



Decoupling vigour and quality in the autumn colours game: Weak individuals can signal, cheating can pay

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ABSTRACT

According to the coevolution theory, autumn colours are a warning signal to insects, signalling the level of chemical defences or availability of nutrients. Because in the original model tree vigour and defences were positively correlated, it is not clear whether signalling would still be stable when they are decoupled, and the fact that weak trees often display bright autumn colours is usually presented as evidence against the coevolution theory. I show that in a theoretical model of insect–tree coevolution, signalling is still stable when vigour and defences are decoupled. Weak trees can signal. Moreover, partial cheating is possible. The different equilibria depend on the importance of vigour and defences against insect attack, of vigour in the production of the signal, and of pleiotropic effects between colour and defences. These results provide precise predictions that can be used for planning future empirical test.

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1. Introduction

1.1. Autumn colours

The adaptive value of the autumn colours of leaves is still a matter of controversy (Ougham et al., 2008). Autumn colours are produced mainly by carotenoids (yellow–orange) and anthocyanins (red–purple). While carotenoids, which are present all year, may become visible because of the seasonal breakdown of chlorophyll, anthocyanins are actively produced in autumn (Sanger, 1971; Lee, 2002a, b; Lee and Gould, 2002; Archetti et al., 2008). What use is the production of a pigment in leaves that are about to be shed?

Red may protect the leaf from the damaging effects of light at low temperatures (photo-inhibition and photo-oxidation), allowing a more efficient resorption of nutrients, especially nitrogen (the photo-protection theory: Pringsheim, 1879–1882; Gould et al., 1995; Hoch et al., 2001; Feild et al., 2001; Lee and Gould, 2002). Alternatively, red might be a warning signal of the status of the tree (indicating high levels of defences or low nutritional capacity) to animals, particularly feeding insects like aphids (the coevolution theory: Archetti, 2000; Hamilton and Brown, 2001; Archetti and Brown, 2004). Other hypotheses are also possible

(Archetti, 2008) but very few tests are available (Ougham et al., 2008; Archetti et al., 2008).

1.2. The coevolution theory

According to the coevolution theory red is a signal of the status of the tree to insects that migrate to (or move among) the trees in autumn: (i) insects migrating to the trees in autumn avoid red leaves and colonise preferentially green leaves; (ii) trees with red leaves have better chemical defences or worst nutritional capacity or any other characteristic that induces a lower fitness in the insects. In this scenario, therefore, colour and preference coevolve in an arms race: autumn colours are an adaptation of the trees to reduce their parasite load and insect preference for green is an adaptation to find the most suitable host trees.

There is no debate on the importance of the first point (colour preference), although it is debated whether insects actually avoid red leaves (the tests performed so far seem to support this claim: Archetti and Leather, 2005; Hagen et al., 2003, 2004; Karageorgou and Manetas, 2006; Döring et al., 2008; see also Furuta, 1986; contrasting evidence has been reported by Schaefer and Rolshausen, 2007; Rolshausen and Schaefer, 2007; reviewed by Archetti et al., 2008). This is not the point of this paper.

The second main point of the theory, however, the link between autumn colour and defences, is much more controversial. According to the coevolution theory, autumn colours are a signal that the tree has strong chemical defences or lower

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nutritional quality, or any other characteristic that would induce a lower fitness in the insects. This is often confused with the following statement: that the trees with red leaves are the most *vigorous* ones. This misunderstanding has created much confusion, and because there is some evidence that *weak* trees often display strong autumn colours (Schaberg et al., 2003; Ougham et al., 2005), it may seem to undermine the coevolution theory.

1.3. Vigour and quality

This misunderstanding (that trees with red leaves must be the most *vigorous* ones) is probably due to the fact that in the original model of the coevolution theory (Archetti, 2000) I did not decouple vigour from defences. In that model I assumed that the trees with high levels of defences were always the most *vigorous* ones. This creates a system in which the trees that signal are the ones with high levels of defences—and these are also the most *vigorous* ones (an example of handicap signalling: Zahavi, 1975; Grafen, 1990).

That model (Archetti, 2000) assumed that the vigour of the tree was positively correlated with the level of defences. This is not necessary, however. As Archetti and Brown (2004) pointed out, stronger autumn colours need not be associated with more *vigorous* trees. Hamilton and Brown (2001) were also careful on this point, and even suggested that it might be the weaker trees that need to signal more. The link must be with the quality of the tree that is relevant for the insects, that is chemical defences or nutritional capacity or any characteristic that may affect insect fitness. And this is not necessarily positively correlated with tree vigour.

Even Ougham et al. (2005) in their criticism of the coevolution theory suggested that the theory can still work if the weak trees are the ones more in need to avoid parasites. Indeed this fact is not controversial in the theory of biological signalling: the requirement for the evolutionary stability of signalling is that the ratio of the fitness cost of the signal and the benefit received be lower in individuals giving stronger signal, either because the signal is less costly for a signaller of high quality or because individuals give stronger signals when in greater need (Maynard-Smith and Harper, 2003).

In the classical model of biological signalling, developed in the context of animal sexual selection, the quality that is relevant for the signaller (the male) and the quality that is relevant for the receiver (the female) are the same: the male's vigour, which affects both the cost of the signal for the male and the fitness of the female. In the autumn colours signalling game, however, the quality that is relevant for the cost of the signal (tree vigour) is not the same that is relevant for the receiver (the level of chemical defences); a *vigorous* tree is not necessarily one with high defences (or low nutrition or anything that affects negatively the fitness of the insects), and a *weak* tree is not necessarily one with low defences.

1.4. Rationale of the paper

My purpose is to analyse the autumn colours signalling game decoupling the quality that affects the cost of the signal (the vigour of the tree) and the quality that is relevant for the receiver (the level of defences or any quality that affects the fitness of the insects). In the original model of the coevolution theory (Archetti, 2000) these two qualities were coupled (*vigorous* trees were the ones with higher levels of defences). What happens when vigour and defences are decoupled? Is signalling still stable in this case? Is it still honest? (that is, do the receivers benefit from trusting the signal?) Are the trees that display more autumn colours also more *vigorous*?

2. The model

I model the following scenario: trees are colonised by insects looking for a host in autumn. The fitness of a tree is affected by the damage induced by the insects and by the cost of autumn colours; the fitness of the insects depends on the quality of the tree they colonise. Trees can signal their status to the insects using leaf colour. Insects must find the most suitable hosts but cannot perceive the vigour nor the defences of the trees—they can only perceive the colour. The problem is to understand whether a signalling system in which the trees use red as a warning signal, and insects trust the signal, is stable.

2.1. Strategies

I use a discrete model in which a tree is assigned two possible values (high and low) for three parameters: vigour, defences and colour.

Colour (s): a tree can be either red (**S**) or green (**s**) in autumn.

Vigour (v): a tree can be either strong (**V**) or weak (**v**). This is the quality from the point of view of the tree itself: it can affect the tree's cost for the production of the signal and its fitness in response to insect attack but does not affect insect fitness at all.

Defences (d): a tree can have high (**D**) or low (**d**) defences against insects. I will talk about defences for simplicity, but this does not necessarily mean chemical defences: it could be any characteristic of the tree that affects insect fitness, for example low nutritional capacity (less nutrients available to insects) would be equivalent to high chemical defences.

Vigour and defences are decided by nature (the environment or genetically determined). I assume an equal frequency of **d** and **D** trees ($f_d = f_D = 1/2$) and of **v** and **V** trees ($f_v = f_V = 1/2$). Because what matters is their relative value, this assumption does not affect the generality of the results and only means that low defences are as likely as high defences, and weak trees are as likely as strong trees; that is the threshold defining high and low is exactly the average value of the population.

In the original model of the coevolution theory (Archetti, 2000) vigour and defences were considered to be the same parameter (named "quality"): as a result there were only four possible tree strategies. In this model vigour and defences can be decoupled, that is a tree can have, for example, high vigour and low defences. Given vigour and defences (chosen by nature), a tree's strategy consists in being **s** or **S** according to its own vigour (v) and defences (d). I assume that the probability $x_{i,vds}$ of being **S** for a vd tree playing strategy i is either 0 or 1. As a consequence there are 16 possible tree strategies i (Table 1). For example strategy $i = 2$ means signalling (red) **S** only if *vigorous* and with high levels of defences (**VD**).

Insects cannot perceive directly vigour nor defences but must rely on the signal (colour) to choose their host. I assume there are only three possible insect strategies j : preference for **s**, preference for **S** and no preference (Table 2). With this model of preference, there are two indeterminate cases when there is only one kind of tree colour and insects with a preference for the other colour ($i = 1, j = 3$ and $i = 16, j = 2$). I assume that insects in these two cases fail to find a host and their fitness is zero.

2.2. Fitness

The rate of survival of a vds tree in autumn is λ_{vds} . In this phase fitness depends only on the cost of the signal. The rate of survival of a vds tree after autumn is ϕ_{vds} . In this phase fitness depends on the cost of being colonised by insects. Therefore the fitness of a

Table 1

The probability (x_{ivds}) of being **S** for a tree i according to its conditions v and d .

i	S (red)	x_{ivds}	x_{ivD}	x_{ivd}	x_{ivDS}
1	Never	0	0	0	0
2	If VD	0	0	0	1
3	If Vd	0	0	1	0
4	If V	0	0	1	1
5	If vD	0	1	0	0
6	If D	0	1	0	1
7	If vD or Vd	0	1	1	0
8	If not vd	0	1	1	1
9	If vd	1	0	0	0
10	If vd or VD	1	0	0	1
11	If d	1	0	1	0
12	If not vd	1	0	1	1
13	If v	1	1	0	0
14	If not Vd	1	1	0	1
15	If not VD	1	1	1	0
16	Always	1	1	1	1

The probability of being **s** is $1-x_{ivds}$.

Table 2

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

j	Preference	y_{js}	y_{js}
1	No preference	f_s	f_s
2	Prefer green	1	0
3	Prefer red	0	1

tree playing strategy i can be defined by

$$T_i = \sum_{vds} f_v d^x x_{ivds} \lambda_{vds} \phi_{vds}$$

where

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

in which a_j is the frequency of insect strategy j , σ'_{vd} is the cost ($0 < \sigma'_{vd} < 1$) due to the attack of the insect population on vd trees and N is the number of trees on which the attack is concentrated. For each kind of insect j , with frequency $(1 - y_{js})$ colour s is avoided and the fitness of the tree is 1; with frequency y_{js} the insects accept colour s : in this case a tree of that colour is chosen with probability $1/Nf_s$ and in this case the tree has fitness $(1 - \sigma'_{vd})$; with probability $(Nf_s - 1)/Nf_s$ the tree is not chosen and has fitness 1.

N can be incorporated in σ'_{vd} without loss of generality and we can substitute σ'_{vd} with σ_{vd} , which is the cost due to part of the insect population that attacks the tree. ϕ_{vds} reduces to

$$\phi_{vds} = \sum_j a_j (1 - y_{js} \sigma_{vd} / f_s)$$

The fitness of an insect playing strategy j is defined by

$$A_j = \sum_s y_{js} \sum_d f_{ds} \gamma_d / f_s - \epsilon_j$$

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_d is the fitness of an insect on a d tree. I assume that insect fitness does not depend on the tree's vigour v or colour s but only on its defences d . ϵ_j is a small cost paid by choosy insects ($\epsilon_j > 0$ for $j = 2, 3$; $\epsilon_j = 0$ for $j = 1$).

The following assumptions can be considered true in any situation: insects perform better on trees with low defences ($\gamma_D < \gamma_d$); the damage due to insects is lower in trees with high levels of defences ($0 < \sigma_{vD} < \sigma_{vd}$) and in vigorous trees ($0 < \sigma_{vd} < \sigma_{vd}$). Other conditions will vary and decide the stability of the strategies.

2.3. Stability

Trees can prefer to pay the cost of having insects rather than the cost of producing the signal either because producing a signal is too costly (for example because of the loss of photosynthesis or the cost of producing anthocyanins) or because the cost of insects is low (for example if the defences are so effective that no damage is done by the insects). Or the trees can prefer to avoid the cost of having insects and pay the cost of producing the signal, either because producing the signal has a low cost or because the cost of being invaded by insects is high (for example if the defences are not effective). Different strategies, therefore, might be stable under different parameters.

The aim of the analysis is to find couples of strategies, one for the trees (i^*) and one for the insects (j^*), that are evolutionarily stable (ESS—Maynard-Smith, 1982), that is couples (i^*, j^*) that satisfy the conditions $T_{i^*} > T_i$ and $A_{j^*} > A_j$ for all other insect strategies j and all other tree strategies i . Therefore the fitness of all tree strategies is calculated with each insect strategy j^* fixed in the population ($f_{j^*} = 1$) to check whether, and for which parameters, a tree strategy i^* satisfies the condition $T_{i^*} > T_i$ for all other tree strategies i . At the same time, the fitness of all the insect strategies is calculated with each tree strategy i^* fixed in the population ($f_{i^*} = 1$) to check whether, and for which parameters, an insect strategy j^* satisfies the condition $A_{j^*} > A_j$ for all other insect strategies j . The stability analysis was performed with Mathematica 6.0 (Wolfram Research).

3. Results

3.1. Vigour linked to defences

Consider, first, the following case: constrain v to d and V to D , and call them q ($= v$ and d) and Q ($= V$ and D). With this constraint the model is identical to the original coevolution model (Archetti, 2000); vigour and defences are not decoupled. This means that only the following tree strategies are allowed: Never signal; Signal if Q ; Signal if q ; Always signal.

There is a non-signalling equilibrium ($j = 1$; Trees: Never signal) and a signalling equilibrium ($j = 2$; Trees: signal if Q). The signalling equilibrium is stable if

$$\sigma_q / 2 < 1 - \lambda_{qS} / \lambda_{qS}$$

$$\sigma_Q / 2 > 1 - \lambda_{QS} / \lambda_{QS}$$

This means that the relative cost paid for the production of the signal $1 - \lambda_{qS} / \lambda_{qS}$ must be smaller than the (half) cost due to insect attack for Q trees but the relative cost paid for the production of the signal must be higher than the (half) cost due to insect attack for q trees. This is a form of handicap principle (Archetti, 2000; Grafen, 1990; Zahavi, 1975). The signal is honest.

It is important to notice that at the signalling equilibrium only Q trees signal, therefore the actual cost for the production of the colour can even be zero (see also Maynard-Smith and Harper, 2003). It is true that a cost prevents q trees from signalling, but this cost prevents them from signalling indeed, and it is not paid at equilibrium. The relevant cost is the one paid by signalling

trees, and this cost can also be zero. In other words, it must be $\lambda_{qS} < \lambda_{qs}$, but it could well be $\lambda_{qS} = \lambda_{qs}$.

This result, so far, is not different from the original model (Archetti, 2000) where v and d were not decoupled. The results are more interesting when we consider the complete version of the model, in which d and v are allowed to be decoupled.

3.2. Decoupling vigour and defences

The stability analysis shows that signalling can be stable with insect strategy $j = 2$ and five tree strategies i : 2, 5, 6, 8 and 14 (Table 3). Other signalling strategies are not stable. For example with $i = 4$ (signal if **V**) only insects with no preference are stable, but with this insect strategy only tree strategy $i = 1$ is stable. A non-signalling equilibrium always exists with insect strategy $j = 1$ (no preference) and tree strategy $i = 1$ (never signal), as in Archetti (2000). The unstable equilibria and the non-signalling equilibria are trivial and will not be discussed further; in the rest of the paper I will focus on the different possible signalling equilibria.

The conditions for the stability of the insect strategy $j = 2$ with the five stable tree strategies (Table 3) can be considered always true for ϵ_j small. Stability for the trees depends on the relative value of the cost for the production of the colour and on the damage due to insect attack, as in the original model (Archetti, 2000) but in a more complex way. For each tree strategy there are four conditions of the form $\sigma_{vds}/f_s < \text{or} > 1 - \lambda_{vds}/\lambda_{vds}$ (Table 3). For $i = 6$, for example, these conditions are

$$\begin{aligned} \sigma_{vds}/2 > 1 - \lambda_{vds}/\lambda_{vds} \\ \sigma_{vds}/2 < 1 - \lambda_{vds}/\lambda_{vds} \\ \sigma_{vds}/2 > 1 - \lambda_{vds}/\lambda_{vds} \\ \sigma_{vds}/2 < 1 - \lambda_{vds}/\lambda_{vds} \end{aligned}$$

The quantity $1 - \lambda_{vds}/\lambda_{vds}$ is the relative cost for the production of colour for a tree **S** compared to a tree **s** with the same vd values. Therefore the inequality signs in Table 3 mean that the (half) cost due to insect attack must be larger ($>$) or smaller ($<$) than the relative cost of the production of colour for trees with the given vd values. The relative cost of the defences, instead, is not relevant for the equilibria.

Trees adopting strategy $i = 2$ signal only when they are **VD**, that is when they are vigorous and have truly high levels of defences. This is partial conceal because **vd** trees do not signal. This case is stable if (see Table 3) the cost of the signal is lower than the cost due to insect attack in **VD** trees but higher in all other cases.

Trees adopting strategy $i = 5$ signal only when they are **vd**, that is when they are weak (and have truly high levels of defences). This is also partial conceal, because **VD** trees do not signal. This case is stable if (see Table 3) the cost of the signal is

Table 3
The sign ($<$ or $>$) of the four conditions σ_{vds}/f_s ($<$ or $>$) $1 - \lambda_{vds}/\lambda_{vds}$ for the stability of the five tree strategies i that can be stable with insect strategy $j = 2$ (preference for green), and the value of f_s .

i	S (red)	vd				f_s	Insects
		VD	Vd	vD	vd		
2	If VD	$>$	$<$	$<$	$<$	3/4	$\epsilon_2 < (\gamma_d - \gamma_D)/6$
5	If vd	$<$	$<$	$>$	$<$	3/4	$\epsilon_2 < (\gamma_d - \gamma_D)/6$
6	If D	$>$	$<$	$>$	$<$	1/2	$\epsilon_2 < (\gamma_d - \gamma_D)/2$
8	If not vd	$>$	$>$	$>$	$<$	1/4	$\epsilon_2 < (\gamma_d - \gamma_D)/2$
14	If not Vd	$>$	$<$	$>$	$>$	1/4	$\epsilon_2 < (\gamma_d - \gamma_D)/2$

The conditions for the stability of insect strategy $j = 2$ are also shown.

lower than the cost due to insect attack in **vd** trees but higher in all other cases.

From the point of view of the insects $i = 2$ and 5 are stable because (with $f_d = f_v = 1/2$) insects preferring green end up on **D** trees only 1/3 of the times (**vd** in the case of $i = 2$; **VD** in the case of $i = 5$) while insects preferring red would always end up on **D** trees (**VD** in the case of $i = 2$; **vd** in the case of $i = 5$) and insects with no preference would end up on **D** trees 1/2 of the times. This is not the best possible equilibrium for insects (the best would be always avoiding **D** trees) but it is stable.

Trees adopting strategy $i = 6$ signal if and only if they really have a high level of defences (**D**); vigour is irrelevant. Therefore the insects always choose the trees with the low defences. This case is stable if (see Table 3) the cost of the signal is lower than the cost due to insect attack in **D** trees but higher in **d** trees, irrespective of vigour. This is the optimal scenario for aphids because they always manage to avoid trees with high levels of defences.

Trees adopting strategy $i = 8$ signal if and only if they are not **vd** (therefore **VD**, **Vd** and **vD** signal). This is partial deceit (dishonest) because **Vd** trees signal. This case is stable if (see Table 3) the cost of the signal is lower than the cost due to insect attack in all trees except **vd** trees (in which this cost is higher).

Trees adopting strategy $i = 14$ signal if and only if they are not **Vd** (therefore **VD**, **vd** and **vD** signal). This is also partial deceit because **vd** trees signal. This case is stable if (see Table 3) the cost of the signal is lower than the cost due to insect attack in all trees except **Vd** trees (in which this cost is higher).

From the point of view of the insects $i = 8$ and 14 are stable because insects preferring green never end up on **D** trees, although 1/3 of the times (with $f_d = f_v = 1/2$) they avoid **d** trees too (**Vd** in the case of $i = 8$; **vd** in the case of $i = 14$); insects preferring red would end up on **D** trees 2/3 of the times) and insects with no preference would end up on **D** trees 1/2 of the times.

Therefore, in summary, when vigour and defences are decoupled, signalling can still be stable but it is not necessarily honest. Trees with low defences (**d**) can signal. Moreover, signalling is not restricted to vigorous trees. Weak trees (**v**) can signal. These equilibria are possible under different conditions as discussed in the next section.

4. Discussion

4.1. Different equilibria with different effects

I will discuss four possible effects (see Table 4) that may affect the likelihood of these combinations. There may be more, but these seem to be the ones relevant for the model, given the biological scenario involved.

1. *Pleiotropy between colour and defences*: If the cost of the production of the colour is lower for **D** trees than for **d** trees, or if **D** trees are necessarily more coloured than **d** trees, for example because of a pleiotropic effect between colour and defences (red pigments and chemical defences are produced by the same biochemical pathway), then, everything else being equal (no effect of defences on insect attack, no effect of vigour on insect attack, no effect of vigour on the cost of the signal), **D** trees are expected to signal more than **d** trees. Pleiotropy, therefore, make all strategies more likely to be stable, but especially strategy $i = 6$ (see Table 4).

2. *Defences affect the fitness of the tree after insect attack*: If **d** trees are more susceptible to the damages induced by insects than **D** trees, then, everything else being equal (no pleiotropic effects, no effect of vigour on insect attack, no effect of vigour on the cost of the signal), they should signal more than **D** trees because they

Table 4

Honesty and likelihood of the five stable signalling equilibria i for trees with insect strategy $j = 2$ (preference for green).

i	S (red)	Honesty	Effects ^a			
			1	2	3	4
2	If VD	Partially concealing	+	–	+	–
5	If vD	Partially concealing	+	–	–	+
6	If D	Honest	++	--		
8	If not vd	Partially dishonest	+	–	+	–
14	If not Vd	Partially dishonest	+	–	–	+

^a The number of times that the equilibria requirements violate (–) or match (+) the assumptions of the four effects described in the text. 1 = Pleiotropy between colour and defences; 2 = defences affect the fitness of the tree after insect attack; 3 = vigour affects the cost of the signal; and 4 = vigour affects the fitness of the tree after insect attack.

need more to avoid insects. This effect may be more important in weak trees (**v**) if, in addition, weak trees are more susceptible to the effects of insect attack. If high levels of chemical defences are efficient in protecting the tree after insect attack, therefore, the likelihood of all signalling strategies is reduced, but especially the likelihood of the honest strategy $i = 6$ (see Table 4).

3. *Vigour affects the cost of the signal*: If **V** trees pay a lower cost for the signal than **v** trees, then, everything else being equal (no pleiotropic effects, no effect of vigour on insect attack, no effect of defences on insect attack), **V** trees are expected to signal more than **v** trees. If the vigour of the tree affects significantly the cost of the signal, therefore, strategies $i = 2$ and 8 are more likely and strategies $i = 5$ and 14 less likely (see Table 4).

4. *Vigour affects the fitness of the tree after insect attack*: If **v** trees are more susceptible to the damages induced by insects than **V** trees, then, everything else being equal (no pleiotropic effects, no effect of defences on insect attack, no effect of vigour on the cost of the signal), they should signal more because they need to avoid insects more than **V** trees. This effect may be more important in trees with low defences (**d**) if, in addition, **d** trees are more susceptible to the effects of insect attack. If the vigour of the tree affects significantly the effect of insect attack on the tree's fitness, therefore, strategies $i = 2$ and 8 are less likely and strategies $i = 5$ and 14 more likely (see Table 4).

These four effects (Table 4) are likely to occur at the same time, therefore they must be weighted according to their relative importance. Different combinations of the four effects may lead to different signalling equilibria, or in some cases to no signalling at all.

4.2. Evidence for the different effects and possible tests

A pleiotropic effect that leads to an association between colour and defences is not unlikely (Ougham et al., 2005) but showing that trees with more (or more intense) red leaves have more chemical defences would not reveal a pleiotropic effect. Moreover, it must be kept in mind that chemical defences are not the only possibility. High levels of defences would be equivalent, in the model, to poor nutritional capacity for the insects. This can perhaps be measured directly, or as an alternative approach, the growth rates of insects could be an indirect measure of d (this approach has been used by Ramirez et al., 2008). There is little doubt that the quality of the tree as a host is crucial for the insects: Moran and Witham (1990), for example, report a differential survival of aphids on *Populus* ranging between 0% and 78%. The importance of vigour and defences against insects for the fitness of the tree, however, is more difficult to measure. It is possible, and there is evidence for this (Ougham et al., 2005),

that tree vigour affects the impact of insect attack on the tree and that weak trees need more than healthy trees to avoid parasites. On the other hand it is likely that vigorous trees can afford the production of the signal more easily than weak trees. What matters is the relative importance of the four effects combined. This will vary from species to species, and possibly even within each species. Measuring these effects is difficult, but it might be possible to estimate their relative importance.

4.3. Honesty and cheating

Seven combinations of parameters exist for the five stable strategies, for which, given a certain v , signalling occurs only with one value of d or, given a certain d , signalling occurs only with one value of v .

The following cases are *honest* (the true level of defences is signalled):

- D** signals and **d** does not, irrespective of vigour ($i = 6$).
- VD** signals and **Vd** does not ($i = 2$ and 14).
- vD** signals and **vd** does not ($i = 5$ and 8).

The following cases are *dishonest* (**d** trees can sometimes signal):

- Vd** signals and **vd** does not ($i = 8$).
- vd** signals and **Vd** does not ($i = 14$).

The following cases are *concealing* (**D** trees do not always signal):

- VD** signals and **vD** does not ($i = 2$).
- vD** signals and **VD** does not ($i = 5$).

All the five strategies except $i = 6$ are a mixture of these cases, and therefore only partially honest. Strategies $i = 8$ and 14 are partially dishonest and strategies $i = 2$ and 5 are partially concealing.

4.4. Weak trees can signal

There is some evidence that the extent and earliness of onset of red coloration is positively correlated with foliar nitrogen deficiency in some cases (Schaberg et al., 2003; Ougham et al., 2005): this suggests that in these cases it is the weak trees that signal. As the model shows, this does not contradict the coevolution theory: the theory is still valid if it is the weakest trees that have a higher need of avoiding parasites. Weak trees can signal. In other cases (Hagen et al., 2004) there is evidence that it is the vigorous trees that display more intense colours. These apparently opposite results can be explained in the light of the present model: they might be the different stable outcomes of signalling under different conditions. As I have shown the relative importance of defences (on insect fitness and on tree fitness), vigour (for the tree against insect attack) and pleiotropy (between colour and defences) will affect the stable signalling equilibria. If we want to develop rigorous tests of the theory we must be able to weight the relative importance of these four (and possibly other) effects as suggested by the model.

It should also be noted that support for a positive correlation between vigour and autumn colours (Hagen et al., 2004) was found in a species with yellow, rather than red, autumn colours. Yellow is due to the breakdown of chlorophyll rather than to a *de novo* production of pigments in autumn (Archetti et al., 2008), and of red and yellow autumn colours are likely to be different. In the

case of *Betula pubescens* in Northern Norway it is possible that the loss of photosynthesis due to an earlier breakdown of chlorophyll represents an important cost that only vigorous trees can afford, because the growing season is very short, but in other species the cost of reduced photosynthesis might be irrelevant (Ougham et al., 2005).

4.5. Relevance for comparative analyses

The model has also implications for comparative analysis. The weighted combinations of the four effect can lead, in some cases, to no signalling at all (the non-signalling equilibrium is always a possible alternative) even in the presence of insects. It is questionable, therefore, how powerful interspecific comparative analyses can be in revealing a correlation between insect presence and presence of autumn colour (Hamilton and Brown, 2001) if the details of the system (importance of vigour and defences on tree fitness, importance of pleiotropy between colour and defences, importance of vigour for the production of the colour) are unknown. It might be that a coevolutionary arms race is going on between insects and trees with parameters (vigour, quality, pleiotropy) that do not lead to any stable signalling equilibrium. We should not necessarily expect, therefore, that autumn colours are present in all cases where a coevolutionary interaction occurs.

5. Conclusion

It is clear that signalling is possible when vigour and defences are decoupled. Signalling is not necessarily completely honest: trees with low defences can sometimes signal. And it is not necessarily restricted to vigorous trees: weak trees can sometimes signal. The different possible equilibria are stable under different conditions, depending on the relative importance of vigour and defences against insect attack, of vigour in the production of the signal, and of pleiotropic effects between colour and defences. These results could help in planning future experimental tests on the coevolution theory. The model might also be applied to other cases of signalling in which the quality of the signaller is decoupled from the quality sought by the receiver.

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Appendix A. Supporting Information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.jtbi.2008.10.012.

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