

## Letter to the editor

### Colour preference as evidence for the theories on the evolution of autumn colours

The coevolution theory of autumn colours (Archetti, 2000; Hamilton and Brown, 2001; Archetti and Brown, 2004) posits that the bright colours of deciduous tree species in autumn are an adaptation to avoid parasites: if leaf colour signals the level of defenses of the tree, then trees with bright leaves may avoid being colonised by insects (for example aphids) that migrate to the trees in autumn to lay their eggs; at the same time insects, by avoiding bright colours, may avoid trees with high levels of defenses. This signalling system is stable under certain reasonable conditions (Archetti, 2000) and can explain aphid preference for green (Hagen et al., 2003, 2004; Archetti and Leather, 2005; Karageorgou and Manetas, 2006). It can also explain why tree species with bright autumn colours have a higher diversity of associated aphids species (Hamilton and Brown, 2001).

The photoprotection theory (Lee, 2002a,b; Lee and Gould, 2002 and references therein) suggests a different adaptive explanation: autumn colours may have evolved because they protect against the physical damage induced by intense light at low temperatures: trees with bright autumn colours are more protected and can reabsorb nutrients more efficiently (especially nitrogen). The photoprotection theory does not make any assumption or prediction on the behaviour of insects or on coevolution between insects and trees.

Schaefer and Rolshausen (2006) suggest that, while autumn colours may be an adaptation for photoprotection, insects may have evolved to avoid bright trees in order to avoid well-defended trees. If colour and defenses are linked (because of a common biosynthetic pathway) then insects may use colour as an indicator of defenses even if the adaptive value of colour is different (photoprotection). Therefore, they suggest that the observed preference of aphids for green is not necessarily evidence in favour of the coevolution theory: aphids may prefer green only because green trees have less defenses but red did not evolve as a signal to avoid insects.

Schaefer and Rolshausen (2006) therefore assume that autumn colours evolved for the reason suggested by the photoprotection theory but that insect behave as predicted by the coevolution theory or, in other words, that preference for green is compatible with the photoprotection

theory. I would like to clarify why this is wrong or, at least, misleading and valid only in one specific and unlikely case.

The argument of Schaefer and Rolshausen (2006) implies that the link between colour and defenses is fixed and cannot evolve, because it is an intrinsic property of the biochemical pathway of pigment/defense synthesis. In this scenario we may think, for the sake of simplicity, that there are trees with weak defenses (**d**) or strong defenses (**D**), and with dull colours (**s**) or bright colours (**S**). Schaefer and Rolshausen (2006) suggest that the only possible tree strategy is having bright colours with strong defenses and weak colours with weak defenses (**ds/DS**). If this association between colour and defenses cannot evolve, then it is clear that insects will choose green (**s**) because this is always linked with lower defenses (**d**). This is possible, and in this sense Schaefer and Rolshausen (2006) may be correct.

Trees with bright colours (**S**), however, will have a double advantage over trees with dull colours (**d**): they will avoid parasite insects and they will have a better photoprotection. Therefore, it is also clear that if the link between colour and defenses can evolve, other tree strategies can evolve and the strategy **ds/DS** can be unstable because **d** trees do not have any advantage. In the coevolution theory **S** trees have a cost due to the production of colour or earlier cessation of photosynthesis, and this is why levels of colour and levels of defenses become associated (and coevolve with insect preference for green—Archetti, 2000). What association between colour and defenses will evolve if autumn colours are an adaptation against photooxidation? And in this case would insects evolve a preference for green? This can be understood by using the model I have developed to analyse the photoprotection theory (Archetti, 2006) in which all the four possible combinations of colour and defenses can evolve (**ds/Ds**, **ds/DS**, **dS/Ds**, **dS/DS**).

The stability analysis shows that preference for green and tree strategy **ds/DS** (the scenario envisaged by Schaefer and Rolshausen) are not stable if **S** trees have a higher fitness than **s** trees due to photoprotection. This couple of strategies (**ds/DS**, preference for green) is stable only if **S** trees have a higher cost during growth compared to **s** trees. It is easy to see why: if colour confers an advantage other than avoiding insects, then there is no advantage for **d** trees to remain green, even if the production of defenses (**D**) has a cost. Under the assumptions of Schaefer and Rolshausen (2006) autumn colours do evolve but do not become

associated with defenses, and aphids evolve a preference for red, not for green.

While Schaefer and Rolshausen (2006) suggest that the link between colour and defenses exists for some reasons and is not adaptive—and cannot be eliminated—the coevolution theory explains this link between colour and defenses exactly as an adaptation against parasites. Indeed the coevolution theory was born from the theoretical prediction that the link between colour and defenses can evolve as a product of coevolution between trees and insects (Archetti, 2000).

It is true that preference for green is not sufficient (but it is necessary) to prove the coevolution theory, but it is important to understand that preference for green is not compatible with the photoprotection theory. Preference for green is possible under the photoprotection theory only assuming that the link between colour and defenses is immutable and cannot evolve by natural selection. If this is true, however, then we must also assume that the tree species with no autumn colours do not have chemical defenses against parasites. This means that aphids should evolve a preference for host tree species with no bright colours and we should expect to find a higher diversity of aphid species on tree species with no autumn colours—which is exactly the opposite of what Hamilton and Brown (2001) have shown, and also the opposite of what Schaefer and Rolshausen (2006) themselves claim to explain.

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