

Unravelling the evolution of autumn colours: an interdisciplinary approach

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Leaf colour change is commonly observed in temperate deciduous forests in autumn. This is not simply a side effect of leaf senescence, and, in the past decade, several hypotheses have emerged to explain the evolution of autumn colours. Yet a lack of crosstalk between plant physiologists and evolutionary ecologists has resulted in slow progress, and so the adaptive value of this colour change remains a mystery. Here we provide an interdisciplinary summary of the current body of knowledge on autumn colours, and discuss unresolved issues and future avenues of research that might help reveal the evolutionary meaning of this spectacle of nature.

Autumn colours

Every year, when summer draws to a close in the temperate zones, autumnal leaf colour change transforms entire landscapes into brilliant mosaics of yellow, orange and red (Figure 1). Although much is known about the biochemistry and physiology of this colour change, its adaptive value remains a mystery [1]. Interest in autumn colour evolution was renewed recently by the revival of the photoprotection hypothesis by plant physiologists and by the development of the coevolution hypothesis by evolutionary biologists. According to the photoprotection hypothesis [2–5], red pigments protect against the harmful effects of light at low temperatures; according to the coevolution hypothesis, instead, red is a warning signal toward insects migrating to the trees in autumn [6,7]. Derived from these basic ideas, several additional hypotheses have recently appeared.

One of the greatest obstacles to a consolidated explanation for autumn leaf colouration has perhaps been a lack of communication between scientists across the subdisciplines of biology [1,8]. Here we bring together authors from a range of backgrounds (biochemistry, physiology, ecology and evolution) in the first interdisciplinary review of autumn leaf colouration in tree biology. In addition to providing a brief summary of each hypothesis and a review

of recent evidence, we also reflect on conceptual problems, and propose future experiments that should prove useful in evaluating each hypothesis.

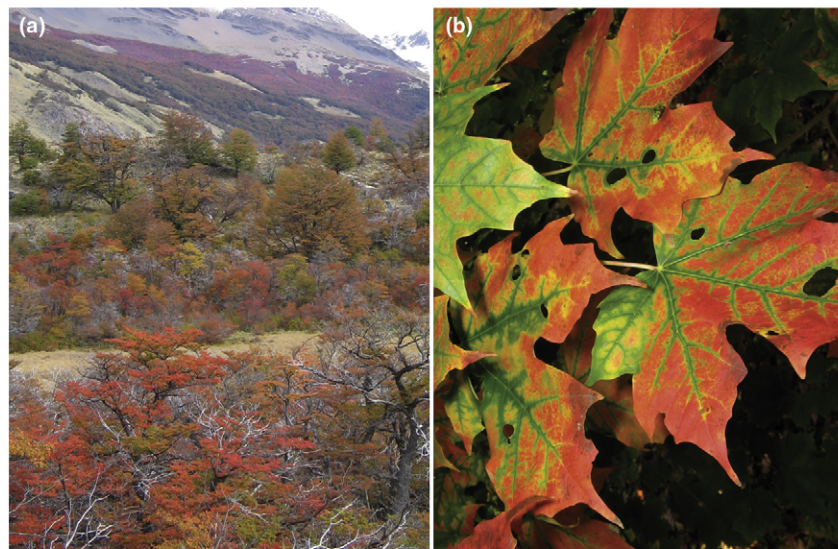
The complexity and variability of autumnal leaf colour change and the emergence of multiple alternative explanations require more and very carefully designed experiments. Nevertheless, as the current hypotheses are now beginning to come under more intense scrutiny, a solution to the mystery of autumn colours might be soon within our grasp.

Why change colour?

Green colouration generally predominates in leaves owing to high concentrations of chlorophyll relative to other pigments. In some cases, however, leaves can have different colours, the senescing leaves of temperate trees being the most dramatic example. It is a common misconception that autumn colours are simply the incidental product of leaf senescence. Autumn colours (Box 1) are due mainly to carotenoids (yellow-orange) and anthocyanins (red-purple). Although carotenoids are present all year round in the leaves, they are masked in mature leaves by the green of chlorophyll; in autumn, they become visible because of the breakdown of chlorophyll into colourless metabolites, but there is no evidence for a *de novo* synthesis [9]. Anthocyanins, by contrast, are newly generated in autumn, shortly before leaf fall [10–13]. Thus, red is produced actively in autumn and is not simply the side effect of leaf senescence. Brown is typically indicative of cell death, and we do not consider it here. Our discussion, therefore, is mainly relevant for red.

Red autumn colours are present in ~10% of the tree species of the temperate regions, whereas yellow is present in ~15% of the species [14]. In some regions of the world these frequencies are much higher, for example in the mixed forests of New England in the USA, where ~70% of woody species turn red and 30% yellow [5], and in the southern beech forests of Patagonia, where pure forests of *Nothofagus* become orange and red in autumn (Figure 1).

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Figure 1. Autumn colours. Autumn colour change in (a) a southern beech *Nothofagus* forest in Patagonia, Argentina and (b) in the leaves of the sugar maple *Acer saccharum* in New England, USA.

Box 1. Biochemistry of autumn colours

We discuss mainly red, but leaves in autumn can also be yellow and brown. Whereas red is due to pigments actively produced in autumn, yellow follows the breakdown of chlorophyll, and brown usually indicates cell death.

Red

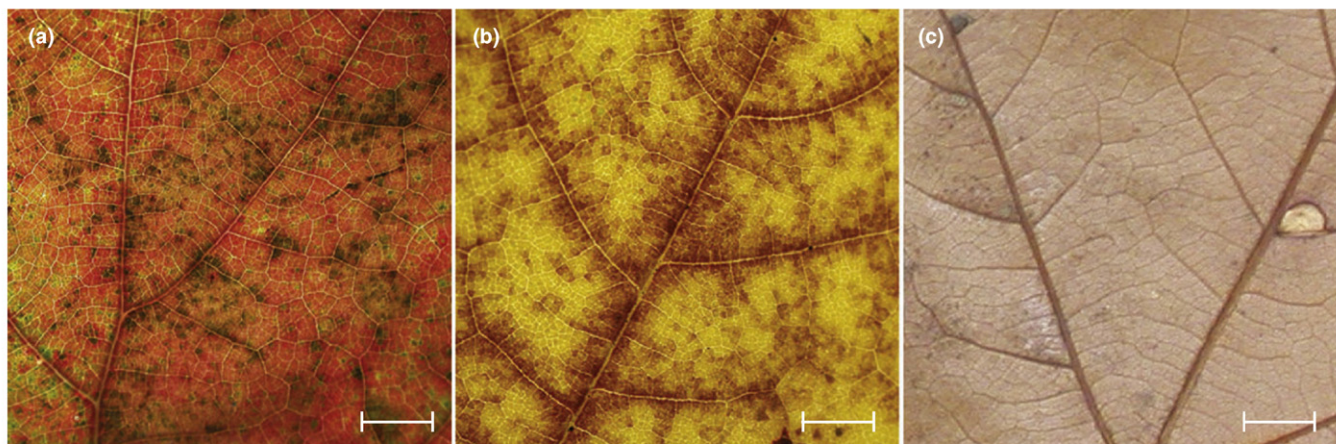
The red and purple colouration in senescing leaves is most commonly due to anthocyanins, which are vacuolar flavonoids (Figure 1a). In autumn, they are synthesised *de novo* once ~50% chlorophyll loss has occurred [5]. Colouration can vary with factors such as chlorophyll concentration (higher chlorophyll concentrations give leaves a purple to brown appearance), pH (basic pH in vacuoles results in blue colouration, whereas more acidic pH results in red), co-pigmentation, glycosylation or the presence of metal ions. In certain specific cases, other pigments contribute to red colouration: for example, betacyanins are present exclusively in the Caryophyllales and have similar properties to anthocyanins; other red pigments found in leaves include 3-deoxy-anthocyanidin, rhodoxanthin and anhydroeschscholtzanthin [9,10].

Yellow

Carotenoids are the pigments responsible for the yellow-orange colours of autumn leaves (Figure 1b). Unlike anthocyanins, they are present in leaves year-round and, similar to chlorophyll, are confined to plastids, where they are located either in the photosynthetic membrane or in the hydrophobic environment of plastoglobules. Carotenoid genes are ancient and ubiquitous among phototrophs [49]. They can undergo subcellular relocation and chemical modification during leaf senescence, but there is little evidence for *de novo* synthesis in autumn [9,33].

Brown

Browning (Figure 1c) is typically indicative of cell death, and reflects polymerisation of quinones [33]. Tannins (another class of phenylpropanoid closely related to anthocyanins) and residual carotenoids are also responsible for browning in late senescence, whereas in early senescence, browning can also result from the combined presence of anthocyanins and chlorophyll [5,10].



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Figure I. Detail of (a) red (oak, *Quercus rubra*), (b) yellow (sugar maple, *Acer saccharum*) and (c) brown (*Q. rubra*) leaves in autumn, from Harvard Forest, MA, USA. Scale bars = 3 mm.

There is an extensive phylogenetic variation, with ~50% of maple (*Acer*) species turning red, and entire taxa with no autumn colours [14].

Extensive variation also exists within species with autumn colours: some individuals drop their leaves when they are still green and others display a variety of colours before falling. Autumn colours have a strong genetic basis, as shown by transplantation experiments in which individuals maintain the timing and intensity of colours typical of the environment in which they evolved, although environmental factors also play a role. A large variation in duration and onset of autumn colouration also occurs [15–17].

Anthocyanins are also produced in a variety of cases that are not associated with senescence, for example in winter evergreens and young leaves; although not the focus of our review, these cases are discussed in **Box 2**.

Adaptive explanations

What use is the production of a red pigment in leaves that are about to be shed? How do we explain the interspecific variation, or the fact that only some species turn red in autumn?

There are two kinds of adaptive explanation for the function of red pigments in autumn leaves: (i) protection against abiotic factors, and (ii) animal–plant interactions. The possible abiotic functions of anthocyanins reduce to three hypotheses [12,18]: photoprotection, osmotic regulation and warming. Many additional possible functions have been proposed that rely on an interaction between plants and animals [18]: coevolution, fruit flag, direct defence, camouflage, anticamouflage and tritrophic mutualism. Only the photoprotection hypothesis [2–4] and the coevolution hypothesis [6,7] have been tested recently, and here we describe recent evidence for both. The other hypotheses (**Box 3**) have either been dismissed, remain untested or can be reduced to other previous hypotheses [18].

The photoprotection hypothesis: protection against the harmful effects of light enhances resorption of nutrients

The idea behind the photoprotection hypothesis dates back to the late 19th century [13], but was revived and proposed in its present form only recently [2–4]. According to this hypothesis, anthocyanins function to relieve photo-oxidative stress by acting directly as a sunscreen shielding leaf tissues against the harmful effects of light at low temperature, or indirectly by quenching reactive oxygen species (ROS) and possibly other photoreactive molecules (e.g. chlorophyll metabolites). ROS and photo-oxidative damage occur when the rate of photon absorption and the concomitant photosynthetic electron flow exceeds the capacity for energy processing via CO₂ assimilation while the energy-dissipating capacity of the chloroplast is surpassed [19]. The risk of photo-oxidative damage is especially high in autumn, because (i) cold temperatures reduce carbon fixation capacity; (ii) there is increased light owing to a thinning canopy, affecting shade-adapted, understory trees; and (iii) there is decreased self-shading by chlorophyll as breakdown occurs [20]. The adaptive function of photoprotection would not be the protection of leaves *per se*

Box 2. Non-autumnal leaf reddening

Red is not necessarily associated with leaf senescence. Anthocyanins are produced in other cases, for example in young leaves and in winter evergreens.

Young leaves

In many tree species, young, expanding leaves are initially red and gradually turn green upon maturation (**Figure 1a**). Although first observed in tropical trees, it occurs also in temperate plants, although its frequency, and whether it is correlated with autumn leaf anthocyanin production, is unknown. In young leaves, light capture ability develops earlier than CO₂ assimilation capacity, an imbalance that might underlie their vulnerability to photoinhibition [50]. Young leaves are also more vulnerable to insect attack [51], and leaf burst in seasonal environments coincides with high insect herbivore pressure. Therefore, hypotheses proposed for autumn leaf reddening (photoprotection or coevolution) could also apply to young leaves.

Comparisons of red and green young leaf phenotypes failed to detect a protective effect of anthocyanins in *Quercus coccifera* [27]. By contrast, insect damage appears higher in green than in red young leaves in the same species [27] and in the tropical genus *Shorea* [52]. Moreover, leaf redness is positively correlated with the leaf chemical defensive potential (total phenolics) [48], as predicted by the coevolution hypothesis. This correlation, however, is not found in all species, suggesting either the involvement of other chemical defences, a high degree of mimicry [27] or a cryptic [53,54] or anticamouflage function [55].

Winter reddening

The leaves of many broad-leaf evergreen species turn red in winter (**Figure 1b**). The photoprotection hypothesis is a reasonable explanation, because cold temperature combined with high light increases the risk of photoinhibition [22,56]. Although some proof exists for a photoprotective function in evergreens [22,24], other studies have been unable to demonstrate such function [57]. There is no evidence that winter reddening confers protection against herbivores in evergreens.

Other cases

The undersurfaces of floating leaves of aquatic plants and understory plants are often red. Red pigments here do not appear to function in backscattering red light, as originally proposed, but could function to attenuate internal light during high-intensity sun flecks [2,58]. Colour might also have a coevolutionary function, but no evidence is available for these cases. Thorny, spiny and prickly plants also often have conspicuous colours. It is possible that their colours are aposematic and associated with poisonous or distasteful effects [59], but a photoprotective role cannot be ruled out.



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Figure 1. Non-autumnal red leaves. (a) Winter reddening in the evergreen *Galax urceolata* and (b) red young leaves of mango (*Mangifera* sp.).

Box 3. Alternative hypotheses of autumn colouration

Alternative hypotheses have been presented to explain the evolution of autumn colouration.

Hypotheses yet to be tested or not well supported by experimental evidence

Osmotic function: anthocyanins could function as a solute to help decrease leaf osmotic potential, thereby contributing to tolerance to drought stress during senescence [60]. Evidence for an osmoticum function is lacking and seems unlikely, as anthocyanins contribute <1% to the osmotic potential of a leaf [56], and other solutes, such as ions or simple sugars, would seem to be more effective.

Leaf warming: anthocyanins convert light into heat, which could warm leaves and increase rates of transpiration and metabolism, or protect against cold temperatures [61]. However, there is evidence against a warming function of anthocyanins in leaves of tropical and temperate climates [5,10].

Fruit flag: autumn colours could attract birds that enable better seed dispersal [62]. This is relevant only for species with bird-dispersed fruits that ripen in autumn, for example the genus *Rhus*; however, the hypothesis was not supported in this genus [63].

Direct defence: anthocyanins could make leaves unpalatable to herbivores or could inhibit fungal growth; however, available evidence suggests that neither is the case [10].

Camouflage: similarly to the young leaves of tropical trees [53,54], red autumn leaves [47] and spring/winter red leaves [27] might be more difficult for herbivores lacking a red photoreceptor to detect.

Anticamouflage: plant colouration could undermine the camouflage of herbivorous insects, thus exposing them to predators and parasitoids [55].

Tritrophic mutualism: autumn colours could attract myrmecophilous aphids, which in turn attract aphid-tending ants; these could defend the trees against other herbivores [64].

Other hypotheses

Insects could prefer yellow leaves because they have more nutrients ('nutrient retranslocation hypothesis' [65]) or avoid red leaves because they have more chemical defences ('defence indication hypothesis' [66]); these are simply predictions about insect behaviour based on the photoprotection and the coevolution hypotheses, rather than new hypotheses on the evolution of autumn colours [18].

The coevolution hypothesis suggests that red is a signal that the tree is not a suitable host for insects, but it is not specific about why. It could be because in trees with red leaves more nutrients are allocated to reproduction and, therefore, are not available in the leaves ('reproductive insurance hypothesis' [67]) or because red leaves are going to fall shortly [8]; these are simply specific examples of the coevolution hypothesis [18].

Aposematism [8] is equivalent to the coevolution hypothesis; however, if autumn colours are a handicap [6], it might be argued that such colouration is conceptually different from aposematism [18,68].

(they are going to fall shortly anyway), but that functional leaves enable a better resorption of nutrients, especially nitrogen and phosphorus [3,4].

Does red colouration have a direct screening effect?

The ability of anthocyanins to absorb light *in vivo* has been demonstrated optically in several studies [10,13]. Whether this translates into photoprotection or not is less clear. Recent studies have shown support for a photoprotective function in senescing leaves [4], young leaves [21] and evergreens [22,23] by demonstrating that red leaves are less light stressed than are non-red leaves under photo-inhibitory conditions. Red leaves also appear to exhibit shade characteristics relative to green conspecifics [24–26], possibly linked to photoprotection. Other recent studies, however, have shown no evidence for a photoprotective effect of anthocyanins, either in senescing [5], young [25,27] or mature [26,28–30] leaves. One source of doubt in some studies is that the strength of the non-anthocyanic photoprotective capacities of the compared green and red leaves was unknown; however, two of these studies [28,30] avoided the problem by comparing green and red sectors of the same leaf. The photoprotective function tested in all of these studies pertained exclusively to protection of the photosynthetic apparatus; there might also be other photo-reactive molecules that anthocyanins might be screening that are specific to senescence (e.g. chlorophyll metabolites).

Does red colouration have an indirect antioxidant effect?

Anthocyanins have been shown to function as *in vivo* antioxidants, effectively neutralising various ROS [13,31,32]. Hydrogen peroxide is the most probable target for neutralisation by anthocyanins, because it is the only ROS known to be able to penetrate both chloroplast, where ROS are produced, and vacuole, where anthocyanins are

stored [33]. Experiments using leaf extracts have, however, yielded conflicting results. Leaf extracts from red morphs have higher antioxidant capacity compared with green morphs in *Elatostema rugosum* [34] but not in *Quintinia serrata* [35] or *Galax urceolata* [22]. No studies have yet specifically tested an antioxidant function of anthocyanins in senescing leaves.

Does photoprotection enable enhanced resorption of nutrients?

Results comparing relative nutrient absorption efficiency between leaves differing in anthocyanin content are also conflicting. An earlier study [4] found no difference in nitrogen resorption efficiency by anthocyanic species or phenotypes relative to acyanic ones, a fact that is inconsistent with the hypothesis. By contrast, two later studies are consistent with the hypothesis: one showed a negative intraspecific correlation between anthocyanin and foliar nitrogen in a variety of species in New England [5] (the need for photoprotection, however, failed to explain the greater leaf mass per area of autumn-red species [5]), whereas a second showed that anthocyanic phenotypes of *Cornus sericea*, *Vaccinium elliottii* and *Viburnum sargentii* translocate significantly more foliar nitrogen than do acyanic mutant phenotypes [36]. Sugar maples *Acer saccharum* with limited nitrogen and which would benefit most from enhanced nitrogen resorption have greater and earlier anthocyanin expression, consistent with photoprotection [17]; moreover, in sugar maple, anthocyanins might delay the progression of the abscission layer through the leaf–branch interface, providing greater opportunities for nitrogen resorption before leaf drop [37]. Despite this evidence linking anthocyanins and increased translocation of nitrogen, the results are purely correlative. As of yet, there is no described mechanism by which the absorption of light by anthocyanins results in enhanced nutrient uptake.

Box 4. Autumn colours as seen through the eyes of insects

To test whether insects can differentiate between green and red leaves, one must be precise about what red and green mean. An objective classification into colour names can be achieved by measuring leaf colours with a spectrophotometer and feeding the resulting reflectance spectra into an objective colour-naming model specific for human vision [47]. However, because the colour perception of humans versus insects is so different, predicting insect colour preference for leaves whose colour has been defined by a human observer is impossible [47].

In particular, leaf colours that form distinct clusters in the human colour space (red versus green) might not be distinguishable by insects that lack a red receptor (such as aphids [38]). Leaves that appear red or green to a human observer might differ only in intensity for aphids, so that visual differences might be lost under varying illumination conditions [45]. Therefore, a test with artificial red and green paint [46] cannot freely be extrapolated to leaf colours.

A general colour preference model was recently developed to test whether the colour of red and green leaves would be perceptually equal for aphids [47]. To build the model, landing rates of aphids in coloured traps were analysed by using information on the colour spectra of the traps and the photo-receptor physiology of the insects (Figure 1). This model can assess the attractiveness of any given colour spectrum for aphids, including leaf colours.

The model showed that, despite their lack of a red receptor, aphids can distinguish between red and green leaf spectra and that, on average, the colour of red leaves is 70% less attractive than that of green leaves [47]. According to the model, this effect could be relatively robust against changes in illumination. Yellow, by contrast, is more attractive than is green for aphids [47], a fact that was not recognised in a previous study on aphids in autumn [16].

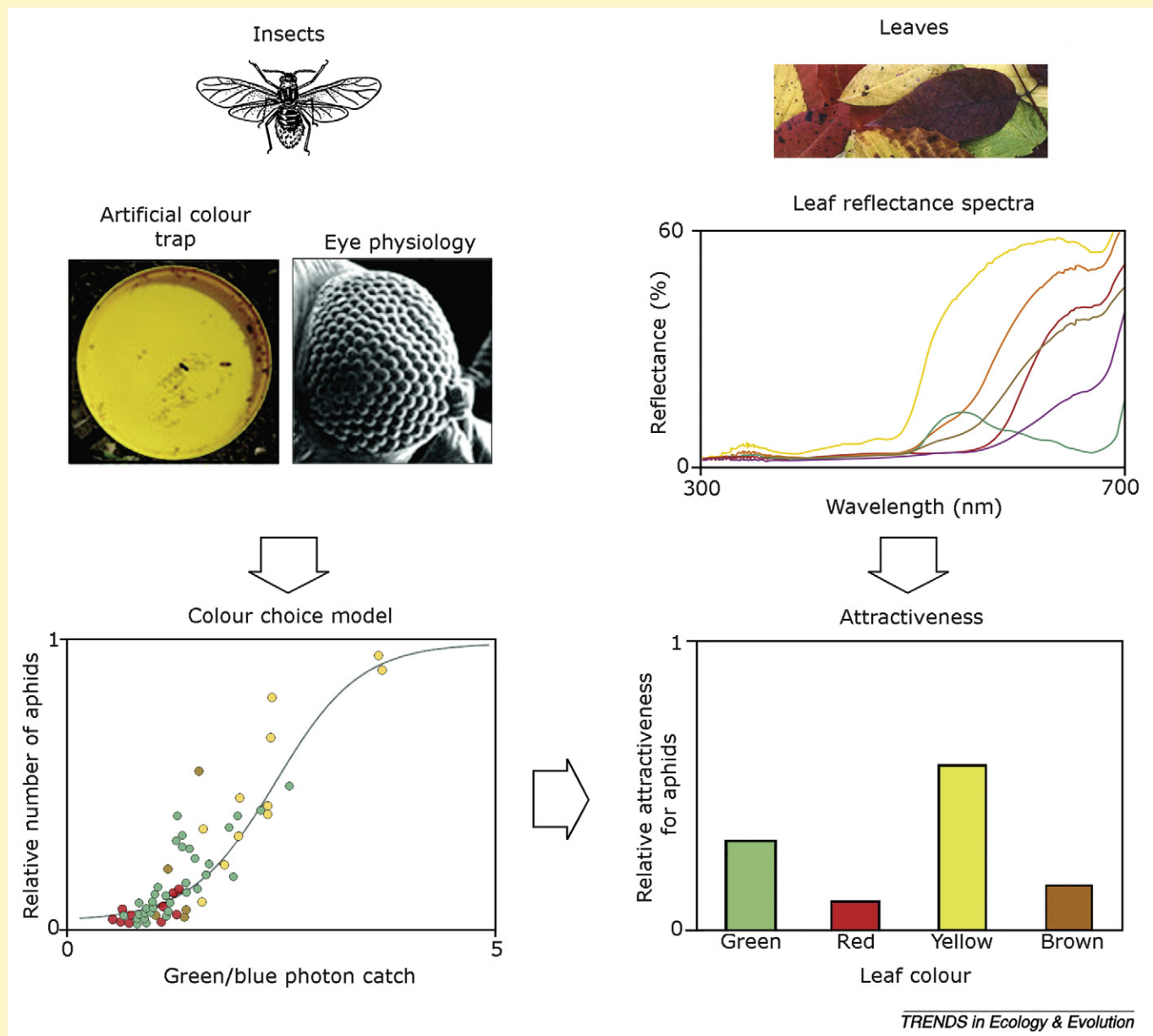


Figure 1. Measuring colour preference in insects. An objective colour measure (the leaf reflectance spectra) of leaves is integrated with a colour choice model for aphids (derived from artificial colour trap measures and the physiology of aphid colour vision) to obtain a measure of the attractiveness for aphids of leaf colours according to colour names based on human vision.

The coevolution hypothesis: red as a warning signal reduces insect attack

According to the coevolution hypothesis, autumn colouration is a signal of quality directed to insects that migrate to the trees in autumn: red might be a signal that the tree is not a suitable host for insects, because of high levels of chemical defences, lower nutritional quality or imminent leaf fall, or any other characteristic that would induce a lower fitness in the insects [6,7,38,39]. Possible receivers of the signal are insect species that migrate to the trees in autumn. Many aphid species, for example [40], migrate from their summer host (usually a herbaceous plant) to trees in autumn: they land on the leaves and lay their eggs on the trees' twigs, often close to the winter buds; the eggs hatch in spring, when aphids develop on the tree before migrating to their summer host.

Because autumn migration is a crucial step in the life cycle of many insects [40], they are under strong selective pressure to find the most suitable host, and because many insects respond to colours they could use leaf colour as a signal of the quality of the tree. The tree, by contrast, would benefit from reducing its insect load, because insects can cause considerable damage to their host trees, particularly in spring, when the next generation hatches from the eggs laid in autumn. Insects cause damage not only through direct feeding but also because they are vectors of viruses, pathogenic fungi and bacteria. Insects moving to the trees in autumn would preferentially colonise green rather than red leaves, and trees with red leaves would reduce their insect load. Autumn colours and the preference of insects for green leaves would therefore coevolve in an arms race: red leaves as an adaptation to reduce insect-induced fitness costs, and insect preference for green leaves as an adaptation to find the most suitable host trees.

Red, even if it is a costly signal, is not expected to be displayed only by vigorous trees; it is possible that weak trees display stronger autumn colours because they are the ones with more need to avoid insects [38,39]. Species with highest nutrient availability, for example, could afford to

replace tissue lost to increased herbivory, and therefore invest less in defences and more in spring growth.

Comparative evidence

Comparative analysis of 262 tree species shows that the species with autumn colours (for example *Acer* species) correspond to those with an evolutionary history of interaction with aphids in autumn [7]. This could explain the interspecific diversity of autumn colours, as species with no need to signal would not need to evolve autumn colours. This analysis [7], however, lacks a proper phylogenetic basis, and needs to be confirmed by further studies.

Do autumn-migrating insects prefer green over red leaves?

Before the initial proposal of the coevolution hypothesis, a study on Japanese maples *Acer palmatum* [15] had already shown that aphids are more abundant on green and yellow leaves than they are on red leaves. The first empirical test, however, was not until 2003 on mountain birch *Betula pubescens* in Norway: this study showed that trees with green leaves suffered more herbivory than did trees with autumn colours [41,42]. *B. pubescens*, however, turns yellow rather than red in autumn. Herbivory was measured indirectly in spring, not observed directly in autumn and was not due to aphids. The first study to monitor insect choice in autumn on a species with red autumn colours [16] showed that the peak of autumn migration of *Rhopalosiphum padi* aphids to their winter host (*Prunus padus*) corresponds to the peak of leaf colour variation, and that aphid number was negatively correlated with the intensity of autumn colouration (the percent of red versus green leaves). Similar results were eventually found for aphids on *Nothofagus alexandrii* in Chile [43] and on *Sorbus aucuparia* in Germany [44]. Lower herbivory (not due to aphids) on red leaves was also found for the young red leaves of *Quercus coccifera* in Greece [27].

These studies suggest that insects, aphids in particular, prefer green over red leaves, but raise an intriguing ques-

Box 5. Outstanding questions

- How does photoprotection result in enhanced nutrient uptake? Future experiments should explain how the beneficial effect of photoprotection results in better nutrient mobilisation. Current evidence is purely correlative (red leaves reabsorb more nutrients).
- How can we explain the contrasting results on the photoprotection hypothesis? We need more studies, or a reassessment of contrasting cases, to explain the potential adaptive benefit of anthocyanins against abiotic factors (direct screening, antioxidant function, resorption of nutrients).
- Are anthocyanins optimal for a direct screening function? Leaf anthocyanins absorb most strongly in the green waveband, where the probability of photon absorption by chlorophylls (and therefore damage) is low [22,56].
- Are anthocyanins optimal for an indirect antioxidant function? Colourless flavonoids and phenolics from the same biosynthetic pathway as anthocyanins have similar or greater antioxidative strength, higher concentrations and are more optimally located within cells/tissues to fulfill an antioxidant function [56,69–71].
- Are autumn colours a true signal? If red and colour preference coevolved, is red a true signal or an index [68]? Does mimicry exist among trees with autumn colours? [8]. Evidence that insects prefer

green over red leaves is also compatible with sensory exploitation of insect vision by trees (camouflage [27,47]): in this case, however, leaves should be blue rather than red [47].

- Is there a fitness cost for insects that colonise autumn-red trees? If true, is this due to chemical defences, availability of nutrients or other factors that affect the fitness of the insects? The only available evidence is indirect (a positive correlation between anthocyanins and phenolics [48]).
- What is the fitness cost for trees that are colonised by insects? Avoiding herbivory, phloem feeding and the transmission of disease is certainly important for a tree, but we lack a quantitative measure of the fitness effects of reducing insect load.
- What species, besides aphids, are important for the coevolution hypothesis? Empirical work on the coevolution hypothesis has focussed on aphids, but the idea could be extended to other insect pests that migrate to the trees in autumn.
- Does coevolution apply to yellow leaves? Carotenoids are not usually manufactured in autumn, but loss of chlorophyll is costly because it reduces photosynthesis, and this might be relevant for species living at high latitudes, where the growing season is short. Aphids are attracted by yellow, but it might be a warning signal for other insects [41,42].

tion: because many insects appear to lack a red photoreceptor, how can they reliably distinguish green from red? [45]. One study [46] did not find any differences in preference by aphids between red and green artificial colours (Box 4), and it was suggested that aphids are not attracted or repelled by the colour but by some associated quality, such as chemicals or volatiles [46]. The results of a recent study [47] combining artificial colour traps with the colour spectra of the autumn leaves of 113 tree species, however, reveal that aphids would be 68% less attracted by the colour of red leaves (Box 4) [47], which is consistent with the coevolution hypothesis and previous field studies [16,43,44]. Importantly, however, this is not enough to confirm that red is a signal, because it does not show that preference in the aphids evolved as a response to leaf colours.

Are there benefits for insects choosing non-red leaves?

If red leaves are a signal that the tree is not a suitable host, then insects should perform better on trees that have green leaves in autumn. Evidence to support this idea is, however, still inconclusive. In the first empirical studies on autumn colours, it was not possible to measure aphid growth rates. In one case, however, it was known from previous studies on the same trees that aphids grow better in spring on trees that retain their leaves for longer in autumn [16], and that these trees were the ones with green leaves in autumn. The only study that directly tested differences in aphid growth rates in spring [43] did not show any difference in aphid growth rates between autumn-red and autumn-green trees, although this was studied with individual red leaves of trees that were otherwise almost entirely yellow or green. Another recent study [48] shows that anthocyanin (red) content is positively correlated with phenolics in several species, which suggests a positive correlation between autumn colours and chemical defences, consistent with the coevolution hypothesis.

Perspectives

Although the photoprotection and the coevolution hypotheses have received much attention recently, we need more data and more carefully designed experiments (Box 5) to be able to accept or reject either hypothesis categorically. The photoprotection hypothesis is controversial but still tenable. Its main predictions (direct screening, antioxidant function and efficient resorption of nutrients) have been confirmed by some studies and rejected by others. The coevolution hypothesis has yet to be tested as intensely as the photoprotection hypothesis. The available tests performed so far (comparative evidence and colour preference) are consistent with the hypothesis, but more studies are necessary to confirm these results, and there are outstanding points (e.g. the link between colour and defences). The basic assumptions and predictions of other hypotheses (Box 3) still need to be tested.

Although empirical field tests are going to be necessary to explain the intraspecific variation in autumn colours, comparative analyses are still needed to account for the interspecific variation; currently, comparative data are available only for the coevolution hypothesis [7] and in

part for the photoprotection hypothesis [5]. Any hypothesis that is not able to address this problem is likely to be only of limited interest. Information on the distribution of autumn colours is scattered throughout the literature, and a compiled list of leaf colours in different species, not only trees, would be most welcome [14].

Perhaps because of the proliferation of hypotheses, it has been suggested [8] that autumn colours have multiple roles, from photoprotection to protection against herbivores. Although this is certainly possible, we believe that it is still premature to look for a pluralistic approach. Individual hypotheses must still be tested thoroughly.

It is curious how autumn colours, given that they are such an astonishing and well-known phenomenon, have continuously escaped the attention of evolutionary biologists. The explanation of their adaptive value might not be far away, as many data are already available about the proximate mechanisms, and efforts to join forces between different fields are under way. For the moment, we have many leads to follow, and an expectation of unexplored and fascinating mysteries to unravel.

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