Tannin evolution by niche construction: a spatial stoichiometric model

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Among plant traits, plant secondary metabolites such as tannins mediate plant-herbivore interactions but also have after-life effects on litter decomposition and nutrient cycling, which could influence their evolution. By modeling the flow of nitrogen and carbon through plants and soil in a spatially explicit context, we explored the relative contribution of herbivory and plant-soil feedbacks as drivers of tannin evolution. We assumed soil nitrogen to be composed of labile and recalcitrant compartments, the latter made of tannin-protein complexes accessible by plants via associations with mycorrhizal fungi. In unproductive environments and for plants with low biomass turnover rates, we show that when tannins modify soil properties locally, plant-soil feedbacks alone can drive their evolution. We further predict the existence of positive coevolutionary feedbacks between associations with mycorrhizae and tannins, possibly triggered by the evolution of the latter as protection against herbivores. In line with our results, tannins are mostly present in conservative plants, associated with mycorrhizae and inhabiting unproductive environments. Our work suggests that plant-soil feedbacks can be key to the evolution of certain plant traits, in what can be interpreted as niche construction mechanisms.

INTRODUCTION

Through their impact on litter, soil and nutrient dynamics, plant traits are key drivers of ecosystem functioning. Many components of a plant's environment are determined by the plant itself, each plant genotype shaping its own environment [49, 60]. In turn, these altered environmental conditions will affect the selective pressures acting on plant traits, thereby constituting an ecological-evolutionary feedback loop named "niche construction" [33, 41]. Many plant traits may have evolved because of their niche construction abilities, including flammability [52], germination timing [11] and plant-soil feedbacks [50]. At the same time, environmental factors may interact with niche-constructing traits, either preventing or enhancing their evolution. For instance, flammability will more likely evolve in dry rather than wet environments. Most models of niche construction, however, do not include such explicit biological mechanisms and species traits [26, 28, 30, 50]. This has the advantage of generality, but the interplay between environmental factors and niche constructing traits can hardly be addressed in such models, as it should depend on the specific mechanisms involved in each ecological setting. Here, we propose that the evolution of tannin production in plants is a useful case study to investigate the evolutionary interplay between environment and niche constructing traits. Tannins can trigger plant-soil feedback loops because they complex organic nitrogen; and the importance of such feedbacks should depend on the fertility of the environment.

Among the large variety of plants defensive structures and compounds, tannins are a widely distributed class of plant secondary metabolites [39], with a wide array of intra- and interspecific variation in their production [25]. Although tannins have been extensively studied as anti-herbivore defense [7, 14], they also affect nutrient cycling. After leaf senescence or plant death, they enter the soil as a component of litter, where they can greatly impact nutrient dynamics [18, 21, 25, 40], limiting leaching [22, 40] and slowing-down decomposition and microbial activities [6, 8, 20, 49]. Tannins complex macromolecules such as proteins which triggers the formation of recalcitrant

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organic matter, from which nutrient accessibility is reduced. This reduction of resource availability, however, may not only be a detrimental side-effect of an anti-herbivore strategy. Tannins promote local nutrient retention, which could be advantageous if plants can retrieve nutrients directly from recalcitrant organic matter, thereby circumventing mineralization by free microorganisms [1, 40]. Mycorrhizal associations with symbiotic fungi may grant this ability to plants. Several studies have assessed the ability of the different groups of mycorrhizae to take up nutrients from organic matter [48], which was demonstrated for plants associated with ericoid mycorrhizae [5, 21, 62], which often abound in heathland and peatlands (we review results on the ability of different types of mycorrhizae to access recalcitrant organic matter in the Discussion).

For those mycorrhizal associations that can access nutrients from tannin-protein complexes, tannin production could be a major process by which plants control their own resources, retaining nutrients in the local environment of the plant, and affecting the outcome of plant-microbe competition in favor of plants. This raises the question of the role plant-soil feedbacks in the evolution of tannins production, and the ecological conditions that could promote this role.

The observed correlation between nutrient limitation and tannin production [13, 38] could result from plants limiting nutrient losses through the formation of protein-tannin complexes, as a strategy to cope with an unfertile environment. Yet, one would expect the opposite correlation if the reduction of nutrient cycling by tannins is detrimental to plants [58]. In fact, based on an eco-evolutionary model, and in apparent contradiction with empirical findings [44], Barot et al. [4] suggested that plants should evolve fast decomposing litter in nutrient-poor environments. Since tannins slow down mineralization, the question of whether the afterlife effects of tannins are beneficial or detrimental to plants in unfertile ecosystems is thus still open. If beneficial, tannin evolution could be driven by plant-soil feedbacks without additional selective pressure as an anti-herbivore defense. If detrimental, tannin evolution would be the outcome of a trade-off between anti-herbivore defense and the reduction of nutrient cycling.

Here we address this question and reconcile observations and theoretical predictions. To do so, we developed and analyzed a mechanistic evolutionary model, which includes the effects of tannins on both herbivory and plant-soil feedbacks. Because tannins are carbon (C) based compounds, and because their afterlife effect notably affects nitrogen (N) cycling, our model explicitly accounts for plants C:N stoichiometry. In terms of nutrients, we focus on N because this element is limiting in most terrestrial environments [59], and because most of the plant N is contained in proteins that are important substrates for tannin complexation. Moreover, because tannin-protein complexes are insoluble, immobile and remain near the tannin-producing plants, our

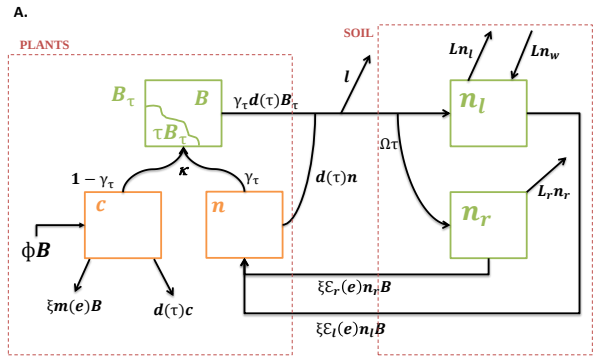

FIG. 1. Scheme of the mean-field model. On the left, the three plant compartments. Carbon (c) and nutrient (n) stocks are used by the plant for the growth of its effective biomass (B_τ), which includes tannins. Following senescence, nutrients enter one of the two soil compartments, on the right. Nutrients complexed by tannins enter the recalcitrant nutrient pool (n_r), the remaining nutrients enter the labile nutrient pool (n_l). Nutrients are then absorbed by plants, at the expense of carbon costs.

model also accounts for spatial structure. Plants associations with specific mycorrhizae will be able to reabsorb N from tannin-protein complexes, in addition to labile N. Our model therefore describes the ecological dynamics of plants growing in an N-limited substrate, plus the evolutionary dynamics of tannin production and symbiotic associations with mycorrhizae, in a stoichiometric and spatial context. We address the following questions:

1) Can plant-soil feedbacks trigger tannin evolution, even in the absence of herbivory?

2) What is the influence of ecosystem fertility on tannin evolution?

3) Can there be coevolution of symbiotic mycorrhizae and tannin production?

Our results suggest that for plants with low biomass turnover rates inhabiting unfertile environments, spatial structure can promote the coevolution of tannin production and mycorrhizal associations. This can occur without selective pressure on tannins as a anti-herbivore defense, following a niche construction mechanism.

METHODS

We follow C and N flows through plants and soil under stoichiometric constraints. Tannin content (τ) and the capacity (e) to benefit from symbiotic associations with mycorrhizae are hereditary phenotypes. We first model the dynamics of the biomass and soil nutrient content of a "typical" plant in a typical location: a mean-field model assuming plants to be well mixed in

Evolutionary traits	interpretation
τ	proportion of tannins in biomass
e	symbiotic capacity

variables	interpretation	nondimensional
t	time	$s = Lt$
B_τ	biomass	$x_\tau = B_\tau / B_\phi$
B	effective biomass	$x = B/B_\phi$
n	stored N	$p = n/B$ or $P = n/\gamma B$
c	stored C	$q = c/B$
n_l	labile N in soil	$y_l = n_l/n_w$
n_r	recalcitrant N	$y_r = n_r/n_w$

TABLE I. Evolutionary traits, dynamical variables and their adimensional counterpart.

the landscape. We then relax this assumption by considering space explicitly and allowing stochastic birth and death events; thus extending the mean-field model into a spatially explicit cellular automaton. We will show, however, that qualitatively accurate predictions about tannin evolution in a spatially explicit setting can be made from the analysis of the much simpler mean-field model.

Plant growth

We denote B_τ the C+N content of plant biomass, with C:N ratio α_τ. A fraction of this biomass, τB_τ, is composed of C associated to tannins and therefore plays no role in physiological processes. What biomass is left we denote $B = (1-\tau)B_\tau$, the "effective biomass", performing growth and absorption with a C:N ratio α independent of τ. We denote γ and γ_τ the proportion of N in B and B_τ, with $1-\gamma$, and $1-\gamma_\tau$, representing[1] the complementary proportions of C in B, and B_τ. As in a chemical reaction, the rate of biomass creation is proportional to the amount that can be created from the N- and C-stocks at that time (denoted n and c) thats is, the minimum between $\frac{n}{\gamma_\tau}$ and $\frac{c}{1-\gamma_\tau}$ [9, 42]. Under these assumptions and a biomass turnover rate d, the dynamics of B_τ follow

$$\frac{dB_\tau}{dt} = \underbrace{\kappa \min\{\frac{n}{\gamma_\tau}, \frac{c}{1-\gamma_\tau}\}}_{\text{growth}} - \underbrace{dB_\tau}_{\text{turnover and herbivory}} \tag{1}$$

[1] α_τ and γ_τ are simple functions of τ and α. To understand why, we can start by decomposing B as $C+N$, so that by definition $\gamma = N/(C+N)$ and $\alpha = C/N$. From this decomposition we immediately get that $\gamma^{-1} = \alpha + 1$. If we now write B_τ as $N + C + C_\tau$ where C_τ is the carbon part attributed to tannins, we similarly get that $\gamma_\tau^{-1} = \alpha_\tau + 1$. Since we also have that $C_\tau = \tau B_\tau = \tau(C_\tau + C + N)$ we deduce that $\gamma_\tau^{-1} = \frac{C_\tau}{N} + \frac{C+N}{N} = \tau\gamma_\tau^{-1} + \gamma^{-1}$ so that $\gamma_\tau = (1-\tau)\gamma$. Since γ and γ_τ can be expressed as functions of the C:N ratios α and α_τ, we get that $\frac{1}{1+\alpha_\tau} = \frac{1-\tau}{1+\alpha}$ which leads to $\alpha_\tau = \frac{\alpha+\tau}{1-\tau}$.

where κ is a metabolic rate, supposed constant. We model the effect of herbivory, and the protection against it that tannins provide by assuming d to be a decreasing function of τ when herbivores are present[2].

Physiological dynamics and stoichiometry

There are two soil N-compartments: labile and recalcitrant (n_l and n_r, respectively). Recalcitrant N is produced by plants themselves when tannins complex N-containing proteins during leaf senescence and during the first steps of litter decomposition [40]. Recalcitrant N is less subject to leaching and volatilization but is more difficult to absorb than labile N [22]. A critical assumption of our model is that symbiotic associations with mycorrhizae are necessary to absorb recalcitrant N [47, 48, 62]. We model this requirement by writing the labile and recalcitrant absorption efficiencies resp. $\mathcal{E}_l$ and $\mathcal{E}_r$ as explicit functions of e, the symbiotic capacity, namely $\mathcal{E}_l(e) = \mathcal{E}_l^- + e(\mathcal{E}_l^+ - \mathcal{E}_l^-)$, and $\mathcal{E}_r(e) = e\mathcal{E}_r^+$, where the exponents $^-$ and $^+$ reflect respectively the minimum and maximum values of the absorption efficiencies (see Table II). Thus symbiotic capacity enhances both absorption efficiencies, and without it recalcitrant N cannot be absorbed. We assumed this capacity to come at an accelerating maintenance C-cost, m, of the mycorrhized root network: $m(e) = \frac{m_0}{1-e}$ where m_0 is the baseline maintenance cost (see Table II). We note ξ the rate at which the absorption process is running, generating a cost ξm. Thus C and N stocks follow

$$\frac{dn}{dt} = \underbrace{\xi \sum_{i=l,r} \mathcal{E}_i n_i B}_{\text{absorption}} - \gamma_\tau \underbrace{\kappa \min\{\frac{n}{\gamma_\tau}, \frac{c}{1-\gamma_\tau}\}}_{\text{growth}} - \underbrace{dn}_{\text{turnover}}$$

$$\frac{dc}{dt} = \underbrace{\phi B}_{\text{photosynthesis}} - \underbrace{\xi m B}_{\text{maintenance}} - (1-\gamma_\tau) \underbrace{\kappa \min\{\frac{n}{\gamma_\tau}, \frac{c}{1-\gamma_\tau}\}}_{\text{growth}} - \underbrace{dc}_{\text{turnover}}$$

Physiological dynamics are best expressed in terms of concentrations $p = n/B$ and $q = c/B$ [32]. Using $\frac{dp}{dt} = \frac{dn}{dt}\frac{1}{B} - \frac{dB}{dt}\frac{n}{B^2}$ the above system becomes:

$$\begin{cases} \frac{dp}{dt} = & \xi \sum_{i=l,r} \mathcal{E}_i n_i - (p+\gamma)\,\mathcal{K}(p,q) \\ \frac{dq}{dt} = & \phi - m\xi - (q+1-\gamma)\,\mathcal{K}(p,q) \end{cases} \tag{2}$$

where $\mathcal{K}(p,q) = (1-\tau)\,\kappa \min\{\frac{p}{\gamma_\tau}, \frac{q}{1-\gamma_\tau}\}$. We assume physiological dynamics (2) to be faster than ecological dynamics rapidly reaching a moving equilibrium

[2] E.g. $d(\tau) = d(1) + (1-\tau)H$ where $(1-\tau)H$ is the rate of herbivory, reduced by tannins from H to eventually 0 when $\tau = 1$.

(p_*, q_*) defined by $\frac{dp}{dt}|_{(p_*,q_*)} = \frac{dq}{dt}|_{(p_*,q_*)} = 0$. This equilibrium gives the plants stocks concentrations at any given time, and depends on the pace of absorption ξ. We assume the latter to be plastic and that plants optimize their absorption to remain at stoichiometric balance, implying that $p_*/q_* = \alpha_\tau$. This and Eq.(2) lead to $m\xi = \phi/(1+\alpha_\tau \sum_{i=l,r} \frac{\mathcal{E}_i n_i}{m})$. Stocks being at stoichiometric balance implies that $\mathcal{K}(p_*, q_*) = \kappa p_*/\gamma$. From Eq. (2) we deduce

$$P^2 + P = \frac{\phi}{\kappa\gamma} \frac{\sum_i \frac{\mathcal{E}_i n_i}{m}}{1+\alpha_\tau \sum_i \frac{\mathcal{E}_i n_i}{m}} \tag{3}$$

where $P = p_*/\gamma$ is the ratio of stocks n over the N-content of effective biomass γB. It is the effective nutrient stock, which drives productivity. Indeed, once Eq. (1) is written as:

$$\frac{dB_\tau}{dt} = \kappa \left(P - \frac{d}{\kappa}\right) B_\tau \tag{4}$$

we see that productivity (rate of biomass creation) is κP. That P satisfies (3) defines a type-II functional response to soil N content. Finally, to permit some degree of bottom-up control, we assume a density dependence for photosynthesis ϕ, saturating as B_τ grows beyond a critical mass B_ϕ. Concretely we write $\phi(B_\tau) = \phi_0/(1+B_\tau/B_\phi)$, which, as long as $B_\tau < B_\phi$, is approximately equal to $\phi_0(1-B_\tau/B_\phi)$.

Absorption and recycling

In a mean-field limit (i.e. neglecting the spatial structure of plant patches), we model the dynamics of inorganic labile N in the soil as

$$\frac{dn_l}{dt} = -\underbrace{\xi \mathcal{E}_l n_l B}_{\text{absorption}} + \bar{\ell}\, \underbrace{d \max\{0, (P+1)\gamma B - \Omega\tau B_\tau\}}_{\text{complexation and recycling}} + \underbrace{L\,(n_w - n_l)}_{\text{in and out flows}}$$

Let us explain this equation, starting from the simplest term, the one representing exogenous nutrient flows (the rightmost term). Here n_w denotes the bare soil N-content, i.e. its wash-out value [12, 32]. L is the leaching rate of N, which we will use in the next section to set a timescale reference.

In the second term from the right, i.e. the recycling term, $\gamma PB = n$ is the N-stock of plants, so that $\bar{\ell} d\gamma PB$ is the rate at which this stock is sent back into the soil by senescence (hence the occurence of d), where $\bar{\ell} = 1 - \ell$ reflects losses[3] during transition between compartments due to leaching and volatilization [55]. γB is the amount of N in plant effective biomass, so that $\bar{\ell} d\gamma B$ is the rate at which it is released. τB_τ is the amount of tannins in plants, so that $\bar{\ell} d\tau B_\tau$ is the amount of released tannins. Each units of these will complex some amount Ω of released N turning it into its recalcitrant form. If tannin content is too high, all organic N is complexed and the labile recycling term vanishes (hence the max$(0, .)$ function).

The third term from the right, the absorption term, simply models the N absorption by plants, following the modeling choices of the previous section on physiological dynamics. The amount $\bar{\ell} d\Omega\tau B_\tau$ of recycled N is complexed, flowing into the recalcitrant compartment n_r. This is the only inflow in n_r and its dynamics follows

$$\frac{dn_r}{dt} = -\underbrace{\xi \mathcal{E}_r n_r B}_{\text{absorption}} + \underbrace{\bar{\ell} d \min\{\Omega\tau B_\tau, (P+1)\gamma B\}}_{\text{complexation and recycling}} - \underbrace{L_r n_r}_{\text{leaching}}$$

for which we will typically assume $L_r < L$.

Adimensionalization and relevant parameters

The nondimensional ratios of parameters appearing in the physiological equations suggest that there is a limited number of relevant nondimensional parameters to consider. Indeed there is, and in this section we adimensionalize the model to reveal them. This will substantially reduce the parametric space and ultimately, will allow a more global understanding of the model's behavior. We use the labile leaching rate L to set the reference time scale, writing $s = Lt$. We then define $\mu = \kappa/L$ and $h = d/\kappa$. Writing $x_\tau = B_\tau/B_\phi$ leads to the nondimensional equation for plant growth

$$\frac{dx_\tau}{ds} = \mu(P-h)x_\tau \tag{5}$$

We then put $\varphi = \frac{\phi}{\kappa\gamma}$. Notice here the occurrence of γ, reflecting the fact that photosynthesis is performed mostly from N-compounds of the plant (so that ϕ should in fact be proportional to γ). We write $\mathcal{N} = \frac{\mathcal{E}_l n_w}{m}$, the latter defining the ecosystem's effective N-enrichment. Finaly, we transform B_ϕ into $\mathcal{B} = \frac{\gamma \mathcal{E}_l B_\phi}{m}$ and set $\mathcal{L} = L_r/L$ and $\beta_i = \frac{\mathcal{E}_i}{\mathcal{E}_l}$. Nondimensional soil N-content are defined in reference to the labile wash-out value n_w as $y_i = n_i/n_w$. This leads us to the following condition satisfied by P:

$$P^2 + P = \mathcal{A} \tag{6}$$

$\mathcal{A} = \sum_i \mathcal{A}_i$ represents the total absorption effort where $\mathcal{A}_i$ is the one restricted to soil N of type i, which reads

$$\mathcal{A}_i = \frac{\varphi \beta_i \mathcal{N} y_i}{1+\alpha_\tau \sum_i \beta_i \mathcal{N} y_i}.$$

[3] Necessary to avoid unrealistic divergences.

To write the soil dynamics in compact yet intuitive form we define nondimensional recycling rates as

$$\mathcal{R}_l = \bar{\ell} h \max\{0, P + 1 - \Omega_\tau\}$$

and

$$\mathcal{R}_r = \bar{\ell} h \min\{P + 1, \Omega_\tau\}$$

where $\Omega_\tau = \frac{\Omega}{\gamma}\frac{\tau}{1-\tau}$ is an effective complexation parameter. This leads us to nondimensional soil dynamics

$$\begin{cases} \frac{dy_l}{ds} = & 1 - y_l + \frac{\mu\mathcal{B}}{\mathcal{N}}(\mathcal{R}_l - \mathcal{A}_l)x \\ \frac{dy_r}{ds} = & -\mathcal{L}y_r + \frac{\mu\mathcal{B}}{\mathcal{N}}(\mathcal{R}_r - \mathcal{A}_r)x \end{cases} \quad (7)$$

in which we clearly see the antagonistic contributions of absorption and recycling. Note that symbiotic capacity e only enters in the absorption terms $\mathcal{A}_i$, via

$$\beta_l\mathcal{N} = (1+\delta\beta_l e)(1-e)\mathcal{N}_0;\ \beta_r\mathcal{N} = \delta\beta_r e(1-e)\mathcal{N}_0 \quad (8)$$

where $\delta\beta_l = \frac{\mathcal{E}_l^+ - \mathcal{E}_l^-}{\mathcal{E}_l^-}$ and $\delta\beta_r = \frac{\mathcal{E}_r^+}{\mathcal{E}_l^-}$ are the maximal relative gain in absorption efficiency. Nondimensional parameters are summarized in Table III.

Cellular automaton

We consider a landscape of S patches each populated by at most one individual at a time; representing either a single or several genetically similar plants. A populated patch grows according to the above model, absorbing and recycling N locally. N diffuses continuously across patches, the diffusion term affecting nutrients in patch k – either labile , $y_l^{(k)}$ or recalcitrant $y_r^{(k)}$ – being

$$\mathcal{D}_i\Big(\sum_{p\in Nei(k)} y_i^{(p)} - \frac{y_i^{(k)}}{\#Nei(k)}\Big);\ i = l, r$$

where $Nei(k)$ denotes the set of neighbors of patch k and $\mathcal{D}_i, i = l, r$, are the nondimensional diffusion rates (i.e. normalized by labile leaching rate L). The first term (the sum) represents in-flow from neighboring patches of patch k while the second represents outflows from patch k towards its neighbors. In simulations we considered the simplest possible landscape: a one-dimensional periodic lattice, so that $Nei(k) = \{k-1, k+1\} \bmod (S)$. We will typically assume $\mathcal{D}_l$ to be much larger than $\mathcal{D}_r$, making recalcitrant N less mobile, whereas labile N tends to uniformly spread in the landscape. We then add a stochastic layer, allowing individuals to randomly die and/or reproduce in an empty patch. We assume that larger individuals are less likely to die than smaller (e.g. younger) ones and, similarly, that the birth rate of individuals increases with their biomass. Concretely, we set

$$r_{\text{death}}(x_\tau) = r^+_{\text{death}}\, e^{-\lambda x_\tau}\ ; r_{\text{birth}}(x_\tau) = r^+_{\text{birth}}(1 - e^{-\lambda x_\tau})$$

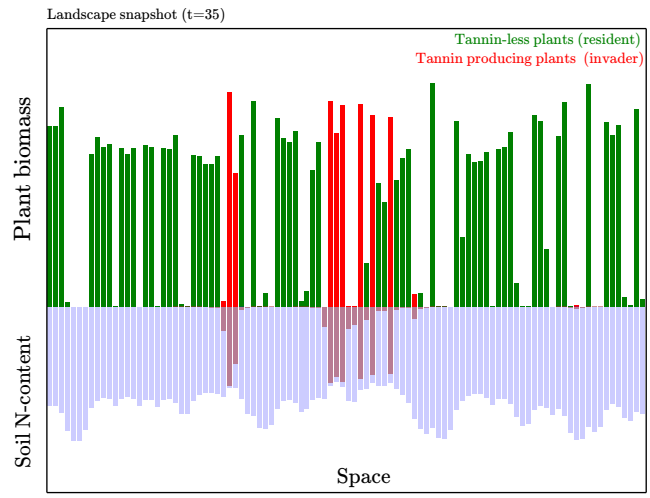

FIG. 2. Snapshot of the cellular automaton. Each green or red bar represent the biomass of an individual, which could represent either a single plant, or several genetically similar plants. Inverted bars represent soil N-content in its labile and recalcitrant form (blue and brown respectively). We follow here the invasion attempt of tannin producing plants (in red) in a landscape populated by a tannin-less resident population (in green).

We assume that individuals contribute to the recruitment in near-by empty patches, and to a lesser extent, to the recruitment in distant patches. Concretely, we write the recruitment rate in an empty patch k as

$$r_{\text{recruitment}}(k) = \sum_{n>0} P(n) \sum_{p\in Nei^{(n)}(k)} \frac{r_{\text{birth}}(x_\tau(p))}{\#Nei^{(n)}(p)}$$

where $P(n)$ is the fraction of a plant reproductive effort to patches at distance n. In the case of a recruitment event, a new individual starts growing from a small initial biomass. In our simulations we will superpose a geometrically decreasing kernel up to $n = 3$ to a uniform contribution of the remaining effort to all other patches (representing the fraction of seeds transported in the wind or by animals to arbitrarily distant locations[4]) We tuned those parameters to always have a densely populated landscape. Indeed, if stochasticity allows many patches to be empty at any given time, the dynamics become neutral and we cannot expect to exhibit selective pressures. We will simulate invasion attempts of tannin-producing plants in a landscape populated by tannin-less plants. We will suppose both phenotypes to have equal symbiotic capacity, so that the resident may absorb recalcitrant N as well as invading plants. A snapshot of a typical run of the automaton is presented in Fig 2, where we can see the impact of tannin producing individuals on soil variables surrounding their respective patches. Parameters of the cellular automaton are summarized in Table III.

[4] Precisely we put, for some $\delta, K < 1$, $P(1) = (1-\delta)K$, $P(2) = (1-\delta)K(1-K)$, $P(3) = (1-\delta)(1-K)^2$ to which we add the mean-field contribution $\frac{\delta}{S}\sum_p r_{\text{birth}}(x_\tau(p))$.

Parameters	interpretation	units
α_τ	plants C:N ratio	–
α	effective C:N ratio	–
γ_τ	fraction of N in plant biomass	–
γ	fraction of N in effective biomass	–
κ	metabolic rate	time^{-1}
d	turnover rate	time^{-1}
H	herbivory rate	time^{-1}
$\mathcal{E}_l^-$	min labile absorption efficiency	mass^{-1}
$\mathcal{E}_l^+$	max labile absorption efficiency	mass^{-1}
$\mathcal{E}_r^+$	max recalcitrant absorption efficiency	mass^{-1}
m_0	min maintenance cost	–
ξ	plastic absorption rate	time^{-1}
ϕ_0	max photosynthesis rate	time^{-1}
B_ϕ	saturating biomass for photosynthesis	mass
L	labile leaching rate	time^{-1}
ℓ	N volatilization	–
n_w	bare soil N content	mass
L_r	recalcitrant leaching rate	time^{-1}
Ω	Tannins complexation power	–
D_l	labile diffusion rate	time^{-1}
D_r	recalcitrant diffusion rate	time^{-1}
r^+_{birth}	max birth rate of individuals	–
r^+_{death}	max death rate of individuals	–
λ	demographic effect of biomass	–
K	seed dispersal kernel	–
δ	fraction of seeds uniformly dispersed	–

TABLE II. Model parameters (in order of appearance) and their dimensions.

MODEL ANALYSES

Invasibility of the tannin phenotype

We start with an analytical approach consisting in deriving the conditions for tannin producing plants to invade a resident population of tannin-less plants. This reasoning relies on the analysis of the invasion fitness function [15], i.e. the initial growth rate of a mutant population in the presence of a resident population at equilibrium. It only depends on the adimensional mean-field model as written in the Adimensionalization section of the Methods. The reasoning goes as follows: a resident population sets the state of soil labile N and available light that a rare mutant population x_τ will experience. The latter's fitness reads

$$W(\tau,0) = \frac{1}{x_\tau}\frac{dx_\tau}{ds}|_{x_\tau=0\,;\,x_0=x_*}$$

where by definition $W(0,0) = 0$ [15]. The sign of the fitness gradient

$$\partial_\tau W(\tau,0)|_{\tau=0}$$

provides a notion of the invasibility of the resident population: if positive, a mutation leading to a small change in the phenotype τ can invade. From (5) and (3) we have that

$$\partial_\tau W \approx \mu\left(\partial_\tau \mathcal{A} - \partial_\tau h\right) \tag{9}$$

This makes intuitive sense: if the phenotypic change increases the absorption effort $\mathcal{A}$ and/or decreases the turnover rate h, the mutant population should be able to invade. Tannins can be selected for as a protection against herbivores since $\partial_\tau|_0 h = -\mathcal{H}$ where $\mathcal{H}$ is the relative rate of biomass removal by herbivores. In their absence, we assumed no impact on turnover, so that $\partial_\tau h = 0$. In this case the selective force can only come through an increase in N-absorption.

Implicit spatial structure

If mutant plants are not well mixed in the landscape, and/or if seedlings reach a small – but not arbitrarily small – biomass before feeling the competition with other plants, then we should expect tannins to affect the soil composition surrounding mutants. We account for this by defining an unknown parameter z, an *a priori* complex function of spatial processes but defined to be independent of turnover rate h and soil enrichment $\mathcal{N}$. More precisely, we define z so that $z\mu h\tau = \mathcal{N}y_r$ where y_r would be the adimensional local density of complexed N, proportional to the turnover rate and tannin content. Indeed, if we write n_r^τ the amount of recalcitrant N formed in the vicinity of a mutant with biomass B_{mut}, this N content should be proportional to $\tau\frac{d}{D_r+L_r}\gamma B_{\text{mut}}$. In terms of the nondimensional parametrization, this translates as $\mathcal{N}y_r$ being proportional to $\tau\mu h\frac{\mathcal{B}}{\mathcal{D}_r+\mathcal{L}}x_{\text{mut}}$. Therefore, keeping track of μ, h and τ are aggregating all other parameters (known and unknown) in a the nondimensional parameter z, we get that $\mathcal{N}y_r = z\mu h\tau$. All in all, this means that the tannins produced by mutants have a direct effect on their absorption term $\mathcal{A}$. Concretely, to consider the invasion of tannin producing mutants in a landscape populated by tannin-less residents, we evaluate eq. 9 at $\tau = 0$, with a change in absorption taken as

$$\partial_\tau|_{\tau=0}\mathcal{A} = \partial_\tau\left\{\frac{\varphi(\mathcal{N}y_l + \beta_r\mu hz\tau)}{1+\alpha_\tau(\mathcal{N}y_l+\beta_r\mu hz\tau)}\right\}|_{\tau=0} \tag{10}$$

evaluated at the equilibrium values of y_l and x (thus φ) of the resident. The invasibility analysis relies entirely on eqs. 9-10, and thus only depends, for any given value of z, on $\mu, h, \mathcal{N}, \varphi, \alpha$ and β_r. This analysis will lead to qualitative predictions about tannin evolution that can be tested on simulations of the cellular automaton.

Coevolution of tannins and symbiotic capacity

We analyze the outcome of the coevolution of tannins τ and symbiotic capacity e as follows [31]. For any values (e,τ) we solve for the ecological equilibrium associated to a resident population with phenotypes τ and e following the dynamics of eqs. (5) and (7). We then determine the fitness gradient at this point by

Relevant parameters for tannin invasibility

parameters	effects on τ	interpretation	expression	values
μ	$\nearrow$	metabolic rate	κ/L_l	5
h	$\nearrow\searrow$	intrinsic turn-over rate	d/κ	0.6
$\mathcal{N}$	$\searrow$	soil fertility	$\mathcal{E}_l n_w/m$	0.6
$\mathcal{H}$	$\nearrow$	max herbivory rate	H/κ	0.01
$\mathcal{B}$	$\nearrow$	saturating biomass	$\gamma\mathcal{E}_l B_\phi/m$	1
φ_0	$\nearrow$	photosynthesis rate	$\phi_0/(\kappa\gamma)$	10
β_r	$\nearrow$	recalcitrant N absorption	$\mathcal{E}_r/\mathcal{E}_l$	1
z	$\nearrow$	spatial structure	–	0.03
α	$\searrow$	C:N ratio	–	0.5
ℓ	$\nearrow$	nutrient losses	–	0.2

Relevant parameters for coevolution analysis

parameters	effects on (e,τ)	interpretation	expression	values
$\mathcal{L}$	$\searrow$	recalcitrant leaching	L_r/L	0.1
$\delta\beta_l$	$\nearrow$	gain in absorption	$(\mathcal{E}_l^+ - \mathcal{E}_l^-)/\mathcal{E}_l^-$	1.1
$\delta\beta_r$	$\nearrow$	gain in absorption	$\mathcal{E}_r^+/\mathcal{E}_l^-$	1.1
$\mathcal{N}_0$	$\searrow$	minimal soil fertility	$\mathcal{E}_l^- n_w/m$	0.6
Ω	$\nearrow$	complexation power	–	1

Parameters of the cellular automaton

parameters	effects on τ	interpretation	expression	values
$\mathcal{D}_l$	$\searrow$	labile diffusion	D_l/L	10
$\mathcal{D}_r$	$\nearrow\searrow$	recalcitrant diffusion	D_r/L	0.1
r^+_{birth}	tuned	max birth rate	–	1
r^+_{death}	to	max death rate	–	0.2
λ	avoid	sensitivity of birth and	–	$1/x_*$
	neutrality	death rates to biomass	–	
K	–	seed dispersal kernel		0.6
δ	–	fraction of uniform dispersal	–	0.2

TABLE III. Nondimensional parameters relevant to the invasibility analysis (and their qualitative effects on tannin evolution) followed with additional parameters relevant to study the coevolution between tannins and symbiotic capacity, along with their values in simulations. Also reported are the additional parameters specific to the cellular automaton.

evaluating the initial growth rate of slightly different mutant phenotypes $(e+\delta e, \tau+\delta\tau)$. The fitness gradient has two components, one in the direction of symbiotic capacity and one in the direction of tannins:

$$\nabla W|_{e,\tau} = (\partial_e W|_{e,\tau}\ ;\ \partial_\tau W|_{e,\tau}) \tag{11}$$

We calculate the first component by generalizing the invasibility analysis (9) to the case of a tannin producing resident. As we did for the latter, we account for spatial structure by writing $\mathcal{N}y_r(\tau+\delta\tau) = \mathcal{N}y_r(\tau) + z\mu h\delta\tau$, where z implicitly accounts for spatial structure. For the second component we use the expressions of $\mathcal{N}\beta_i$ given in Eq. (8). The continuous coevolutionary steady state (co-CSS) will correspond to an intersection between the isocline of symbiotic capacity $\{(e,\tau) \in \mathbb{R}^2_+ \mid \partial_e W|_{e,\tau} = 0\}$ and the one of tannin content $\{(e,\tau) \in \mathbb{R}^2_+ \mid \partial_\tau W|_{e,\tau} = 0\}$.

RESULTS

Our analysis predicts the effect of all the model's parameters on the selective advantages of tannin production (Table III). In the following sections, we focus on the influence of two key parameters, the effective bare soil N content $\mathcal{N}$ and the plants' relative turnover (h). Effective bare soil N content ($\mathcal{N} = \mathcal{E}_l n_w/m$) is a proxy for soil fertility, it allows to test if the model predicts that unfertile ecosystems favor tannin production, as observed in nature. Plants relative turnover ($h = d/\kappa$) is a proxy for plant life strategy, high h plants will enhance nutrient cycling while low h plants will slow it down. We consider three evolutionary scenarios for plants tannin production: (i) Tannin phenotype evolving in the presence of herbivores but in the absence of spatial structure. (ii) Tannin phenotype evolving under negligible herbivory pressure but taking into account spatial structure. (iii) Tannin phenotype evolving in the presence of herbivores and taking into account spatial structure. All of these scenarios include the plant-soil feedback loop, assuming a symbiotic association with mycorrhizae, but differ with respect to herbivory and spatial structure. We then analyze the outcome of coevolution of tannin and symbiotic associations in the presence and absence of herbivores, accounting for spatial structure, starting from a resident population with neither tannins nor symbiotic association.

Invasibility of tannins

The relationship between tannin invasibility, soil fertility and plants life strategies under the three scenarios is illustrated in Fig. 3, in which we numerically computed the fitness gradient as defined in Eq. (13) as a function of h and $\mathcal{N}$. In the leftmost panel – herbivores and no spatial structure – we observe selective pressure towards protection against herbivores by tannin production at low turn over rates h and relatively low fertility $\mathcal{N}$. Note that as h grows (or $\mathcal{N}$ decreases) plants eventually reach the limits of viability (in grey in Fig 3). In the middle panel – no herbivores but spatial structure – we observe that local recycling of recalcitrant N by tannin-producing mutants should strongly promote their settlement at low fertility and intermediate values of turnover rate. Finally, the rightmost – herbivores and spatial structure – combines the previously described behaviors, showing that, for low soil fertility, tannin production can be beneficial at both low and intermediate values of turn over rates, but for essentially different reasons. At low turn over rate tannins are mostly selected for their herbivore deterrent properties, whereas at intermediate turnover they mostly favor plants by forming a local N pool less subject to leaching.

To get a more global understanding of the factors promoting tannin evolution we can derive an analytical approximation of the fitness gradient. For this purpose one needs expressions for the equilibrium state of a tannin-less ecosystem. Using (5), (3) and (7) with $\tau = 0$

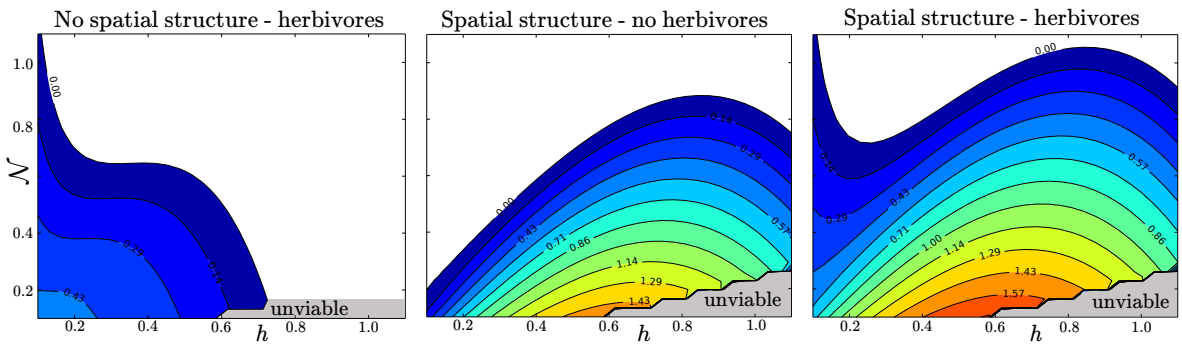

FIG. 3. Role of turnover rate h and soil fertility $\mathcal{N}$ on the invasibility of tannins. We plotted the fitness gradient at $\tau = 0$, a positive value predicts that tannin-producing plants should be selected for. In all panels, the facts that the limits of viability (in grey) increases in steps is a numerical artifact (see main text for the smooth analytical expression). Left panel: non spatial model ($z = 0$) with herbivory ($\mathcal{H} = 10^{-2}$). In this case, recalcitrant N play no role in the invasion fitness of tannins. middle panel: Spatially implicit context without herbivory ($z = 0.03$, $\mathcal{H} = 0$). Right panel: spatial structure and herbivory. Note that increasing z would inflate the invasibility domain (see main text for an analytical expression).

yields

$$\mu\mathcal{B}x_* \approx \frac{\mathcal{N}(1-y_l^*)}{\ell h} \text{ and } \mathcal{N}y_l^* \approx \frac{h}{\varphi_* - h\alpha} \tag{12}$$

The symbols indexed with "$*$" denote resident equilibrium values. The second equation gives us the viable domain, at the limits of which $y_l^* = 1$ and $\varphi_* = \varphi_0$, so that, in the $(h, \mathcal{N})$ plane it is a curve defined by $\mathcal{N} = \frac{h}{\varphi_0 - h\alpha}$ of which we see the low h part in Fig. 3. Algebraic manipulations of (9-10) then lead to the following expression for the fitness gradient of the tannin phenotype

$$\partial_\tau|_0 W \approx \frac{\mu h^2}{\varphi_*}\left(\frac{\mu h \beta_r z}{|\mathcal{N}y_l^*|^2} - 1\right) - \mu\mathcal{H} \tag{13}$$

Putting $z = 0$ amounts to neglecting spatial structure, while $\mathcal{H} = 0$ neglects the effect of herbivores. The effects of the latter being rather straightforward, we focus instead on scenario (ii), corresponding to $z > 0$ and $\mathcal{H} = 0$. Using that $\mathcal{N}y_l^* \approx \mathcal{N} - \mu\ell\mathcal{B}hx_*$, the limits of invasibility (corresponding to the term in parenthesis in (13) set to zero) read:

$$\mathcal{N} \leq \sqrt{\mu h \beta_r z} + \mu\ell\mathcal{B}hx_* \tag{14}$$

The first term on the r.h.s. is a monotonous convex function of h. Increasing the spatial parameter z increases the contribution of this term, thus simply inflating the invasibility domain. The rightmost term, by virtue of Eq.(12), is always smaller than $\mathcal{N}$ so that the invasibility domain vanishes for small enough z. This term is not monotonous. In fact, when h is small, x_* approaches 1, saturating photosynthesis rate. On the contrary x_* reduces as h grows. Thus x_* goes from 1 to 0 as h grows, vanishing precisely at the limits of viability. Thus hx_* is humped shaped which explains the humped shaped invasibility domain observed in the two last panels of Fig. 3. We can deduce an expected positive effect on tannin evolution of μ and parameters related to photosynthesis intake, $\mathcal{B}$ and φ_0 the latter delaying the photosynthesis saturation point and inflating the viability domain. The qualitative effect of every parameter is summarized in Table III.

Simulations of the cellular automaton: the selective advantage of altruism

In the left panel of Fig 4 we confronted our qualitative predictions to simulations of the cellular automaton, without herbivory. For the same values of parameters as in Fig 3 we ran simulations of invasions attempts of a tannin producing population ($\tau = 0.2$), starting from a few aggregated individuals in a landscape populated by tannin-less plants. We monitored the ultimate fraction of mutants and compared the outcome of these simulations to the invasibility domain from the middle panel of Fig 3. Except near the inviable domain where less successful invasions were recorded than expected, we see that simulations of the cellular automaton are in qualitative agreement with the invasibility predictions. This provides support to our analysis suggesting that, at least qualitatively, tannin evolution depends only on the few key parameters previously identified (h and $\mathcal{N}$, but also the other nondimensional parameters of the mean-field model as summarized in Table III). Beyond corroborating our analysis, simulations of the cellular automaton allowed us to relate tannin evolution to the evolution of altruism by group selection [57]. To do so we ran invasion attempts as above keeping $h, \mathcal{N}$ fixed but for many values of recalcitrant diffusion rate $\mathcal{D}_r$. We monitored the frequency of successful invasions to estimate the probability of invasion as a function of $\mathcal{D}_r$, as shown in the right panel of Fig 4. At the individual level, in terms of survival and birth rate, the least diffusion of recalcitrant N the better $-$a selfish "behavior". Yet at the population level, in terms of probability of invasion, we observe that intermediate values of diffusion

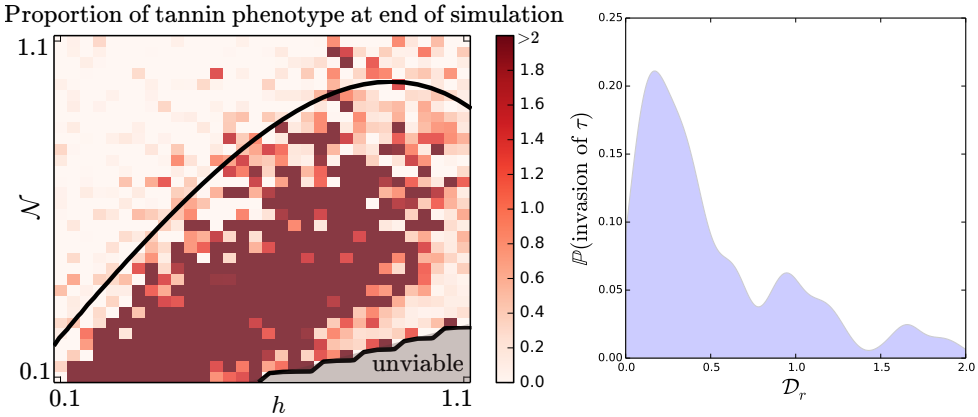

FIG. 4. Left: confrontation of the qualitative predictions of fig.(3) to simulations of the cellular automaton. Each cell represents the ultimate fraction of mutants (with $\tau = 0.2$) after 400 time steps. The landscape is a periodic lattice comprised of $S = 250$ cells. We start from 5 spatially aggregated mutants in a landscape populated by tannin-less plants. New-born individuals have an initial biomass 10^{-3} smaller than the one of an average resident. N-diffusion rates are set to $\mathcal{D}_l = 5$ and $\mathcal{D}_r = 0.1$. We compare to the invasibility domain from the middle panel of fig.(3) by adjusting the free parameter z (here $z = 0.03$). Except near the inviable domain where less successful invasions are observed than expected, we observe a good qualitative agreement between the two. Right: evidence of selection of altruism. We varied the recalcitrant diffusion rate $\mathcal{D}_r$ from 0 to 2 and estimated the invasion probability function from the histogram of diffusion rates for which the ultimate proportion of mutant biomass was larger than one. At the individual level, in terms of survival and birth rate, the least diffusion of recalcitrant N the better. Yet at the population level, in terms of probability of invasion, intermediate values of diffusion appear more beneficial. For large values we recover a "tragedy of the commons" scenario, where "cheaters" benefit without costs from complexed N.

−corresponding to altruistic "behaviors"− are more beneficial. For larger values of nutrient diffusion we recover a "tragedy of the commons" scenario, where "cheaters" benefit without costs from the complexed N pool, and individuals contributing to this pool, having no extra benefits, are eventually excluded.

Coevolution of symbiotic capacity

In Fig. 5, we drew the coevolutionary steady state of tannins and symbiotic capacity, co-CSS [31]. The fitness gradient (11) has two components and the co-CSS corresponds to an intersection between the fitness gradient isocline of symbiotic capacity (in Grey in Fig. 5) and the one of tannin content (in black). We find that coevolution can have important consequences, especially if symbiotic capacity is not favored without tannins. In this case herbivory can promote a slight increase of tannins which will promote symbiotic capacity, and in turn promote a larger tannin content[5].

[5] Incidentally we could derive the following analytical approximation for the fitness gradient:

$$\nabla W|_{e,\tau} \approx \mu \left(\frac{h^2}{\varphi_*} \left(\frac{\mu \beta_r z}{\langle \mathcal{N}\beta, y \rangle^2} - \partial_\tau \alpha_\tau \right) - \mathcal{H} \; ; \; \frac{h^2}{\varphi_*} \frac{\langle \partial_e \mathcal{N}\beta, y \rangle}{\langle \mathcal{N}\beta, y \rangle^2} \right)$$

where $\langle \mathcal{N}\beta, y \rangle = \sum_i \mathcal{N}\beta_i y_i$. We used this expression to deduce the qualitative effects of parameters on coevolution, summarized in Table III.

DISCUSSION

Plant soil feedbacks alone can trigger tannin evolution

In a spatial context, we predict that plant-soil feedbacks can trigger the evolution of tannin production, even in the absence of selective pressures due to herbivores (Fig 3 center panel, Fig 4 left panel). The results of our modeling approach are in line with the "litter perspective" proposed by Hättenschwiler et al. [17] as an alternative to the "green foliage perspective" for the evolution of tannins. Plants may benefit from the afterlife effects of tannins, instead of suffering from a reduction of nutrient cycling [4]. In line with empirical findings [21, 24], our model assumes that the main mechanism explaining the impact of tannins in soil is their ability to complex proteins, which forms a recalcitrant N pool that can be reabsorbed by mycorrhizae. Our model predicts that tannins should evolve only if a given plant has a preferential access to this recalcitrant pool, and cannot evolve if it is shared with all plants. In our model, a tannin-producing plant creates a local pool of recalcitrant N, which can only be reabsorbed by this plant. The mechanisms underlying such exclusivity may be spatial, if neighboring plants are too far away to access the local pool, or biological, if mycorrhizae are better adapted to reabsorb the recalcitrant nutrients formed by their host [21, 62]. Tannin production cannot evolve when the recalcitrant pool is shared by all plants, because tannin producing plants must be protected from the invasion of cheaters able to absorb recalcitrant N without paying the cost of tannin production. Our model is in this sense similar to those fo-

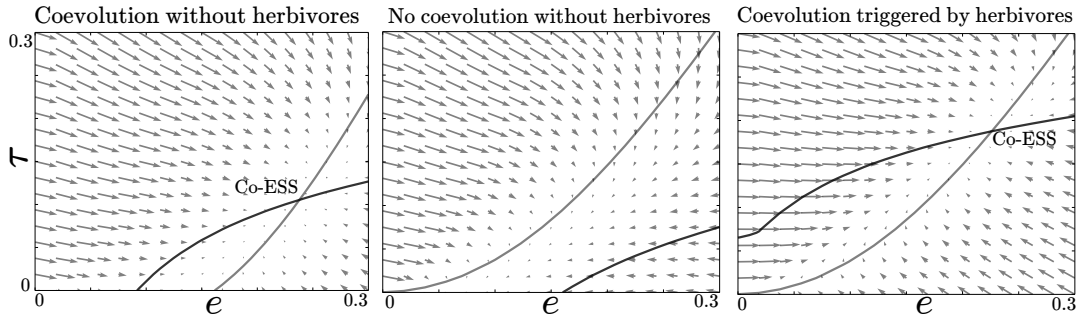

FIG. 5. Coevolution of tannins and symbiotic capacity. In Grey is the fitness gradient isocline of symbiotic capacity, In black the fitness gradient isocline of the tannin phenotype. The coevolutionary stable state (co-CSS) is at the intersection of the two. Leftmost panel: we chose parameters $\delta\beta_i$ controlling the effect of symbiotic capacity on absorption efficiencies (8) such that symbiotic capacity would be favored even in the absence of tannins. In this case, we predict a coevolutionary positive feedback, with tannin evolution increasing the selective advantage of symbiotic associations and vice versa, until a co-ESS is reached. Middle panel: Here we chose $\delta\beta_i$ so that symbiotic capacity is not favored in the absence of tannins. In this case, we predict no evolution of tannin production nor symbiotic capacity. Rightmost panel: Additional pressure from herbivory, however, can trigger a coevolutionary positive feedback.

cused on the evolution of altruism [29], facilitation [27] and shared chemical resources among microorganisms [2]. Yet our model is not a mere illustration of altruism evolution, for two reasons. First, in models of altruism evolution [29, 57, 61], the altruistic trait is beneficial to any phenotype. Our model is one of competition for resources in which no individual is strictly altruistic. Tannin production could both lead to the competitive exclusion of non-symbiotic plants [21] and to the facilitation of plants associated with mycorrhizae. Second, we consider here a whole ecosystem including abiotic compartments, instead of a single monospecific population. Hence, selection does not operate at the group-level [57], but at the ecosystem-level (cf. next section).

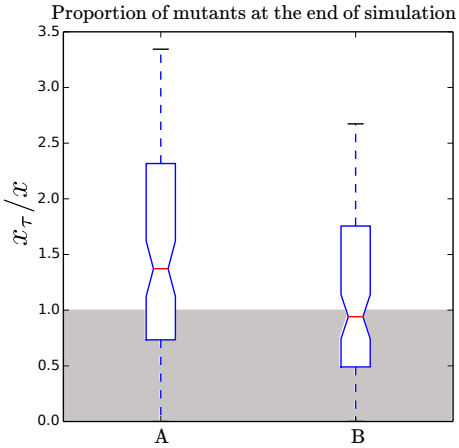

FIG. 6. The effect of ecological inheritance in the cellular automaton. Case A: with ecological inheritance, after the death of a tannin-producing individual, other plants can benefit from the pool of recalcitrant N that it formed during its lifetime. The box plot represents the outcome of simulation runs (100 runs up to t=200), starting from a few tannin producing-mutants in a landscape populated by a tannin-less resident. Case B: when an individual died, we set to zero the recalcitrant pool that it formed during its lifetime, thus removing the effect of ecological inheritance. The overall larger values for the ultimate proportion of mutants in case A demonstrates the importance of ecological inheritance for the invasion success of tannins. All parameters are the same as those used in Fig 4, but with $\mathcal{D}_r = 0$.

Tannin evolution under a niche-construction perspective

The evolution of tannins through plant soil feedbacks can be understood as a case of niche construction, i.e. organisms' ability to modify their environment for their own benefit, or for the benefit of related organisms which will occupy the improved environment after their death [26, 30, 41]. Our model based on empirical processes simulated a mechanism in which tannins initiate an eco-evolutionary loop between organisms and their environments. The death of a tannin producing individual leaves a N-rich patch available for recruitment from neighbors that are likely to be of his kin. Individuals could inherit the environment transformed by their ancestors, a property termed *ecological inheritance* [41]. As illustrated in Fig 6, this effect was substantial and positive in our model: when ecological inheritance is turned off (after the death of a tannin producing plant, the recalcitrant nutrient pool is set to zero), the invasion of tannin producing mutants becomes less likely (Fig 6, right). This is analogous to high organismic dispersion in models of altruism evolution, in such situations genetic inheritance is diffused in the whole landscape and altruism cannot evolve [29, 57]. Most evolutionary models consider the evolution of phenotypes whose fitness can be fully understood at the organismic level. In the case of tannin evolution, the fitness of this phenotype can be understood at the organismic level in the presence of herbivores, but not in the presence of the plant-soil feedbacks. The feedback involves plants, nutrient compartments, and mycorrhizae within the soil. Furthermore competition occurs between ecosystems having contrasted material cycles [35, 36]. A whole ecosystem therefore persists through time via genetic and ecological inheritance. Within the framework of multi-level selection [43], we therefore propose to interpret tannin

evolution as the emergence of a new unit of selection at the ecosystem-level [16, 54].

Nutrient-poor ecosystems favor tannin evolution

Because they slow down mineralization, one might expect that tannin should not evolve in unfertile ecosystems [4]. This prediction is not verified empirically, both at the inter and intraspecific level: tannin producing species are mostly found in unfertile environments [13, 38], and plant populations of a single species contain more tannin in nutrient poor environments [19, 23, 24, 40]. Our model resolves this apparent paradox (Fig. 3, middle panel). Tannins can be useful to plants growing in unfertile ecosystems because they allow the formation of recalcitrant nutrient pools less prone to leaching, which can counter-balance the negative effect of a slower mineralization [51]. In the model of Barot et al. [4], the nutrients present in dead organic matter could not be reabsorbed by plants directly, and had to be first decomposed into mineral nutrients, leading to the conclusion that plants must evolve fast mineralization strategies in unfertile ecosystems. In our model plants can have direct access to the recalcitrant pool, provided that they are associated with specific mycorrhizae (cf. next paragraph) and could thus benefit plants in unfertile ecosystems. We found that fertile ecosystems should in fact *prevent* tannin evolution. First, because plant-soil feedbacks initiated by tannins becomes inefficient when labile nutrients are easily available. Second, although protection against herbivores does not require plant-soil feedbacks, fertile ecosystems favor fast growing species which are generally less protected against herbivores [13]. For plant-soil feedbacks to trigger the evolution of tannins, we found that an intermediate turnover rate is required (Figs 3-4). If turnover is too slow plant biomass increases, photosynthesis becomes limited by intraspecific competition and the carbon stock is to low for plants to invest in tannins. By contrast, if turnover is too large then labile nutrients abound and the recalcitrant pool formed by tannins becomes useless. In comparison to other models of nutrient cycling and litter decomposition [4, 10], our model may appear excessively detailed and specific. However, the additional an specific mechanisms at play in our model led to a correct prediction, i.e. tannins should evolve more easily in unfertile ecosystems. This illustrates the trade-off between simplicity, specificity and realism in model building, and how this can affects predictive accuracy.

The importance of symbiosis with mycorrhizae

Our model predicts that tannin-mycorrhizae coevolution can lead to a coevolutionary equilibrium in which plants produce tannins and become associated with mycorrhizal fungi (Fig 5). If plants need to invest in a symbiotic capacity with mycorrhizae when recalcitrant nutrient are absent, this coevolutionary equilibrium can be reached without any defensive role of tannins against herbivory (Fig 5, leftmost panel). But if plants alone have an easy access to labile nutrients, a defensive role of tannins against herbivory is necessary to trigger a coevolutionary positive feedback (Fig 5 rightmost panels).

The ability of mycorrhizae to access nitrogen from tannin-protein complexes is thus a central, and possibly controversial, assumption in our work. Within functional groups of mycorrhizae, the mycorrhizal strategy may have evolved several times from free ancestors, as it is the case for ectomycorrhizae [45]. Consequently, the different groups of mycorrhizae are not phylogenetically related and have distinct enzymatic capacity [46]. Their decomposer capacities are thus expected to depend on their type – ecto-, ericoid- or endomycorrhizae (for short: ECM, ERM, AMF) and of the clade within a given type.

That mycorrhizae can access recalcitrant complexes is still in debate for ECM [34, 45], the dominant mycorrhizal type in temperate and boreal forests. The loss of genes associated with saprotrophic ability during the transition from a free to a mycorrhizal strategy, as well as certain experimental evidence [5], suggest a low ability for complex organic matter decomposition. Simultaneously, an increasing body of litterature suggest the opposite, arguing that ECM selectively mine complex organic nitrogen [3, 53, 56]. Madritch and Lindroth [37] specifically demonstrated an higher N acquisition from high-tannin litter but without exploring the underlying mechanisms, in particular the potential implication of ECM fungi. Again, part of the controversy may arise from the fact that distinct ECM species might have distinct enzymatic abilities.

On the other hand, Wurzburger and Hendrick [62], using 15 N-enriched protein-tannin complexes from leaf litter extracts, convincingly demonstrated the ability to acquire directly nitrogen from tannin-protein complexes for ERM, which often abound in heathland and peatlands, and are often very rich in tannins. AMF, which dominate in grasslands and tropical forests, are usually poor decomposers, and may therefore not be able to acquire nitrogen from tannin-protein complexes. However, as pointed by Hättenschwiler et al. [17], this ability has so far not been tested for tropical AM fungi.

In short, if our results should be relevant for ERM dominated ecosystems (e.g. heathland and peatlands), more studies are needed to clarify the decomposer ability of ECM and tropical AM fungi, and thus establish the precise level of generality of our results.

Incidentally, our study sheds light on the mycorrhizal-associated nutrient economy framework proposed by Phillips et al. [46]. This framework posits that the contrasting modes of nutrient acquisition of different mycorrhizal fungi strongly contributes to explain contrasting C and N cycling patterns

observed in ecosystems dominated by ECM, ERM or AM plants. By modeling together the formation of recalcitrant N through tannin production and the ability of mycorrhizae to access it, our study refines this framework and places the patterns observed by Phillips et al. [46] in a broad evolutionary perspective.

Conclusion

Our model shows that the protective role of tannins against herbivores reinforces tannin evolution, but is not a necessary condition. Plant-soil feedbacks can be strong enough to trigger alone their evolution, provided that the pool of recalcitrant nutrients complexed by tannins is, at least in part, reabsorbed by the mycorrhizae of the same plant, or by its neighboring relatives. Niche construction is here a central aspect of tannin evolution through plant-soil feedbacks.

Ecological conditions modulate this niche construction process. Tannin evolution requires plants to have intermediate biomass turnover rates an inhabit relatively infertile ecosystems, thus highlighting the fact that niche construction is more effective in harsh environments.

Such ecological conditions are generally fulfilled in ecosystems harboring tannin producing plants [13, 38]. Our model suggest that plant-soil feedbacks have played a decisive role in the evolution of tannin production. More generally our work provides a detailed example of how plant traits, via their impact on a plant's environment, can be selected for as part of a niche construction mechanism and induce, in the process, the transformation of a whole local ecosystem.

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