

Autumn colours and the nutrient retranslocation hypothesis: A theoretical assessment

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Abstract

The adaptive value of the bright colours of leaves in autumn is still debated. It is possible that autumn colours are an adaptation to protect the tree against photoinhibition and photooxidation, which allows a more efficient recovery of nutrients. It has been proposed that the preference of aphids for trees that retranslocate nitrogen more efficiently can explain the high diversity of aphids on tree species with bright autumn colours. This scenario however does not take into account the impact of insects on the fitness of the trees and has not been analysed theoretically. Its assumptions and predictions, therefore, remain uncertain. I show with a model of insect–tree interaction that the system can actually evolve under particular conditions. I discuss the differences with the coevolution theory of autumn colours, available evidence and possible tests.

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1. Introduction

1.1. Autumn colours and nutrient retranslocation

Why the leaves of many deciduous tree species change their colour in autumn remains uncertain. It has been proposed that bright colours are warning signals against insects, for example aphids, that lay their eggs on the trees in autumn (the Coevolution Theory—Archetti, 2000; Hamilton and Brown, 2001; Archetti and Brown, 2004). Another possibility is that autumn colours are a protection against photoinhibition and photooxidation (reviewed in Lee, 2002a,b; Lee and Gould, 2002): trees with bright autumn colours may reabsorb nutrients more efficiently in autumn before leaf fall. In this case, however, it is not clear whether insects should develop a preference for certain colours.

Holopainen and Peltonen (2002) proposed the “Nutrient Retranslocation Hypothesis”—but White (2003) claims

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that it is actually a subset of an older idea (White, 1993)—to explain the high diversity of aphids on tree species with bright autumn colours observed by Hamilton and Brown (2001). The Nutrient Retranslocation (“NR”) hypothesis suggests that, because trees with bright (yellow and red) leaves are well protected against photoinhibition and recover nitrogen more efficiently, insects migrating in autumn actively look for trees with bright leaves, because they provide better nutrition (linked with nitrogen).

In this scenario, insects are not the driving force of the evolution of autumn colours, which is suggested instead by the Coevolution Theory (Archetti, 2000; Hamilton and Brown, 2001; Archetti and Brown, 2004). The NR hypothesis therefore is not a new adaptive explanation for autumn colours (this is already assumed to be the protection against photoinhibition and photooxidation) but a prediction about insect preference: aphids and other autumn migrating insects prefer trees with red and yellow leaves because they provide better nutrition.

It is important to point out that leaves with bright colours have *less*, not more, nitrogen than green leaves (Lee, 2002a,b; Lee and Gould, 2002; Lee, personal communication). Trees with brighter leaves, however, or

with bright leaves lasting for longer, may recover nitrogen more efficiently, which would allow them to have more nitrogen available in spring. The NR hypothesis, therefore, makes sense if the insects feed on the tree in spring, like many aphids do for example.

1.2. Analysing costs and benefits

Holopainen and Peltonen (2002) did not introduce in their verbal argument the impact of aphid choice on tree fitness. What would happen if a mutant tree avoided the production of colour in autumn? It would clearly have a cost due to the lack of protection, but also an advantage due to a lack of aphids. If the trees with bright colours were the ones with associated higher defences against aphids, would aphids still prefer red? The NR hypothesis would require a simple theoretical analysis (similar to the one developed for the Coevolution Theory—Archetti, 2000) of cost and benefits to understand its plausibility, but unfortunately Holopainen and Peltonen (2002) did not provide it, therefore its assumptions and predictions remain uncertain.

I will develop a model of aphid–tree interaction and I will analyse the stability and the dynamics of the system to understand under which conditions the scenario proposed by Holopainen and Peltonen (2002) is possible. This will provide a clear statement of assumptions and predictions of the NR hypothesis. Finally, I will discuss these results and available evidence for the NR hypothesis in the context of the evolution of autumn colours.

2. A model of insect–tree coevolution

I describe a situation in which insects use trees as a host for the winter: in autumn they migrate to the trees to lay their eggs, which overwinter on the tree producing new progeny in spring. In spring then the offspring leave the trees to migrate to their secondary host (an herbaceous plant). This is a typical life cycle of many aphid species, therefore, I will refer to aphids in the model, but the model may be relevant for any other insect species with a similar life cycle.

2.1. Strategies

I assume that the fitness of a tree depends on both its own properties and on the attack of aphids. I use a discrete model in which a tree is assigned two possible values (*high* or *low*) for each of two properties: defences and colour. *Defences* (d) measures the level of chemical defences of the tree against aphids, which can be either strong ($d = \mathbf{D}$) or weak ($d = \mathbf{d}$). *Colour* (s) measures the intensity of the autumn leaf colour, which I assume can be either red ($s = \mathbf{S}$) or green ($s = \mathbf{s}$).

I assume that the level of defences (d) is not dependent on the genotype but on tree condition that depends on the environment and I consider an equal frequency of \mathbf{d} and \mathbf{D}

trees ($f_{\mathbf{d}} = f_{\mathbf{D}} = 1/2$). Because what matters is the relative value of d , this assumption does not affect the generality of the results and only means that low defences are equally likely as high defences, that is the threshold defining high and low is exactly the mean value of the population.

Colour (s) is also not genetically determined but is a response to the d phenotype. This response depends on the strategy (i) of the tree. Only the tree strategies (production of colour according to the level of defences), therefore, are genetically determined and are under selection. The level of defences (d) depends on the environment and the colour (s) depends on both d and on the tree strategy (i). I assume that a tree can produce either red (\mathbf{S}) or green (\mathbf{s}) according to its d , but not an intermediate frequency of both colours. This allows four possible tree strategies (see Table 1): always green ($i = 1$); red if \mathbf{D} ($i = 2$); red if \mathbf{d} ($i = 3$); always red ($i = 4$), with frequencies, respectively, t_1, t_2, t_3, t_4 .

Aphids cannot perceive directly d but only s . This means that they can assess the suitability of the tree as host only by evaluating its colour (displayed at the moment of choice in autumn), not the level of defences (acting mainly in the following spring on their progeny). Therefore, there are three possible aphid strategies (j), no preference ($j = 1$), preference for \mathbf{s} ($j = 2$), preference for \mathbf{S} ($j = 3$), with frequencies, respectively, a_1, a_2, a_3 .

The probability y_{js} of choosing a colour s associated with each strategy j depends on the frequency of \mathbf{s} and \mathbf{S} trees ($f_{\mathbf{s}}$ and $f_{\mathbf{S}}$). I use an exponential function ($f_{\mathbf{s}}^{1/M}$) to avoid a discontinuity in $f_{\mathbf{s}} = 0$, that is when there is only one kind of tree colour but only aphids with the opposite preference (Table 2). With this model, with M sufficiently high ($M > 1$) aphids choose always trees corresponding to their preference if these are not very rare, but as the frequency of these trees approaches zero, they also choose trees of the opposite colour.

Table 1

The probability (x_{ids}) of being s for an i tree according to its condition d

i	\mathbf{S} (red)	x_{ids}	$x_{id\mathbf{S}}$	$x_{i\mathbf{D}s}$	$x_{i\mathbf{D}\mathbf{S}}$
1	Never	1	0	1	0
2	If \mathbf{D}	1	0	0	1
3	If \mathbf{d}	0	1	1	0
4	Always	0	1	0	1

Table 2

The probability (y_{js}) of choosing s for a j aphid

j	Preference	$y_{j\mathbf{s}}$	$y_{j\mathbf{S}}$
1	No preference	$f_{\mathbf{s}}$	$f_{\mathbf{S}}$
2	Prefer green	$f_{\mathbf{s}}^{1/M}$	$1 - f_{\mathbf{s}}^{1/M}$
3	Prefer red	$1 - f_{\mathbf{S}}^{1/M}$	$f_{\mathbf{S}}^{1/M}$

2.2. Fitness

The rate of survival of a ds tree in the growth phase is λ_{ds} and its survival in autumn during aphid attack is ϕ_{ds} . Therefore the fitness of a tree strategy i can be defined by

$$W_t(i) = \sum_{ds} f_d x_{ids} \lambda_{ds} \phi_{ds}.$$

The values of x_{ids} define the tree strategies (see Table 1). With $f_d = f_D = \frac{1}{2}$, therefore, the values of $W_t(i)$ are:

$$\begin{aligned} W_t(1) &= \frac{1}{2} \lambda_{ds} \phi_{ds} + \frac{1}{2} \lambda_{Ds} \phi_{Ds}, \\ W_t(2) &= \frac{1}{2} \lambda_{ds} \phi_{ds} + \frac{1}{2} \lambda_{Ds} \phi_{Ds}, \\ W_t(3) &= \frac{1}{2} \lambda_{ds} \phi_{ds} + \frac{1}{2} \lambda_{Ds} \phi_{Ds}, \\ W_t(4) &= \frac{1}{2} \lambda_{ds} \phi_{ds} + \frac{1}{2} \lambda_{Ds} \phi_{Ds}. \end{aligned}$$

The quantity ϕ_{ds} depends on the frequency (a_j) of each aphid strategy j and on the cost (σ'_d) due to the attack of the aphid population on d trees. With frequency $(1 - y_{js})$ the colour s is avoided by the aphids j and the fitness for the tree is equal to 1; with frequency y_{js} the colour is chosen by the aphids: in this case the probability that an individual tree (ds) is chosen is $1/Nf_s$, where N is the number of trees on which the attack is concentrated: in this case the fitness for the tree is $(1 - \sigma'_d)$; otherwise, with frequency $(Nf_s - 1)/Nf_s$, its fitness is 1 because the tree is not attacked. Therefore ϕ_{ds} can be written

$$\phi_{ds} = \sum_j a_j \left\{ \underbrace{(1 - y_{js})}_{\text{colour avoided}} + y_{js} \underbrace{\left[\frac{Nf_s - 1}{Nf_s} + \frac{1}{Nf_s} (1 - \sigma'_d) \right]}_{\text{colour chosen}} \right\}.$$

N can be incorporated in σ'_d without loss of generality and σ'_d can be substituted with $\sigma_d = \sigma'_d/N$, which is the cost due to part of the aphid population that attacks the tree. Thus ϕ_{ds} reduces to

$$\phi_{ds} = \sum_j a_j \{1 - y_{js} \sigma_d / f_s\}.$$

Therefore with $M = \infty$ the values of ϕ_{ds} are:

$$\begin{aligned} \phi_{ds} &= a_1(1 - \sigma_d) + a_2(1 - \sigma_d/f_s) + a_3(1), \\ \phi_{dS} &= a_1(1 - \sigma_d) + a_2(1) + a_3(1 - \sigma_d/f_s), \\ \phi_{Ds} &= a_1(1 - \sigma_D) + a_2(1 - \sigma_D/f_s) + a_3(1), \\ \phi_{DS} &= a_1(1 - \sigma_D) + a_2(1) + a_3(1 - \sigma_D/f_s). \end{aligned}$$

Aphid fitness depends only on their performance on the different kinds of trees and on the frequency of the different tree strategies. Therefore the fitness $W_a(j)$ of aphids with no preference ($j = 1$) or preferring green

($j = 2$) or red ($j = 3$) are, respectively,

$$\begin{aligned} W_a(1) &= f_{ds} \gamma_{ds} + f_{Ds} \gamma_{Ds} + f_{ds} \gamma_{ds} + f_{Ds} \gamma_{Ds}, \\ W_a(2) &= (f_{ds} \gamma_{ds} + f_{Ds} \gamma_{Ds}) / f_s, \\ W_a(3) &= (f_{ds} \gamma_{ds} + f_{Ds} \gamma_{Ds}) / f_s, \end{aligned}$$

where f_{ds} is the frequency of ds trees in the population and f_s is the frequency of s trees in the population; γ_{ds} is the fitness of an aphid on a ds tree.

2.3. Evolutionary stability

I use a game theory model (Maynard-Smith, 1982), with haploid, asexual inheritance; recombination and diploidy are unlikely to make a substantial difference. This model, however, provides only a way to test the evolutionary stability of the system but not a definitive proof that the system can actually evolve. Therefore, it will provide necessary (but not sufficient) assumptions for the NR hypothesis to be stable. After checking the stability of the system I will use a computer simulation to study the origin and the dynamics of the model.

In order to ascertain whether a couple of strategies, one for the trees (i^*) and one for the aphids (j^*), is evolutionarily stable (ESS—Maynard-Smith, 1982), the following system of inequalities must be solved:

$$\begin{cases} W_t(i^*) > W_t(i) \\ W_a(j^*) > W_a(j) \end{cases}$$

for all aphid strategies j and all tree strategies i . Therefore, with each aphid strategy j^* fixed in the population ($f_{j^*} = 1$), the fitness of all the tree strategies must be calculated to check whether, and for which parameters, a tree strategy i^* satisfies the condition $W_t(i^*) > W_t(i)$ for all other tree strategies i . Then, with each tree strategy i^* fixed in the population ($f_{i^*} = 1$) the fitness of all the aphid strategies must be calculated to check whether, and for which parameters, an aphid strategy j^* satisfies the condition $W_a(j^*) > W_a(j)$ for all other aphid strategies j .

Because this does not affect the generality of the stability analysis, I will use $M = \infty$, that is complete preference for red or for green (this leaves us with two particular indeterminate cases in which there is preference for a colour but all trees of the opposite colour: this case is easy to analyse and is always an indifferent equilibrium even with $M < \infty$). These assumptions can be relaxed in the simulations, where I will use $M = 10$ to add more realism to the model.

2.4. Evolutionary dynamics

In the simulations, I will describe the origin and the dynamics of the system. The simulations are based on a simple replicator-dynamics algorithm (haploid, asexual) using the same fitness functions described above but a finite value of M (in this case it is possible that fitness becomes negative for very small values of f_s : if this happens fitness is

set to zero), in which the frequency t_i of a tree strategy i after each generation is $t'_i = t_i W_i(i)/W_i^*$ (where W_i^* is the mean fitness of the tree population), and the frequency a_j of an aphid strategy j after each generation is $a'_j = a_j W_a(j)/W_a^*$ (where W_a^* is the mean fitness of the aphid population).

3. Results

3.1. Evolutionary stability

The general conditions that must be satisfied are $\lambda_{ds} > \lambda_{ds}$ (the production of defences has a cost), $\gamma_{ds} < \gamma_{ds}$ (aphids perform better on trees with low defences) and $\sigma_D < \sigma_d$ (the damage due to aphids is lower in trees with high defences). These conditions are valid also for the Coevolution Theory (Archetti, 2000). The NR hypothesis requires, in addition, that $\gamma_{ds} < \gamma_{ds}$ (because S trees are supposed to provide better nutrition for aphids) and $\lambda_{ds} > \lambda_{ds}$ (because red protects trees against photoinhibition), whereas in the Coevolution Theory $\lambda_{ds} < \lambda_{ds}$ (the production of colour has a cost) and $\gamma_{ds} = \gamma_{ds}$ (aphid performance does not depend on tree colour).

The stability analysis shows that if aphids prefer green ($a_2 = 1$) or have no preference ($a_1 = 1$), then no pure tree strategy is stable. With $a_3 = 1$, instead, stability is possible. It is convenient to define the quantity $\kappa_d = (1 - \lambda_{ds}/\lambda_{ds})$, the relative cost for the absence of colour (due to the damage of photoinhibition and photooxidation) for a tree S compared to a tree S with the same d value. The conditions for the stability of the different tree strategies turn out to depend on the relationship between κ_d and σ_d/f_S as described below. Note that these conditions depend on

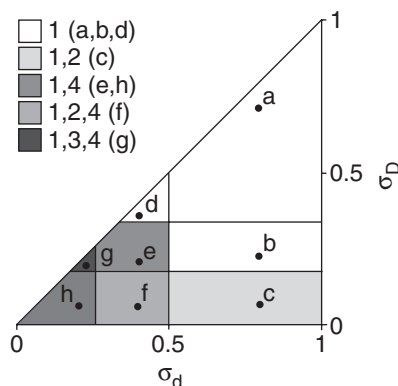


Fig. 1. The possible combinations of stability for pure strategies depending on σ_d with given λ_{ds} ($\lambda_{ds} = 0.5$; $\lambda_{ds} = 1$; $\lambda_{ds} = 0.4$; $\lambda_{ds} = 0.6$). (1) $\sigma_d/f_S > \kappa_d$, $\sigma_D/f_S > \kappa_D$: ($i = 1$) is stable with $a_3 = 1$ but aphid strategies are neutral with $t_1 = 1$. (2) $\sigma_d/f_S > \kappa_d$, $\sigma_D/f_S < \kappa_D$: no couple of pure strategies. (3) $\sigma_d/f_S < \kappa_d$, $\sigma_D/f_S > \kappa_D$: ($t_3 = 1$, $a_3 = 1$) stable. (4) $\sigma_d/f_S < \kappa_d$, $\sigma_D/f_S < \kappa_D$: ($i = 4$) is stable with $a_3 = 1$ but aphid strategies are neutral with $t_4 = 1$. Because stability depends on f_S , which depends on the tree strategies present, for certain parameters more than one stable strategy is possible.

f_S , which depends on the tree strategies. Therefore with certain sets of parameters λ_{ds} and σ_d more than one tree strategy could be stable (Fig. 1).

The inequality sign of the following cases (1–4) means if the cost due to aphid attack (σ_d/f_S) would be larger or smaller than the relative cost due to photoinhibition (κ_d)—if the tree did not have red autumn colours—for trees with the given d values.

- (1) $\sigma_d/f_S > \kappa_d$ and $\sigma_D/f_S > \kappa_D$. Strategy $i = 1$ (always green) is possible with $a_3 = 1$ if $\sigma_d/f_S > \kappa_d$ and $\sigma_D/f_S > \kappa_D$, that is if the impact of aphids on all kinds of trees is high (higher than the relative cost for the absence of the colour): preference for red increases quickly because aphids preferring S trees perform better, but as they increase in frequency green trees (s) have a strong advantage and go to fixation. With $t_1 = 1$, however, there is no possible choice for aphids (only green trees and complete preference for red): this equilibrium, therefore, is not strictly stable, because other aphid strategies have all the same fitness and can invade with $t_1 = 1$.
- (2) $\sigma_d/f_S > \kappa_d$ and $\sigma_D/f_S < \kappa_D$. Strategy $i = 2$ (red if D) with $a_3 = 1$ can be stable with $\sigma_d/f_S > \kappa_d$ and $\sigma_D/f_S < \kappa_D$ but aphid strategy $j = 3$ is not stable with tree strategy $i = 2$ fixed in the population ($t_2 = 1$). Therefore ($i = 2$, $j = 3$) is not an ESS.
- (3) $\sigma_d/f_S < \kappa_d$ and $\sigma_D/f_S > \kappa_D$. Strategy $i = 3$ (red if d) is stable with $a_3 = 1$ if the cost of aphid load is smaller than the cost due to lack of red colour in d trees but not in D trees. This is possible but unlikely because the assumption $\sigma_D < \sigma_d$ allows the conditions $\sigma_d/f_S < \kappa_d$ and $\sigma_D/f_S > \kappa_D$ to be possible only under a limited range of parameters (Fig. 1).
- (4) $\sigma_d/f_S < \kappa_d$ and $\sigma_D/f_S < \kappa_D$. Strategy $i = 4$ (always red), is possible with $a_3 = 1$ under a wide range of parameters (Fig. 1), because the condition $\sigma_D < \sigma_d$ does not contrast with the conditions for its stability ($\sigma_d/f_S < \kappa_d$ and $\sigma_D/f_S < \kappa_D$: the cost due to aphid attack must be smaller than the relative cost due to photoinhibition for all trees). Strategy $j = 3$, however, is not strictly stable with $t_4 = 1$, it is an indifferent equilibrium because there is no possible choice: other aphid strategies have the same fitness and can invade through drift for example, though they cannot spread through natural selection (see dynamics).

3.2. Origin and dynamics with two strategies

So far we have only checked the stability of couples of pure strategies. We have seen that one couple is possible ($t_3 = 1$, $a_3 = 1$) and that two pure tree strategies can be stable ($i = 1$ and $i = 4$) though with no pure aphid strategies. It remains to be seen whether these equilibria can be reached from the origin of the system. We can assume that the initial strategies at the origin of the system were green ($i = 1$) and no preference ($j = 1$). In a

population with these aphid and tree strategies, we can introduce one strategy for the trees and one for the insects and check whether the expected equilibria can be actually reached. Here, I analyse the dynamics introducing only one strategy for the trees and one for the insects. In the next Section I will analyse the case of multiple strategies.

Fig. 2 shows the dynamics of the system when tree strategy $i = 3$ (red if **d**) and aphid strategy $j = 3$ (preference for red) are introduced, using the parameters for which the couple ($i = 3, j = 3$) is stable (red if **d**, preference for red). The only stable equilibrium is indeed ($t_3 = 1, a_3 = 1$) (the upper right corner of Fig. 2), while ($t_3 = 1, a_1 = 1$) (the bottom right corner of Fig. 2: red if **d**, no preference) is unstable; the line $t_3 = [2a_3\lambda_{as}\sigma_d]/[(\lambda_{as}-\lambda_{ds})(1-\sigma_d+a_3\sigma_d)]$ is also a line of unstable equilibria, which divides the frequency space in which t_3 increases (t_3 higher) or decreases (t_3 smaller), while a_3 always increases (except at $t_1 = 1$ and at $a_1 = 1$); the line includes the unstable equilibrium ($t_1 = 1, a_1 = 1$) (the bottom left corner of Fig. 2: no colour, no preference) and the unstable equilibrium ($t_3 = [2\lambda_{as}]/[\lambda_{as}-\lambda_{ds}], a_3 = 1$) (on the top ridge of Fig. 2). The singularity on the left edge ($t_1 = 1$) is explained by the fact that when there are only green trees, because aphid choice has no cost, it is indifferent for aphids to have any preference, as any preference will result in the choice for the same colour (**s**). Preference for red ($a_3 = 1$) can be reached with $t_1 = 1$ (the upper left corner of Fig. 2) but this preference will remain unexpressed in the aphid population because there is only one kind of trees; lower values of a_3 could eventually evolve by drift along the line $t_1 = 1$, but as soon as a few red trees appear in the population ($t_3 > 0$) preference for red (a_3) will go back to fixation (Fig. 2).

The equilibrium ($t_3 = 1, a_3 = 1$) can be actually reached and the process seems more straightforward if red evolves before the evolution of the preference. This is possible, as red is supposed to evolve for reasons that are independent

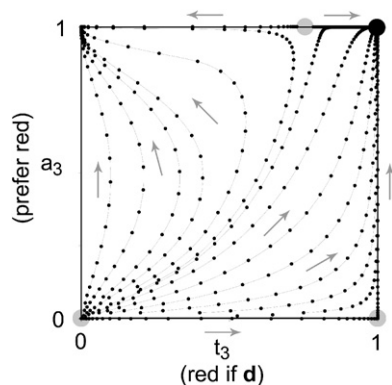


Fig. 2. Evolutionary dynamics and stability of the two tree strategies $i = 1$ (always green) and $i = 3$ (red if **d**) and of the two aphid strategies $j = 1$ (no preference) and $j = 3$ (prefer red); $a_1 = 1 - a_3$, $t_1 = 1 - t_3$; $f_d = f_D = 0.5$; $M = 10$ (with $M = 10,000$ the dynamics is virtually identical); $\lambda_{as} = 0.5$; $\lambda_{ds} = 1$; $\lambda_{Ds} = 0.4$; $\lambda_{DS} = 0.6$; $\sigma_d = 0.2$; $\sigma_D = 0.18$; $\gamma_{as} = 0.6$; $\gamma_{Ds} = 0.4$; $\gamma_{DS} = 0.5$. The black and grey circles are stable and unstable equilibria.

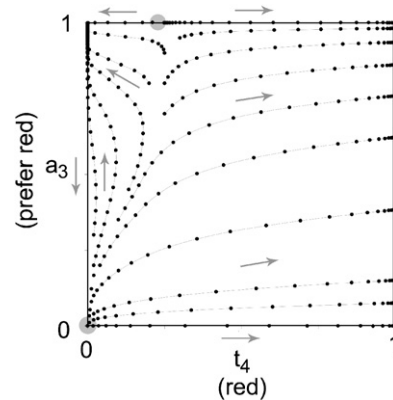


Fig. 3. Evolutionary dynamics and stability of the two tree strategies $i = 1$ (always green) and $i = 4$ (always red) and of the two aphid strategies $j = 1$ (no preference) and $j = 3$ (prefer red). Same parameters as in Fig. 2 except $\sigma_D = 0.05$ (with $M = 10,000$ the dynamics is virtually identical). The black and grey circles are stable and unstable equilibria.

from aphid choice. It is important to remember, however, that the parameter space under which this equilibrium is possible is rather restricted (see above) and that we have not yet investigated the dynamics with other strategies present in the population (see below).

Fig. 3 shows the dynamics of tree strategies $i = 4$ (always red) and aphid strategy $j = 3$ (preference for red), evolving with tree strategies $i = 1$ (always green) and aphid strategy $j = 1$ (no preference) in the parameter space where ($i = 4$) can be stable. The only stable equilibria correspond to the line ($t_4 = 1$) (the right ridge of Fig. 3); the line $t_4 = [a_3(\lambda_{as}\sigma_d + \lambda_{Ds}\sigma_D)] / \{[\lambda_{as}-\lambda_{ds}][1 + (a_3-1)\sigma_d] + [\lambda_{Ds}-\lambda_{DS}][1 + (a_3-1)\sigma_D]\}$ is a line of unstable equilibria, dividing the frequency space in which t_4 increases (t_4 higher) or decreases (t_4 smaller), while a_3 always increases (except at $t_1 = 1, t_4 = 1$ and at $a_1 = 1$); the line includes the unstable equilibrium ($t_1 = 1, a_1 = 1$) (the bottom left corner of Fig. 3: no colour, no preference) and the unstable equilibrium ($t_4 = [\lambda_{as}\sigma_d + \lambda_{Ds}\sigma_D] / [(\lambda_{as}-\lambda_{ds}) + (\lambda_{Ds}-\lambda_{DS})], a_3 = 1$) (on the top ridge of Fig. 3). The singularity on the left edge ($t_1 = 1$) is explained as for the analogous case of Fig. 2.

The equilibrium ($t_4 = 1$) can be reached and the process seems possible under a wider range of initial conditions (Fig. 3). The equilibrium ($t_4 = 1, a_3 = 1$), however, is reached only if the population is already fixed on preference for red; in the other cases the frequency of aphids with preference for red will reach an intermediate value depending on the initial frequencies (Fig. 3): in this situation ($t_4 = 1$) all aphids will choose the same colour as aphids with no preference will have no other choice than choosing **s**. The frequency of aphids might change slightly by mutation or drift along the line of neutral equilibria $t_4 = 1$. Differently from the line ($t_1 = 1$), the line ($t_4 = 1$) is an attractor and ($i = 4$) will reach fixation even if t_4 is slightly less than 1, whereas if t_1 is slightly less than 1 the population will always reach the point ($t_1 = 1, a_3 = 1$).

The simulations described above confirm that the cases ($t_3 = 1, a_3 = 1$) and ($t_4 = 1$) that can be stable according to the ESS analysis can also actually be reached from the origin in the parameter space in which they are stable.

Studying the invasion of $i = 1$ at the origin does not make sense ($i = 1$ is the wild type at the origin) but it remains to be seen whether strategy $i = 1$ (which is possible according to the stability analysis), is actually immune from invasion of other strategies in the parameter space in which it is stable. This will be done in the following section.

Strategy $i = 2$ is not stable with pure aphid strategies, according to the stability analysis, but it is also necessary to ascertain whether it can be reached with multiple strategies present in the population. This will also be done in the following section.

3.3. Origin and dynamics with more than two strategies

In the previous simulations, I have introduced a small fraction of one strategy only in a population fixed for green colour ($t_1 = 1$) and no preference ($a_1 = 1$). It is important to check what happens if more than two strategies are present in the population because more than one strategy can be stable with the same set of parameters (Fig. 1).

Fig. 4, for example, shows that tree strategy $i = 4$ (always red) is much more likely to go to fixation in the parameter space where $i = 3$ (red if **d**) is also stable: the equilibrium ($t_3 = 1, a_3 = 1$) is stable but it can be reached only if the frequency of the other tree strategy (t_4) in the population is very low. The other stable equilibrium is indeed the line $t_4 = 1$. This equilibrium is reached whenever t_4 is higher than the value of the line of unstable equilibria $t_4 = [a_3 \lambda_{DS} \sigma_D] / [(a_3 \sigma_D - \sigma_D + 1)(\lambda_{DS} - \lambda_{DS})]$, which in $a_3 = 1$ is equivalent to $t_4 = [\lambda_{DS} \sigma_D] / [\lambda_{DS} - \lambda_{DS}]$ (the unstable equilibrium on the top ridge of Fig. 4).

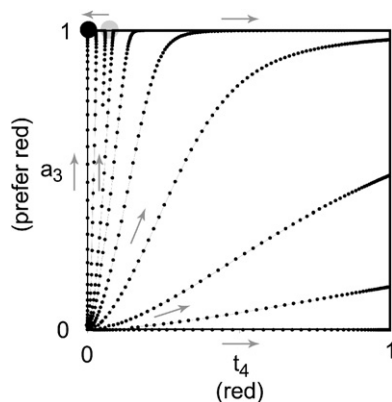


Fig. 4. Evolutionary dynamics and stability of the two tree strategies $i = 3$ (red if **d**) and $i = 4$ (always red) and of the two aphid strategies $j = 1$ (no preference) and $j = 3$ (prefer red). Same parameters as in Fig. 2 except $M = 10,000$ (with $M = 10$ the dynamics is virtually identical but the line of unstable equilibria dividing the space in which t_3 increases or decreases would be indistinguishable from $t_3 = 1$). The black and grey circles are stable and unstable equilibria.

In general, simulations with all strategies present in the population show that equilibria with more than one couple of strategies are possible (Table 3). Tree strategy $i = 4$ is the most common outcome, associated with aphid strategy $j = 3$ or with a mixture of aphid strategies (Table 3). The second more likely equilibrium is the case of no colour associated with preference for red ($t_1 = 1, a_3 = 1$), which may occur only if σ_d and σ_D are large. Note that, however, starting from the origin and introducing a low frequency (initial $a_2, a_3, t_2, t_3, t_4 = 0.05$) of all the other strategies, the result is almost always $t_4 = 1$ and a mixture of a_1 ($0.77 > a_1 > 0.84$) and a_3 ; the only exception is case (a), with σ_d and σ_D large, in which ($t_1 = 1, a_3 = 1$) is the stable equilibrium.

3.4. Summary of the results

To summarize, the most likely couple of ESS under the scenario proposed by the NR hypothesis seems to be production of red irrespective of defences ($i = 4$) and preference for red ($j = 3$), mixed with no preference ($j = 1$). In this case for the trees, it is always convenient to have red colours in autumn because this confers better protection against photoinhibition and photooxidation despite the damage due to aphids (which prefer red). In this situation, aphid strategies are neutral because there is no possible choice and no difference in trees as hosts, as there is no correlation between defences and colour.

If the damage due to aphids is high (σ_d and σ_D large) green ($i = 1$) and preference for red ($j = 3$) is possible. This is possible because when a small amount of red trees are present, preference for red increases quickly; as this preference increases, red trees tend to disappear but preference remains unexpressed in the population, as it has no disadvantage compared to other aphid strategies. Red trees can no longer increase in frequency because aphid preference for red is still present. Some other possibilities exist (see Table 3) but these are rather rare and restricted to certain specific conditions. Other possibilities are not stable or cannot be reached during evolution.

4. Discussion

The NR hypothesis (Holopainen and Peltonen, 2002) is, at least in theory, plausible, because colour and a certain amount of preference can evolve under the assumptions of the model. The hypothesis has now clear assumptions and predictions, which are very different from the Coevolution Theory (Archetti, 2000; Hamilton and Brown, 2001; Archetti and Brown, 2004), as summarized in Table 4. These predictions are testable. I will discuss briefly these assumptions and predictions and the available evidence.

4.1. Aphids prefer autumn colours (red and yellow) and avoid green, or have no clear preference

In the model preference for green evolves only rarely, always mixed with other strategies and in very specific

Table 3
Summary of the results of the stability analysis and of the dynamics according to the parameters

Parameters	Stability		Dynamics
$\sigma_{\mathbf{d}} = 0.8, \sigma_{\mathbf{D}} = 0.7$	(a)	1	$(t_1 = 1, a_3 = 1)$ 99%; $(t_4 = 1, \text{mixed } a_1 \text{ and } a_2)$ 1%
$\sigma_{\mathbf{d}} = 0.8, \sigma_{\mathbf{D}} = 0.2$	(b)	1	$(t_4 = 1, \text{mixed } a_i)$ 75%; $(t_1 = 1, a_1 = 1)$ 13%; $(t_1 = 1, a_1, a_2 \approx 0.5)$ 12%
$\sigma_{\mathbf{d}} = 0.8, \sigma_{\mathbf{D}} = 0.05$	(c)	1, 2	$(t_4 = 1, \text{mixed } a_i)$ 100%
$\sigma_{\mathbf{d}} = 0.4, \sigma_{\mathbf{D}} = 0.35$	(d)	1	$(t_1 = 1, a_3 = 1)$ 62%; $(t_4 = 1, \text{mixed } a_1 \text{ and } a_3)$ 38%
$\sigma_{\mathbf{d}} = 0.4, \sigma_{\mathbf{D}} = 0.2$	(e)	1, 4	$(t_4 = 1, \text{mixed } a_1 \text{ and } a_2)$ 84%; $(t_1 = 1, a_3 = 1)$ 16%;
$\sigma_{\mathbf{d}} = 0.4, \sigma_{\mathbf{D}} = 0.05$	(f)	1, 2, 4	$(t_4 = 1, \text{mixed } a_1 \text{ and } a_3)$ 99%; $(t_1 = 1, \text{mixed } a_1 \text{ and } a_3)$ 1%;
$\sigma_{\mathbf{d}} = 0.2, \sigma_{\mathbf{D}} = 0.18$	(g)	1, 3, 4	$(t_4 = 1, \text{mixed } a_1 \text{ and } a_3)$ 99%; $(t_1 = 1, a_3 = 1)$ 1%
$\sigma_{\mathbf{d}} = 0.2, \sigma_{\mathbf{D}} = 0.05$	(h)	1, 4	$(t_4 = 1, a_3 = 1)$ 100%

“Stability” shows the results of the stability analysis for pure strategies only; (1) $\sigma_d/f_S > \kappa_d, \sigma_D/f_S > \kappa_D$: $t_1 = 1$, aphid strategies neutral; (2) $\sigma_d/f_S > \kappa_d, \sigma_D/f_S < \kappa_D$: no pure strategies; (3) $\sigma_d/f_S < \kappa_d, \sigma_D/f_S > \kappa_D$: ($t_3 = 1, a_3 = 1$) stable; (4) $\sigma_d/f_S < \kappa_d, \sigma_D/f_S < \kappa_D$: ($t_4 = 1$), aphid strategies neutral (see Fig. 1 for a description of the four cases). “Dynamics” shows the results of 1000 cases in which a population starting with random frequencies of all the tree and aphid strategies has reached a stable equilibrium. For the dynamics the results have been obtained using the following values: $\lambda_{ds} = 0.5$; $\lambda_{dS} = 1$; $\lambda_{Ds} = 0.4$; $\lambda_{DS} = 0.6$; $\gamma_{ds} = 0.6$; $\gamma_{dS} = 0.7$; $\gamma_{Ds} = 0.4$; $\gamma_{DS} = 0.5$; $M = 10$; letters (a–h) corresponding to each value of σ_d refer to the points shown in Fig. 1.

Table 4
A comparison of the assumptions and predictions of the NR hypothesis and of the Coevolution Theory

	Nutrient retranslocation	Coevolution
1. Aphid preference	Preference for red ($j = 3$), no preference ($j = 1$) or mixed	Preference for green
2. Tree colour	Always red ($i = 4$) or (unlikely) green ($i = 1$)	Red only if D or green
3. Aphid growth	Better on red trees ($\gamma_{dS} > \gamma_{ds}$)	Better on green trees
4. Tree growth	Colour is an advantage ($\lambda_{dS} > \lambda_{ds}$)	Colour has a cost
5. Damage due to aphids	Damage (σ_d/f_S) lower than the relative cost (κ_d) of absence of photoinhibition at least for d or D (or both)	Damage lower than the relative cost of colour production only for d

For both: $\lambda_{ds} > \lambda_{Ds}$ (the production of defences has a cost), $\gamma_{Ds} < \gamma_{ds}$ (aphids grow better on trees with low defences), $\sigma_D < \sigma_d$ (the damage due to aphids is lower on trees with high defences). For the Coevolution Theory see Archetti (2000). See the discussion for more explanations.

circumstances. Mixed preference for red and no preference is usually the case (see Table 3). This is clearly the opposite of what the Coevolution Theory predicts (Archetti, 2000; Archetti and Brown, 2004). Holopainen and Peltonen (2002) did mention circumstantial evidence that an aphid species (*Eucraphis betulae*) prefers bright leaves in autumn and there is anecdotal evidence that aphids prefer yellow (not red) over green (Moericke, 1969). Other evidence published recently, however, points in the opposite direction (Furuta, 1986; Hagen et al., 2003, 2004; Archetti and Leather, 2005; Karageorgou and Manetas, 2006) or is at least uncertain (Leather, 1986; Glinwood and Petterson, 2000).

4.2. Autumn colours do not depend on the level of defences of the tree

According to the model, under the assumptions of the NR hypothesis, no correlation evolves between level of defence and colour: tree colour (most likely red) does not depend on the level of defences. This does not mean that variation in colour is not expected, but it means that if some variation in colour exist, it does not depend on variations in the level of defences. Therefore, if autumn colours are an adaptation against photooxidation another

explanation for the diversity of colours is necessary (for the Coevolution Theory, instead, the diversity of colours depend on the variation in defensive commitment). There is no evidence so far in favour or against this prediction.

4.3. Aphids will grow better on trees that had brighter or long-lasting autumn colours

Because (according to the NR hypothesis) colour does not depend on the level of defences, aphid growth in spring is expected to depend only on the capacity of the trees to recover nutrients (which may depend on the level of colour). Therefore aphids are expected to grow better on trees that in autumn had, for reasons independent from defences, brighter or long-lasting colours (because they recover nutrients more efficiently). Again, there is no evidence so far in favour or against this assumption.

It is important to remember that leaves with bright colours have *less*, not more, nitrogen than green leaves. Trees with yellow and red leaves do recover nitrogen more efficiently in autumn, but this affects only their nutritional capacity in spring (Lee, 2002a, b; Lee and Gould, 2002; Lee, personal communication). The NR hypothesis, therefore, makes sense if the insects feed on the tree in spring, not in autumn like Holopainen and Peltonen (2002) suggest.

4.4. Autumn colours confer an advantage to the tree during growth

If red allows a better recovery of nutrients then trees with red colours should grow better. The production of colour is not expected to impose a cost on the tree during growth. This point is clearly difficult to test, but gathering indirect evidence might be possible.

4.5. The impact of aphids on the tree's fitness must be lower than the relative cost of photoinhibition in trees with low defences or with high defences (or both)

If it is higher than both then no colour evolves. In fact with high σ_d values the trees at equilibrium do not produce colours. As I have shown, with high σ_d , this occurs because as preference for red increases, red trees tend to disappear and eventually can no longer increase in frequency because aphid preference for red is still present in the population (it remains unexpressed because it has no disadvantage compared to other aphid strategies). This result means that, according to the NR hypothesis, if the impact of aphids is important then autumn colours are not likely to evolve. This is quite the contrary of what Hamilton and Brown (2001) have shown: that tree species in which the impact of aphids is important are the ones with autumn colours. Holopainen and Peltonen (2002), instead, suggest that these trees species with bright colours have more species-specific aphids (as shown by Hamilton and Brown, 2001) because aphids prefer bright leaves. This can be true only if the impact of insects on a tree's fitness is low. The point here, however, is not about the absolute magnitude of the damage but is whether this damage is higher or lower than the damage due to photoinhibition. I know of no studies comparing these two costs in the same system and conditions.

5. Conclusions

Put it simply the NR hypothesis states that, because trees with bright autumn colours are better protected against photoinhibition and photooxidation, insects prefer trees with bright colours because these provide better nutrition. This scenario is possible only if insects feed on the tree in spring and have a low impact on the tree's fitness so that the protection against photooxidation overcomes the damage due to the insects.

The NR hypothesis is now testable. Future tests must allow us to answer the following questions (the answers must be positive for the NR hypothesis):

1. Do insects prefer bright autumn colours?
2. Are autumn colours independent from the defences of the tree?
3. Do insects grow better on trees with bright and prolonged autumn colours?
4. Are autumn colours an advantage for the tree during growth?

5. Is the cost due to insects on the tree lower than the relative cost of photoinhibition?

I hope this analysis will help our understanding of the subject and inspire more empirical tests. As Table 4 shows, the Coevolution Theory has rather different predictions. This is important because coevolution (Archetti, 2000; Hamilton and Brown, 2001; Archetti and Brown, 2004) or photoprotection (Lee, 2002a, b; Lee and Gould, 2002) are the two most likely candidates for an adaptive explanation of autumn colours.

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