As a consequence, the link among plant

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defence, photoprotection, and leaf colour is species-dependent and certainly not binary. It is similarly erroneous to include these as *fixed* traits in the model because plants respond dynamically to both abiotic and biotic stressors. This aspect is particularly important since dynamic plant responses, such as priming, represent the core foundation of the defence indication hypothesis (Schaefer and Rolshausen, 2006). Because of the overly simplistic assumptions, the model is of little use to distinguish between the hypotheses on leaf colouration.

Core assumptions of the model developed by Archetti (2007b), as well as some of the conclusions derived from it, appear to fly in the face of well-established facts of plant biochemistry and physiology. For example, the model builds on the premise that bright (red and yellow) leaves are always better photoprotected than green leaves. This assumption is wrong; while there is good evidence that anthocyanins in red leaves provide novel mechanisms for photoprotection (Neil and Gould, 2003), green leaves are normally rich in xanthophyll pigments, which dissipate excess light energy as heat (Niyogi, 2000), and in colourless antioxidants, some of which are remarkably effective at mitigating photo-oxidative damage (Logan et al., 2006). Thus, green plants are likely to be well defended against photo-oxidative damage and evolutionary stable, as evidenced by the large number of species that remain green throughout their life. The crucial point is that—owing to the invalidity of the fundamental assumption—Archetti's (2007b) stability analysis is not suited to model the evolution of autumnal leaf colouration. Neither is the analysis suited to test the defence indication hypothesis, or to conclude that photoprotection theory and aphid preferences for green are incompatible.

Finally, Archetti (2007b) has misinterpreted the defence indication hypothesis when he states that the link between colour and defences is fixed and cannot evolve under the hypothesis. While the hypothesis indeed expects a fixed link between specific defensive compounds and anthocyanin content, any generalisation is unwarranted. Similarly, plant colours other than red can be produced by a variety of pigments and co-pigments (Davies, 2004) which further debilitates assumptions on a fixed relationship between pigments and photoprotection.

In his letter, Archetti (2007b) maintains that colour preferences of insects are useful to distinguish between the different hypotheses on leaf colouration. As explained previously (Schaefer and Wilkinson, 2004), this is not the case because pigments and defensive secondary compounds have multiple physiological functions of which only some might be relevant in the context of herbivory. Thus, to disentangle cause and effect of leaf colouration we need experiments that test the selective pressures of herbivorous *relative* to those of abiotic factors. Costs and benefits of pigmentation have to be measured in terms of plant physiology, biochemistry and in interactions with herbivores. Such tests are still lacking, partly because they are more difficult to conduct than observational studies, and partly because supporters of the coevolution hypothesis have been reluctant to consider alternative hypotheses. Rather than modelling the theoretical foundations with binary assumptions, it is time to turn a new leaf and devise experiments and models that resemble tasty puddings and realistically test the different scenarios.

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