The coevolution theory of autumn colours

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According to the coevolution theory of autumn colours, the bright colours of leaves in autumn are a warning signal to insects that lay their eggs on the trees in that season. If the colour is linked to the level of defensive commitment of the tree and the insects learn to avoid bright colours, this may lead to a coevolutionary process in which bright trees reduce their parasite load and choosy insects locate the most profitable hosts for the winter. We try to clarify what the theory actually says and to correct some misunderstandings that have been put forward. We also review current research on autumn colours and discuss what needs to be done to test the theory.

Keywords: autumn colours; coevolution; biological signalling; trees; evolution

1. INTRODUCTION

Why do leaves change their colour in autumn? Bright autumn colours occur in many deciduous tree species and are well known to everybody. However, an evolutionary explanation to this question has only recently been put forward. This explanation is the 'coevolution theory' that we will discuss in this paper. The coevolution theory has been developed by us (Archetti 2000; Hamilton & Brown 2001; Brown 2004) from an idea of W. D. Hamilton, and recently there has been a considerable amount of interest on the subject (e.g. Atkinson 2001; Whitfield 2001; Holopainen & Peltonen 2002; Lev-Yadum *et al.* 2002; Wilkinson *et al.* 2002; Hagen *et al.* 2003).

Previous explanations of autumn colours did not really answer the question 'why', in that they did not propose an adaptive value. The usual explanation was that bright colours are a mere by-product of leaf senescence: chlorophyll usually masks the colour of other pigments, carotenoids and flavonoids; in autumn, because of leaf senescence, chlorophyll is degraded and detoxified to colourless products, and this allows the red and yellow hues of carotenoids and flavonoids to stand out; therefore bright colours are just a secondary effect of leaf senescence. Leaf senescence and abscission already have an adaptive explanation: in periods of short daylight and low temperatures (winter) the cost of keeping the leaves is bigger than the benefit induced by photosynthesis (Sanger 1971; Thomas & Stoddart 1980; Goodwin & Mercer 1983). Because bright colours are just a secondary effect of senescence, we do not need further explanations for autumn colours.

This point of view, however, ignores two facts. The first is that leaf fall is not necessarily correlated with autumn colours. Many deciduous tree species do not have bright colours in autumn. Moreover, there is huge variation among individuals of the same species, and some trees lose their leaves when they are still green, while other trees of the same species show bright colours, for a period of time that is also variable. Leaf abscission and senescence may be preadaptations to the phenomenon of autumn colours, but they are by no means the same thing.

The second is that bright colours are not just the effect of the degradation of chlorophyll, but new pigments are actively produced in autumn (Duggelin *et al.* 1988; Chang *et al.* 1989; Matile *et al.* 1992). The *ex novo* synthesis of these pigments in leaves that are going to fall in a short time cannot be seen as a secondary effect of senescence, because this synthesis has a cost. It has been proposed (Merzlyak & Gitelson 1995) that autumn pigments protect chlorophyll from dangerous photo-oxidation processes. Indeed, this is one of the functions of carotenoids in non-senescing leaves. Light energy, usually trapped by chlorophyll, in autumn leaves cannot be harnessed to carbon fixation and may produce reactive oxygen species that could be harmful to the tree. This protective effect might seem useless for leaves just before abscission; however, if membranes and other structures of the leaf are remobilized before abscission, protection from photo-oxidation may play a role in the evolution of autumn colours, at least as a pre-adaptation. However, it cannot explain the huge variation in autumn colours, both among individuals of the same species and among different tree species. Another evolutionary explanation seems necessary to explain this intraspecific and interspecific variation.

2. THE COEVOLUTION THEORY

One of W. D. Hamilton's last hypotheses (though not quite the last) was that bright autumn colours could be the result of coevolution between insects and trees. The idea is that bright colours are a 'signal' revealing the level of defensive commitment of the plant, to insects that migrate to the tree in autumn and exploit it as a host for the winter (for example, aphids). Therefore we call it the 'coevolution' or 'signalling' theory. Coevolution of colour preference and bright colours would allow well-defended plants to reduce parasite load and the parasites to locate the most profitable hosts for the winter.

The signalling hypothesis makes predictions on two interrelated levels: (i) on an interspecific level, species of

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trees suffering greater insect attack invest more in defence and consequently more in defensive signalling than less troubled species; and (ii) on an intraspecific level, individuals of signalling species vary in expression of this signal, with defensively committed individuals producing a more intense display, which proves aversive to the monophagous pests that drive the signal evolution in (i).

Thus, the interspecific and intraspecific arguments are separate but interrelated (mirroring an earlier study on parasite-driven signals in birds (Hamilton & Zuk 1982)). Both are open to rejection. Here, we concentrate on developing the potential for experimental tests of the intraspecific arguments in (ii). Rejection of the intraspecific hypothesis can occur on only a species-by-species basis; thus a key call of this paper is to promote the study of a diversity of candidate interactions. We refer to Hamilton & Brown (2001) for more details on (i).

3. ASSUMPTIONS, PREDICTIONS AND POSSIBLE MISUNDERSTANDINGS

Recent papers (Holopainen & Peltonen 2002; Wilkinson *et al.* 2002) claim that the hypothesis is unlikely to be correct on the basis of our current knowledge of its biological basis. In particular, Wilkinson *et al.* (2002) argue that the principal assumptions of the theory do not match current knowledge of plant pigment biochemistry and aphid ecology. This assertion is based on some observations that are, however, rather inconclusive with regard to the hypothesis. A discussion of these facts can be useful to understand what the hypothesis says and what it does not.

(a) *Match between signal and receiver*

Wilkinson *et al.* (2002) note that aphid migration is not restricted to the time-window of autumnal coloration, and often peaks at other times of the year. If a tree species is engaged in a signal game, it is evidently limited by photosynthetic demands to put on a colourful display during a limited period in autumn. The coevolution theory demands only that the receivers *at that time* are sufficiently important to the signaller to merit putting on a display. If some of a tree's key insect enemies have already found their winter home, no matter. So long as the enemies still on the move are of sufficient economic importance, the assumption of the model is satisfied.

It should also be borne in mind that only a minority of tree–aphid (and indeed tree–non-aphid) interactions are likely to be engaged in a signalling interaction, and by looking at other interactions we may learn little with regard to the signalling hypothesis. Many aphid species do not host-alternate in autumn, for example, but this does not mean that the other species, which do host-alternate (whether among members of the same or different host species), cannot provide a selective pressure for the evolution of warning colours. Looking at Hamilton & Brown's (2001) fig. 1 one can see that only 13 species of tree were infected with three or more specialist aphids. Among these 13 species, some are evidently brighter than others. It is the interaction between these bright species and their specialist pests that demand specific experimental attention. A list of tree species with their autumn colours and the number of their parasite aphids is available from the authors on request.

(b) *Form of the signal*

Leaf colour varies considerably not only from one individual to another but also from one leaf to another on the same branch. Indeed, in some trees, the colour changes even in different parts of the same leaf. However, this is not a problem for the coevolution theory, as Wilkinson *et al.* (2002) claim. What matters is that there is a mean colour for each tree and that there is variation in the mean colour for neighbouring trees. It would be interesting to know whether insects perceive and choose the tree as a whole or choose single leaves or branches, but this does not make any difference for the coevolution theory, which states that the mean load of parasites on a single tree (and therefore the fitness of the tree) will depend on its mean colour.

(c) *Insect preferences*

There is anecdotal evidence that some insects are *attracted* by yellow. Therefore yellow could not be a warning colour. This is an important point, which, if true, would appear to dismiss the hypothesis. Caution is, however, needed against generic claims on behalf of all insects, and on the distinction between attraction and preference. The fact that yellow is a good colour for insect traps, cited by Wilkinson *et al.* (2002) against the hypothesis, is too generic to be taken into account as a general argument against the coevolution theory. Is it true for all species? Is it true in all seasons? Direct observations of insect choice for different colours of autumn leaves are necessary; to our knowledge, and also according to Wilkinson *et al.* (2002), these observations do not exist yet. The few studies that report *indirectly* a preference for a certain colour, indeed, show a preference for green (see below). Holopainen & Peltonen (2002) cite circumstantial evidence that, in some cases, a particular aphid species lands and feeds on yellow leaves, but with no data to support their view that aphids, in general, prefer yellow over green. It may be that anecdotal observations reported by Holopainen & Peltonen (2002) reflect a general behaviour of this species (*Euceraphis betulae*), which, however, does not host-alternate and therefore is not particularly relevant for the theory; they certainly do not offer strong definitive evidence against the coevolution theory. An answer must come from direct evidence of aphid preference for different colours in autumn: evidence that is still lacking (but see below).

Furthermore, great care is needed to distinguish colour *preference* (implying choice) from simple *attraction*. The *attractiveness* of yellow is consistent with the signalling hypothesis, while in contrast it has been shown that, among aphids that are attracted to yellow, individuals have a preference for the most diluted shade (Moericke 1969). Thus this preference for impure yellow will result in avoidance of trees displaying the strongest yellows in favour of others displaying only impure tints. The important cue is therefore relative intensity: individual hosts are competing to produce the most intense colour and thus avoid colonization (Hamilton & Brown 2001). Hamilton and Brown made the analogy with the handicap signalling theory of stotting in gazelles, arguing that 'while a cheetah may select a metaphorically "off colour" gazelle, aphids may literally prefer off-colour trees' (Hamilton & Brown 2001, p. 1492).

(d) *Link between colour and tree condition*

Environmental factors may influence the intensity of leaf colour, and in some cases environmental stress may be so strong that it will result in brighter colours for weaker trees; according to Wilkinson *et al.* (2002) this weakens the coevolution theory. This is not true: one of the predictions of the model is indeed that the signalling system may collapse if environmental conditions are too poor or too rich (Archetti 2000).

Archetti (2000) developed a model in which bright colours were predicted to evolve depending on the vigour of the tree; this is a possibility, but it is not essential for the hypothesis. It must be remembered that the theory predicts, in general, that the degree of colour is correlated with the level of *defensive commitment* of the tree, not necessarily with the *vigour* of the tree. It is entirely possible that it is trees in poor condition that invest more resources in defence against parasites and in autumn colours. Indeed, Schaberg *et al.* (2003) showed that the extent and earliness of onset of red coloration in maple leaves were positively correlated with foliar nitrogen deficiency. Hamilton & Brown (2001) were very cautious about defining the relationship between tree condition and defensive commitment, suggesting even the possibility of a negative relationship. Again, the relationship between dimensions of leaf colour and dimensions of tree quality must be investigated directly.

(e) *Signal costs and signal honesty*

Wilkinson *et al.* (2002) state that, because anthocyanins are synthesized in autumn at a possibly minimal cost, and because loss of carotenoids does not lead to considerable waste for the tree, their signal cannot be considered honest. While illustrating that the biochemical costs of autumnal pigment changes and losses are debatable (but not absent), this argument completely ignores a key set of costs mentioned in Hamilton & Brown (2001) and in Archetti (2000), the costs of an early cessation of photosynthesis. Under this scenario, the colour (red or yellow) serves merely as a marker of photosynthetic cessation (i.e. 'look, no chlorophyll!'), which if undertaken early bears its own unfakeable cost: loss of photosynthesis (see also Hagen *et al.* (2003) for an empirical approach based on *timing* of coloration). It remains to be seen how costly is the cessation of photosynthesis during a season when remobilization of other minerals, and not carbon fixation, is a priority for the tree, but it is worth stressing that signal honesty can be maintained among conflicting players for even low levels of cost, so long as the marginal costs are high and increasing (e.g. Lachmann *et al.* 2001). Finally, if the timing of the colour, rather than its intensity, is the prevailing signal, then this could involve even the dullest autumn colours, including brown, which is not usually considered a 'bright' colour.

Wilkinson *et al.* (2002, p. 402) conclude that 'other hypotheses based on interactions with insects can explain autumn colours', mirroring sentiments expressed in the Hamilton & Brown (2001) article itself: 'here we suggest that this diversity of [autumnal] coloration reflects, in part, a signaling interaction between certain tree species and their most aggressive pests. The comparative data … point to a suggestive pattern of association. Evidently, direct experimental investigations are now required to test these

ideas on characteristically bright tree species and their autumnal pests' (Hamilton & Brown 2001, p. 1492). Holopainen & Peltonen (2002) suggested that leaf colours are a signal of the degree of nutrient translocation going on in the leaves. There is room for multiple interacting determinants of leaf colour and insect recruitment. What we surely need now to reject or accept the hypothesis is not circumstantial evidence or indirect suggestions from old data but direct tests of the assumptions and of the predictions of the hypothesis in different tree–insect systems.

4. WHAT NEEDS TO BE DONE

The first main test, or group of tests, concerns insect preference for colours. The signalling hypothesis predicts that in choice tests they should prefer duller shades of autumnal colours, and/or later emergence of colour. Aphids are particularly likely to be involved in the coevolution of autumn colours, because many species migrate to trees in autumn, they have colour vision, and they can have a strong impact on the fitness of the tree. However, it will be necessary to test the theory with different host–parasite systems, not restricted to aphids. These studies will be preferentially done in the field; however, specific studies in controlled conditions in the laboratory may be useful. For example, to decide whether colour itself is the main determinant of insect choice, insects could be allowed to choose between branches of different colours and then to repeat the test under a monochromatic light. Preference for colour, if observed in the first test, should disappear under a monochromatic (e.g. red) light. A possibility is that colour is merely a by-product of another signal (e.g. an olfactory signal), correlated with the intensity of colour itself.

The degree of leaf retention could be a confounding variable if it is associated with colour. However, note that the hypothesis suggests a role for the degree of leaf retention: indeed, if there is, as we have discussed, a cost for the loss of photosynthetic intake owing to the abscission of leaves, early abscission could also be interpreted as an honest signal of the tree's defensive commitment. Experimental investigations of leaf loss have the advantage of being more amenable to manipulation, allowing a range of leaf-loss conditions independent of tree condition, defence or colour.

An important prerequisite of the hypothesis is that significant colonization of the winter host occurs during a time when there is variation in leaf colour. A confirmation of this will be a necessary, but not sufficient, condition for the hypothesis. It should be possible to have precise data on both insect arrival (by looking at data collected by suction traps, for example) and leaf colours (by direct field observations) for many species in a reasonable amount of time. There will presumably be much variation, because aphids, for example, are a huge group of insects, because their abundance may vary greatly from year to year, and because the timing of the colours will vary from one plant species to another.

The second main test concerns the growth rates of the insects in spring. Insects on trees that displayed bright colours in autumn are expected to grow less rapidly or less healthily if bright trees are defensively stronger, and therefore better equipped to react against pathogens.

Experimental manipulation of the overwinter burden will be important to separate the effects of recruitment and survival. An important task would be to assess the relationship between the condition (strength) of the tree and the timing and intensity of leaf colour change. Clones of the same species could be grown on different conditions of nutrients or light and the difference in colour could be observed. Alternatively, the condition of different trees could be assessed by indirect measurements, for instance fluctuating asymmetry (see Hagen *et al.* 2003).

It would be useful to develop some more general measure of tree condition, as fluctuating asymmetry is not equally applicable to all species, and in all cases it is an indicator of vigour on a longer time-scale than that during which autumn colours develop. The incorporation of an index of tree condition into the study of autumn colours would be welcome, as tree condition is likely to be the motor of variation in tree defensive commitment, signalling and consequent insect attack. Once again, experiments manipulating tree condition and/or resource holding would be most welcome. Note again, however, that defensive commitment is not necessarily correlated with either tree condition or resource holding. Therefore it is also necessary to measure the link between tree condition (vigour) and the degree of defensive commitment, possibly by measuring secondary metabolites or compounds known to be effective against herbivores.

5. WHAT HAS BEEN DONE

Few papers discussed aphid preference for colours before the birth of the coevolution theory. Furuta (1986, 1990) reported aphid preference for green over red autumnal leaves of *Acer palmatum*, and Leather (1990) showed that aphids prefer trees that retain leaves for longest in *Prunus padus*. Leather (1986) did not observe a preference for leaves at different stages of senescence, but he had used very young (small) trees (S. R. Leather, personal communication). Glinwood & Petterson (2000) showed that, in fact, there is a preference of oviparae for non-senescing leaves. Moran & Witham (1990) showed that aphids avoid trees with few leaves and prefer trees that retained leaves for longer in *Populus*.

The first papers to propose the coevolution theory were Archetti (2000) and Hamilton & Brown (2001). Archetti (2000) presented a game-theoretic model incorporating the basic assumptions of the coevolution theory and showing that a signalling system between trees and parasites can evolve as a form of handicap signal (Zahavi 1975, 1977; Grafen 1990*a,b*). Hamilton & Brown (2001) presented a comparative analysis of autumnal colour and aphid diversity across 262 species of deciduous trees. The dataset revealed a positive association between the degree of autumnal coloration and the diversity of monophagous aphids, suggesting that the most troubled tree species invested more in signals of defence. These two papers stimulated interest (e.g. Atkinson 2001; Whitfield 2001; Lev-Yadum *et al.* 2002) and controversy (Holopainen & Peltonen 2002; Wilkinson *et al.* 2002). However, new research efforts with the specific purpose of testing the hypothesis have only recently begun.

Hagen *et al.* (2003) demonstrate for *Betula pubescens* that more colourful trees in autumn suffer less insect damage the following spring (in keeping with the basic within-species prediction of the signalling hypothesis). Although they did not analyse preference directly in autumn, this is the first (to our knowledge) empirical evidence of the first main prediction of the hypothesis, that bright colours reduce the herbivore load of the tree. Hagen *et al.* (2003) also argue that trees suffering greater attack extend their photosynthetic season to recoup resources, and hence are less coloured in September. However, the observed correlation allows alternative causal links, for instance late cessation may *cause* increased same-year attack; i.e. less coloured trees may suffer more attack in the following season *and* instantaneously. This double cost of attack (by both parents and progeny) must be balanced by the cost of early cessation of photosynthesis. The challenge is to determine which of the many correlated traits is causal: tree condition? Insect attack? Tree defence? Experiments are going to be necessary.

Hagen *et al.* (2003) introduce an index of tree condition (fluctuating asymmetry) into the study of autumn colours. This is a very welcome development, as tree condition is likely to be a motor of variation in tree defensive commitment, signalling and consequent insect attack. It is interesting to note that their results support a positive relationship between tree condition and signal intensity (and hence a negative relation with consequent attack).

M. Archetti and S. R. Leather (unpublished data) monitored colonization of the aphid *Rhopalosiphum padi* on individual trees of *Prunus padus* directly in autumn and observed that aphids began to arrive when some of the trees were almost completely red, some of them completely green and most of them variable in colour, and colonization went on until leaf fall. The timing of the signal, at least in this case, is extraordinarily exact. More importantly, a strong preference of aphids for trees with green leaves was observed. This is in agreement with Hagen *et al.* (2003) and is also the first direct evidence of colour preference (for green) in autumn. Moreover, their observations, compared with previous data gathered on the same species, suggest that aphids colonizing trees with green leaves develop better in spring than aphids colonizing trees with bright autumn colours, which is consistent with a positive correlation between tree quality and defensive commitment.

A direct measurement of the relationship between autumn coloration and tree condition was carried out by Hagen *et al.* (2004): they explored the relationship between autumn coloration and level of fluctuating asymmetry in leaves (indicator of the tree's quality) in *B. pubescens* and found that bright autumn birches are in better condition and therefore, they suggest, consequently should be better at fighting off herbivores. However, we must still be cautious on this point; as we have discussed, it would be necessary to measure directly the link between tree condition and the degree of defensive commitment.

6. CONCLUSIONS

The coevolution theory might turn out to be a general explanation for bright colours of leaves. For any future work it will be necessary to select specific tree–insect systems to study autumn colours, which could offer the possibility to study easily both the production of colours and

of defences against parasites, and the preference of insects in autumn and their subsequent growth rates in spring. To assess the generality of the coevolution theory, these studies must be done on a variety of tree–insect species. There is clearly the potential to apply the same logic to colourful bushes and vines, and further to a variety of colourful plant structures, for instance young leaf flushes and wind-dispersed seeds. Theoretical interest remains in linking these potential defensive signal syndromes with the dazzling array of attractive plant signals of fruits and flowers (S. P. Brown, unpublished data). But autumn colours still deserve much investigation, and it is likely that there are many differences in the huge variety of species that show bright colours. It is still too soon to accept or reject the idea, but we are beginning to work in the right direction.

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