

A multi-mutualist simulation: Applying biological market models to diverse mycorrhizal communities

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ABSTRACT

We present a cellular automaton that simulates the interaction between a host tree and multiple potential mycorrhizal symbionts and generates testable hypotheses of how processes at the scale of individual root tips may explain mycorrhizal community composition. Existing theoretical biological market models imply that a single host is able to interact with and select from multiple symbionts to organize an optimal symbiont community. When evaluating the tree–symbiont interaction, two scales must be considered simultaneously: the scale of the entire host plant at which carbon utilization and nutrient demands operate, and the scale of the individual root tip, at which colonization and carbon–nutrient trade occurs. Three strategies that may be employed by the host tree for optimizing carbon use and nutrient acquisition through mycorrhizal symbiont communities are simulated: (1) *carbon pool adjustment*, in which the plant controls only the total amount of carbon to be distributed uniformly throughout the root system, (2) *symbiont selection*, wherein the plant opts either for or against the interaction at each fine root tip, and (3) *selective carbon allocation*, wherein the plant adjusts the amount of carbon allocated to each root tip based on the cost of nutrients. Strategies were tested over various nutrient availabilities (the amount of inorganically and organically bound nutrients). Success was defined on the basis of minimizing carbon expended for nutrient acquisition because this would allow more carbon to be utilized for growth and reproduction. In all cases, the symbiont selection and selective carbon allocation strategies were able to meet the nutritional requirements of the plant, but did not necessarily optimize carbon use. The carbon pool adjustment strategy is the only strategy that does not operate at the individual root tip scale, and the strategy was not successful when inorganic nutrients were scarce since there is no mechanism to exclude suboptimal symbionts. The combination of the symbiont selection strategy and the carbon pool adjustment resulted in optimal carbon use and nutrient acquisition under all environmental conditions but result in monospecific symbiont assemblages. On the other hand, the selective carbon allocation strategy is the only strategy that maintained successful, multi-symbiont communities. The simulations presented here thus imply clear hypotheses about the effect of nutrient availability on symbiont selection and mycorrhizal community richness and composition.

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1. Introduction

Interspecific mutualisms are often conceptually viewed as the sum of costs and benefits to the involved organisms over the duration of the symbiosis (e.g., Roughgarden, 1975; Koide and Elliot, 1989; Bronstein, 1994, 2001). This perspective has led to the application of economic theory towards describing and understanding the evolutionary stability of mutualisms in nature (Axelrod and Hamilton, 1981; Noë and Hammerstein, 1994; Schwartz and Hoeksema, 1998). More particularly, some theoretical approaches to understanding mutualist associations have relied on economic

relationships between potential partners in which each member of the mutualism specializes in the acquisition of a particular commodity (Noë and Hammerstein, 1994; Schwartz and Hoeksema, 1998; Hoeksema and Schwartz, 2003; Kummel and Salant, 2006). In these biological market models, when mutualistic relationships are stable and maintained it is because both partners experience a net gain in resources required for growth. Such a “division of labor” perspective has also provided insight into cooperation and competition among semi-autonomous ramets of clonal plants (Stuefer et al., 1996; Roiloa et al., 2007; Tannenbaum, 2007).

Biological market models postulate how two heterospecific individuals benefit from a mutualistic relationship (e.g., Schwartz and Hoeksema, 1998). The host is generally assumed to select for or against the symbiont depending on whether the association is perceived as beneficial or detrimental. In cases with multiple potential

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partners, the association between the two partners that yields the highest mutual fitness should be the most desirable according to the market models.

The relationship between ectomycorrhizal fungi and their woody plant associates is an ideal context in which to apply biological market models (to simplify, the term host will refer to the plant and the term symbiont to the fungus, as in Wilkinson and Sherrat, 2001). Mycorrhizal mutualisms are prevalent in all terrestrial biomes, with ectomycorrhizal fungi especially common in temperate and boreal forests (Smith and Read, 1997). Moreover, in temperate and boreal forests, the ectomycorrhizal fungal community is strikingly diverse (Trappe, 1977; Molina et al., 1992; Bruns, 1995; Gardes and Bruns, 1996; DeBellis et al., 2006). In mycorrhizal symbioses, the traded commodities are sugar from the host plant and resources bound in the soil matrix, especially nitrogen and phosphorus, from the fungal symbiont. It is advantageous for the plant host to allocate as little carbon to the fungus as possible, while still acquiring sufficient nutrients to maintain plant functions and support new growth and reproduction; this allows the host to allocate more carbon to growth and reproduction, thereby maximizing fitness. The fungus must provide sufficient nutrients to the plant in order to maintain its association with the plant while obtaining the most carbon possible in order to maximize its own fitness.

A simulation model is the appropriate step from theoretical models towards empirical studies, especially for developing testable hypotheses based on trade relationships between a host and multiple potential symbionts (as suggested in Johnson et al., 2006). A cellular automaton is particularly appropriate for biological market models. Each cell in the simulation may be viewed as an individual root tip in the root system of a single plant available for colonization by mycorrhizal fungi. Occupation probability is determined at the level of the cell (i.e., root tip), but the overall strategy behind the decisions is based on whole-plant abundances of carbon and nutrients.

The approach used here can make testable predictions about the structure of a symbiont assemblage associated with a given host. Since many ectomycorrhizal fungi are obligate mutualists, rather than facultative, association with any available host is preferable to no association. Likewise, many plants are unable to absorb organically bound nutrients and are thus obligate mutualists with so called protein-fungi (Abuzinadah and Read, 1986; Read and Perez-Moreno, 2003) under certain environmental conditions. However, given multiple potential fungal symbionts, the mutualistic interaction between an individual host plant and any single symbiont species is facultative rather than obligate since the host may interact preferentially with another fungal species given differing environmental conditions and symbiont availability. Environmental conditions, especially those related to the available forms of nutrients, are thus likely to determine the demand for and cost of maintaining associations with mutualistic fungi. This is central to the simulations presented here.

Different functional types are likely to have different interactions with hosts. For example, during forest establishment a particular functional type may be a mutualist, and as resource availability changes, the same functional type may become a cheater (receiving sugars from the host but offering few or no nutrients in payment). Host plants would perceive a symbiont as a cheater if the price of the nutrients at the symbiont's location is higher than the average price paid at the whole-plant level. If host plants are able to selectively associate with more beneficial fungi, the economic relationship determined by the physiological attributes of fungal functional types and nutrient availability would shape the mycorrhizal fungal community.

For the purposes of the simulations reported herein, the key axes by which fungal functional types differ are: (1) the ability to access

nutrients in inorganic molecules or bound in organic compounds and (2) the amount of carbon the fungus requires (from the plant) for a given amount of nutrients. We assume a strict positive correlation between these functional traits; therefore, the greater ability the fungus has to obtain nutrients from organic compounds, the more costly that fungus is to maintain for the plant (based on Gibson and Deacon, 1990).

Three major plant strategies for allocating carbon to roots are tested using the simulation: carbon pool adjustment, symbiont selection, and selective carbon allocation. In the carbon pool adjustment strategy, carbon is equally allocated to all roots irrespective of the colonizing fungi, and adjustments in the amount of carbon allocated to the root system are made at the whole-plant level. The fate of the fungal symbiont in each cell is based on the probability of the fungus remaining viable given the amount of carbon made available by the host in that cell. The carbon pool adjustment strategy is equivalent to a null hypothesis as the plant is unable to distinguish different fungal symbionts, but can merely adjust carbon allocation to the whole root system (i.e., potentially available to symbionts) or to growth. A host solely utilizing the carbon pool strategy has no defense against cheating symbionts, thus we predict that this strategy will be inefficient when nutrients are costly (i.e., predominantly available in organic forms).

The symbiont selection strategy is equivalent to partner choice (or control) by the host plant (Kiers and van der Heijden, 2006; Johnstone and Bshary, 2008), a concept well documented in legume-rhizobia symbioses (Simms and Taylor, 2002; Sachs et al., 2004; Simms et al., 2006). In the model presented here, carbon allocation to individual root tips is recipient determined: the fungus involved in the mutualism determines the amount of carbon allocated to each cell; however, the host plant determines the probability of the fungus remaining in the cell. If the fungus is beneficial (from the host's perspective), it will remain in the cell; if it is not beneficial, it will be expelled. Mechanisms by which the host plants may select against fungal symbionts after colonization include selective turnover of fine roots (Bruns, 1995; Hoeksema and Kummel, 2003) or withholding carbohydrates available to fungal symbionts by ceasing invertase activity (Nehls et al., 2007; Nehls, 2008).

In the symbiont selection strategy the host chooses the most appropriate symbiont for the given environmental conditions, but the carbon allocated to each symbiont is recipient determined. Thus, the symbiont community, rather than the host tree, determines the amount of carbon allocated to maintain symbiotic associations and this occurs at the scale of the individual fine roots. We predict that hosts utilizing the symbiont selection strategy will have single fungal functional type communities (of the most appropriate available symbiont), but not optimize the carbon allocated to growth, especially when nutrients are costly—the available carbon will be exhausted in maintaining the symbiont community.

The selective carbon allocation strategy is related to partner choice, but includes rewards for beneficial symbionts and sanctions against perceived-cheating symbionts rather than merely maintaining or expelling symbionts. Utilizing sanctions against cheating symbionts is a proposed mechanism for long-term stability of mutualisms (Denison, 2000; West et al., 2002, 2007), and has been shown experimentally in the legume-rhizobia mutualism (Kiers et al., 2006). Furthermore, sanctions provide a means for ensuring fair trade for resources (Schwartz and Hoeksema, 1998; Denison, 2000) and efficiently utilizing diverse symbiont communities (Hoeksema and Kummel, 2003; Kummel and Salant, 2006). For these simulations, the amount of carbon allocated to an individual fungus is initially recipient determined, but is then modified by the donor based on the cost and benefit of the association. Since the host plant can control the extent to which fungal symbionts are utilized, under this strategy we expect diverse symbiotic communities composed

Table 1

A key to notations used to define parameters and functions in the cellular automaton. Symbols for fungal functional types are defined in Table 2.

Notation	Description
C_{TOTAL}	The total amount of carbon the tree is able to allocate to the root system
C_G	The portion of C_{TOTAL} that is allocated to plant growth
C_F	The portion of C_{TOTAL} that is allocated to fungal symbionts
C_{MIS}	The portion of C_{TOTAL} that is mismanaged, either the portion C_G for which there is insufficient nutrients, or allocated to C_F but not used optimally to acquire nutrients
C_{REMAIN}	The amount of C left for colonizing fungi (symbiont selection and selective carbon allocation strategies)
N_{ACQ}	The total amount of nutrients acquired by the host in one time cycle
N_{MIN}	The minimum amount of nutrients required to sustain the host
N_{REQ}	The amount of nutrients required to sustain the host and new growth
N_{EXCESS}	$N_{ACQ} - N_{REQ}$ when $N_{ACQ} > N_{REQ}$
PRICE	The average price paid for nutrients by the host
p_{cell}	The price paid for nutrients within a single cell
$prob_f$	The probability of the fungus remaining in the cell for the next cycle
c_f	The amount of carbon allocated to a cell
n_{total}	The maximum amount of nutrients a fungus can acquire in the cell it occupies
$n_{transfer}$	The amount of nutrients the fungus transfers to the plant in the cell
in_{cell}	The amount of inorganic nutrients in a cell
on_{cell}	The amount of organically bound nutrients in a cell
in_{uptake}	The amount of inorganic nutrients taken up by the fungus
on_{uptake}	The amount of organic nutrients taken up by the fungus
N_g	The amount of nutrients require to support one unit of C_G

of multiple functional types appropriate for the environmental conditions.

In addition to testing the three major strategies individually, we combined the carbon pool adjustment and symbiont selection strategies for another series of tests. The symbiont selection strategy addresses the vulnerability to cheaters of the carbon pool adjustment strategy, and the carbon pool adjustment strategy accounts for the lack of host control of carbon utilization in the symbiont selection strategy. We expect hosts utilizing the combined strategies to form single functional type symbiont communities (as per the symbiont selection), but able to control the number of associations (since the host control the total amount of carbon used to maintain symbiotic associations), thus optimizing the amount of carbon allocated to growth.

2. Methods

In the model, a plant in full sun produces a pool of carbon beyond its requirements for maintenance. This excess pool is hereafter referred to as C_{TOTAL} (for reference, Table 1 lists explanations for model parameter abbreviations). There are two fates for carbon in C_{TOTAL} : (1) the carbon is allocated to new growth (C_G); or (2) the carbon is used in the trade for nutrients via the fungal symbiosis (C_F). A portion of the C_{TOTAL} carbon pool may be mismanaged (C_{MIS}) through allocation to fungal symbionts that do not provide adequate nutrients, allocated to growth when there are insufficient nutrients for growth, or acquiring nutrients in excess of the required amount (therefore not optimizing C_G). The plant maximizes fitness by allocating as much carbon to C_G as possible, and obtaining a sufficient amount of nutrients, all while minimizing C_{MIS} . The relationship between the amount of nutrients acquired (N_{ACQ}) and the amount of nutrients required (N_{REQ}) determine if the plant is acquiring sufficient nutrients ($N_{ACQ} = N_{REQ}$), excess nutrients ($N_{ACQ} > N_{REQ}$), or has nutrient deficiency ($N_{ACQ} < N_{REQ}$). N_{REQ} is calculated as the minimum amount of nutrients to sustain the tree based on its size (N_{MIN}) plus an N value proportional to the amount of carbon allocated to growth calculated as $N_g \times C_G$

(described below underneath tree parameters), analogous to the consumption vector of Schwartz and Hoeksema (1998). In general, if there is a nutrient deficiency, the plant must allocate more carbon to C_F at the expense of C_G . If there are excess acquired nutrients (i.e., exceeds the requirement of nutrients to maintain the tree and support the new growth), the plant may allocate more carbon to C_G and less to C_F (Fig. 1). Importantly, in this model the tree is not able to store either carbon produced or nutrients acquired in a previous step to be utilized in a later step.

2.1. Fungal functional type definitions

Simulations utilize a range of fungal functional types, which span the range of likely traits, with no other attempt to mimic any particular fungal species. The fungal types are defined based on their ability to acquire and transfer inorganic and organic nutrients, the minimum amount of carbon required, the cost of transferring a unit of nutrients to the plant, and the probability of remaining in the cell given an amount of carbon. There are six defined mutualist fungal types, numbered from 1 to 6 (Table 2). These mutualist fungi range from those that are unable to acquire nutrients bound in organic substrates to fungi that can acquire almost all of the organically bound nutrients. The more organically bound

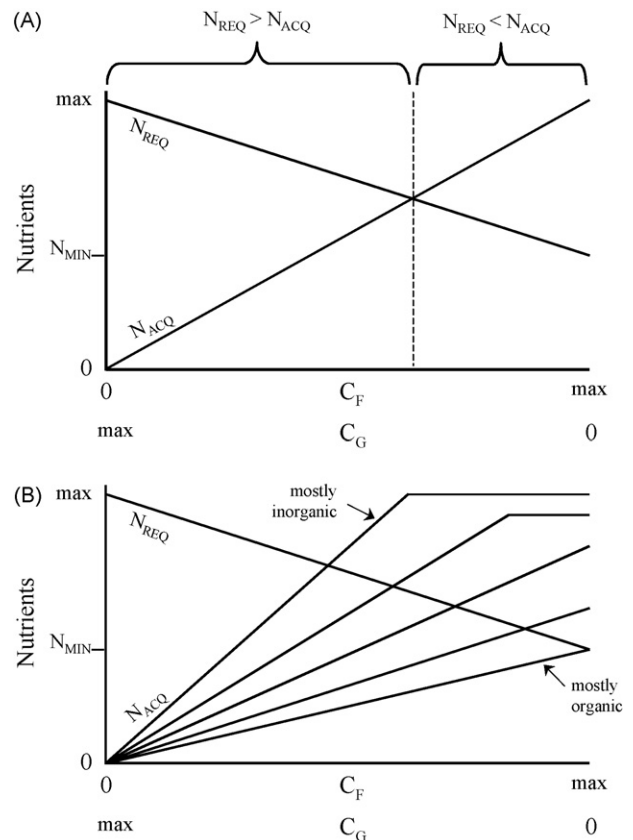


Fig. 1. (A) Conceptual representation of N_{ACQ} and N_{REQ} values based on the partitioning of the C_{TOTAL} pool into the C_F and C_G subpools. The intersection of the N_{ACQ} and N_{REQ} lines represents the equilibrium condition where the host optimally manages C_F and C_G pools and $C_{MIS} = 0$. When $N_{REQ} < N_{ACQ}$, excess nutrients are acquired; conversely, when $N_{REQ} > N_{ACQ}$, too much carbon is allocated to C_G . In both cases, $C_{MIS} > 0$. (B) The effects of inorganic nutrient availability on the N_{ACQ} slope. The N_{ACQ} slope is inversely related to the average price per unit nutrient, and the different lines represent environments ranging from those with mostly inorganic nutrients to those with mostly organic nutrients. Hosts in environments with lower inorganic nutrient availability must allocate more carbon to C_F in order to acquire sufficient nutrient quantities. The plateaus are due to physiological constraints on the amount of nutrients the fungus is capable of transferring to the host over a period of time. Refer to Table 1 for the definitions of parameters.

Table 2

Fungal functional types defined based on characteristic parameters: C_{\min} is the minimum amount of carbon on which the fungus can survive; C_{cost} is the amount of carbon the fungus requires to transfer one unit of nutrients; IN is the proportion of inorganic nutrients the fungus can access; IN_{\max} is the maximum amount of inorganic nutrients the fungus can transfer to the host in one step; ON is the proportion of organic nutrients the fungus can access; ON_{\max} is the maximum amount of organic nutrients the fungus can transfer to the host in one step; and N_{\max} is the maximum amount of nutrients the fungus can transfer to the host in one step.

Functional type	C_{\min}	C_{cost}	IN	IN_{\max}	ON	ON_{\max}	N_{\max}
1	0.25	1.00	1.0	2.0	0.00	0.00	2.00
2	0.40	1.15	1.0	2.0	0.15	0.25	2.25
3	0.55	1.30	1.0	2.0	0.30	0.50	2.50
4	0.70	1.45	1.0	2.0	0.45	0.75	2.75
5	0.85	1.60	1.0	2.0	0.60	1.00	3.00
6	1.00	1.75	1.0	2.0	0.75	1.25	3.25

nutrients the functional type is able to acquire, the more carbon it requires to function. The proportion of inorganic nutrients that can be acquired is the same for all fungal types ($IN = 1.0$). Likewise, the total amount of inorganic nutrients that can be transferred from the fungus to the host in one time step is also identical for all fungal types ($IN_{\max} = 2.0$).

The probability of a fungus remaining in a cell (prob_f) is based on the following equation:

$$\text{prob}_f = \frac{c_f - C_{\min}}{N_{\max} \times C_{\text{cost}}} \quad (1)$$

in which c_f is the amount of carbon allocated to each cell, C_{\min} is the minimum amount of carbon on which the fungus can survive, N_{\max} is the maximum amount of nutrients the fungus can transfer to the tree in one time step, and C_{cost} is the amount of carbon required by the fungus to transfer one unit of nutrients. The greater c_f is relative to C_{\min} , the higher the probability of the fungus remaining in the cell. The denominator calculation scales the carbon provided relative to the maximum capability of the fungus to transfer nutrients to the tree. It is possible that $c_f < C_{\min}$, and that $(c_f - C_{\min}) > (N_{\max} \times C_{\text{cost}})$; however, since probability is defined $0 \leq \text{prob}_f \leq 1$, if the calculated prob_f is less than zero, it is treated as 0, and if it is greater than 1, it is treated as 1. The range is truncated because these simulations consider each fungus within each cell as a unique individual, unable to increase in size—future simulations may allow functional types to colonize adjacent cells when c_f is high ($\text{prob}_f > 1$), or for individuals occupying multiple cells to contract in size when c_f is low ($\text{prob}_f < 0$).

2.2. Cellular automaton

The simulations were performed using a two-dimensional cellular automaton format on a 100×100 grid of cells. Each cell contains spores of all fungal functional types, thus dispersal limitation is not considered in these simulations. There are four major occurrences in each cell during each discrete time step: (1) colonization; (2) the trade of nutrients for carbon; (3) the calculation of the trade value—the price of nutrients for each cell; and (4) modification of carbon allocation and/or fungal probability alteration. For the simulations, colonization occurs solely via spore germination; therefore, hyphal growth into neighboring cells to compete for colonization is not considered. Nutrients taken up by the fungus are then transferred to the tree in exchange for the carbon sugars produced by the tree. The amount of nutrients the fungi offer depends on the functional type of the fungus, the amount of available nutrients within the cell, and the amount of carbon supplied to the fungus by the tree (Fig. 1B). The fungus in each cell attempts to deliver nutrients appropriate to the amount of carbon it receives; however, the environmental conditions may prevent fair trade. For example, different fungal types have different capabilities for taking up nutri-

ents bound in organic compounds (Table 2). Thus, if functional type 1 occupies a cell with a vast quantity of organically bound nutrients and no inorganic nutrients, it will be unable to deliver any nutrients to the plant regardless of the amount of carbon that is supplied.

2.3. Colonization

Cell order is randomized for colonization such that the identity and location of the cell has no bearing on the sequence in which the simulation evaluates the cell. This randomization is critical for colonization in the symbiont selection and selective carbon allocation strategies, in which the fungal symbiont determines the initial c_f , as explained below. Likewise, the order for the fungi is randomized for each colonization attempt. For the initial colonization step in the carbon pool adjustment strategy, colonization is attempted in all cells, with successful colonization based on the output of a random number generator and the probability of a spore germinating (equal for all functional types). For each cell, the simulation cycles through a random order of fungal functional types and moves on to test the next cell if there is either a successful colonization event (the cell is occupied) or if all fungal functional types are unsuccessful in germinating (the cell remains vacant).

Initial colonization in the symbiont selection and selective carbon allocation strategies differs from that in the carbon pool adjustment strategy. Since the fungal functional type determines c_f , and there is a finite amount of available carbon (C_{TOTAL}), there is a possibility that a fungal community will draw more carbon than is available to the roots. Since the cellular automaton simulation cycles through the cells one at a time, the cells assessed towards the end of the cycle would have a higher probability of vacancy than those earlier in the cycle. Thus randomization of cell order is critical in the colonization cycles. For the initial colonization cycle in the symbiont selection and selective carbon allocation strategies, the c_f for the cell is subtracted from the remaining available pool (C_{REMAIN}) until the available pool is exhausted. For the first colonization cycle, the initial C_{REMAIN} is equal to C_{TOTAL} .

All colonization after the first cycle in all three strategies occurs only on vacant cells. Cells are vacant if an earlier colonization attempt fails and the cell is thus vacant in the previous cycle, or if the fungus fails to remain in the cell based on prob_f (through either the action of the host or the fungus, based on the operating strategy). The order in which colonization attempts occur in vacant cells is randomized as in the initial colonization cycle. In the carbon pool adjustment strategy, colonization attempts occur in all vacant cells. In the symbiont selection and selective carbon allocation strategies, colonization attempts occur in vacant cells until C_{REMAIN} is exhausted.

2.4. Calculation of trade coefficients

After cells are colonized by fungi, the simulation calculates for each cell the amount of nutrients the fungus in that cell can access, and then the amount of nutrients it can transfer based on c_f . The amount of nutrients transferred is calculated using the following algorithm:

$$on_{\text{cell}} \times ON = on_{\text{uptake}} \quad (2)$$

$$\text{If } on_{\text{uptake}} > ON_{\max}, \quad \text{then } : on_{\text{uptake}} = ON_{\max} \quad (3)$$

$$in_{\text{cell}} \times IN = in_{\text{uptake}} \quad (4)$$

$$\text{If } in_{\text{uptake}} > IN_{\max}, \quad \text{then } : in_{\text{uptake}} = IN_{\max} \quad (5)$$

$$on_{\text{uptake}} + in_{\text{uptake}} = n_{\text{total}} \quad (6)$$

$$\frac{c_f}{C_{\text{cost}}} = n_{\text{transfer}} \quad (7)$$

Table 3
Strategy-specific responses to nutrient surpluses or deficiencies.

$N_{ACQ} - N_{REQ}$	C_{MIS}	Condition	Carbon pool adjustment	Symbiont selection	Selective carbon allocation
+	+	Nutrient excess, host has not maximized C_G allocation	Allocate some C_F to C_G (Eqs. (9)–(11))	Selects for favorable symbionts and against “cheating” symbionts under all conditions except equilibrium	Incrementally increases C to favorable symbionts and decreases C to “cheating” symbionts
–	+	Nutrient deficiency, not enough nutrients to support a portion of C_G pool	Allocate some C_G to C_F (Eqs. (12)–(19))		
–	0	Nutrient deficiency when $C_F = C_{TOTAL}$	PRICE too high for host to acquire sufficient nutrients, but host unable to evict “cheating” symbionts		
0	0	Equilibrium	Pool sizes remain unchanged	Stable symbiont community since host determines $prob_f$	Incrementally increasing and decreasing carbon allocated to each symbiont causes turnover of symbiont community since $prob_f < 1$ for higher priced functional types

$$\text{If : } n_{\text{transfer}} > n_{\text{total}}, \text{ then : } n_{\text{transfer}} = n_{\text{total}} \quad (8)$$

In which on_{cell} and in_{cell} are the available amounts of organic nutrients and inorganic nutrients in each cell, respectively. If $n_{\text{transfer}} > n_{\text{total}}$, the fungus transfers the maximum amount of inorganic nutrients (in_{uptake} as calculated in Eqs. (4) and (5)) and the remaining n_{transfer} is of the organic nutrients ($on_{\text{uptake}} = n_{\text{transfer}} - in_{\text{uptake}}$).

After n_{transfer} is calculated, the cell price (p_{cell}) is determined by c_f/n_{transfer} . Tree wide pools of nutrients acquired and total carbon transferred to the roots are calculated by summing the corresponding values of c_f and n_{transfer} from all cells. Also, average price paid for nutrients (PRICE) is calculated as the average of all cell prices.

2.5. Modification of cell carbon and probability

Methods of cell carbon/symbiont modification depend on which strategy is being simulated. There are several general attributes calculated tree-wide for each time step that apply to all three strategies. First is the calculation of carbon partitioning of the C_{TOTAL} pool into C_F , C_G and C_{MIS} sub-pools. Tree-wide C_F is calculated by summing c_f of all cells in the grid. Tree-wide C_G is generally a pre-determined amount calculated by the simulation to maximize C_G , and is detailed in the carbon pool adjustment strategy. There are two conditions that create the C_{MIS} pool: (1) when nutrients are acquired in excess to the nutrient requirement of the plant, and (2) when nutrient acquisition is insufficient to support the growth of the plant. Calculation of C_{MIS} from the first condition is through multiplying the amount of excess acquired nutrients ($N_{EXCESS} = N_{ACQ} - N_{REQ}$) by the average price the tree paid for nutrients. In the second condition, the excess amount of carbon allocated to C_G is transferred to the C_{MIS} pool (Eq. (15)).

Second, the calculation of the tree-wide nutrient pools is common to all strategies. Tree-wide N_{ACQ} is calculated as the sum of all n_{transfer} values in the grid. N_{REQ} is calculated by adding the N_{MIN} (minimum amount of nutrients needed to sustain the tree without growth and reproduction) to ($C_G \times N_g$), which is the amount of nutrients required to satisfy the carbon allocated to growth. Based on the relationship of N_{ACQ} to N_{REQ} , the tree may have a nutrient deficiency, have a nutrient surplus, or acquire a sufficient amount of nutrients. Furthermore, each strategy for modifying carbon pools and fungal probabilities is based on the relationship of N_{ACQ} to N_{REQ} .

2.6. Carbon pool adjustment

The carbon pool adjustment strategy is the simplest strategy as all cells receive the same amount of carbon from the tree regardless of the fungal functional type or even the presence of a fungus. For the first step, the entire C_{TOTAL} pool is distributed to all cells—each cell receiving $C_{TOTAL}/10,000$ units of carbon (there are 10,000 cells in the simulation). The carbon distribution is adjusted after each time step in order to maximize C_G while maintaining sufficient nutrient uptake. The strategy adjusts the C allocation based on nutrient uptake (see Table 3 for basic overview). If the amount of nutrients acquired is exactly sufficient, such that $N_{ACQ} = N_{REQ}$, the pool sizes are not adjusted.

If there is a nutrient surplus (which often occurs after the initial step, when all of C_{TOTAL} is allocated to C_F), the C_{MIS} pool as calculated above for nutrient excess, is partitioned into C_G and C_F as to maximize the amount of C allocated to C_G while taking into account the new nutrient requirement needed to accommodate the new size of the C_G pool based on the nutrient price from the previous step. The new tree-wide C pools are calculated as follows:

$$C_{MIS} = (N_{ACQ} - N_{REQ}) \times \text{PRICE} \quad (9)$$

$$C_{Gj} = \frac{C_{Gi} + C_{MIS}}{1 + N_g \times \text{PRICE}} \quad (10)$$

$$C_{Fj} = C_{TOTAL} - C_{Gj} \quad (11)$$

C_{Gi} is the C_G pool from the previous step; C_{Gj} is the C_G pool for the next step. Eq. (9) calculates the size of the C_{MIS} pool based on the results of the previous step. Eq. (10) is used to determine C_{Gj} (an annotated derivation of Eq. (10) can be found in Appendix A). The new tree-wide C_F pool (C_{Fj}) is then equally distributed to all cells. Thus, if nutrients are acquired in excess in one time step, less carbon will be allocated to each cell in the next step. The probability of the fungus remaining in the cell is based on the amount of carbon it receives; therefore, if less carbon is allocated to c_f in each cell, fungi with higher carbon demands (i.e., higher C_{min}) will have lower probability of remaining in the cell.

If the tree fails to acquire a sufficient level of nutrients, the tree must allocate more carbon to C_F , while still maximizing C_G . There are two conditions in which the tree may not acquire enough nutrients. In the first condition, the plant has allocated too much carbon to C_G , and thus the C_{MIS} pool consists of all of the C_G that cannot be supported by the nutrients. The second condition occurs when all of C_{TOTAL} is allocated to C_F and the tree still fails to acquire sufficient

nutrients (N_{MIN} is the nutrient requirement for the plant to exist at its current state with no growth; thus, even when $C_G = 0$, the plant still requires some nutrients, see Fig. 1); essentially, the price of the nutrients is too high. To ameliorate the first condition, the tree must convert some of the C_G pool to C_F . The C pool sizes for the next time step are adjusted using the following equations:

$$\text{PRICE}_i = \frac{C_{Fi}}{N_{\text{ACQ}i}} \quad (12)$$

$$\text{Nutrient deficit} = N_{\text{REQ}i} - N_{\text{ACQ}i} \quad (13)$$

$$N_{\text{REQ}i} = N_{\text{MIN}} + C_{Gi} \times N_g \quad (14)$$

$$C_{\text{MIS}} = C_{Gi} - \frac{N_{\text{ACQ}i} - N_{\text{MIN}}}{N_g} \quad (15)$$

$$C_{Gf} = C_{Gi} - C_{Gj} \quad (16)$$

$$C_{Fj} = C_{\text{TOTAL}} - C_{Gj} \quad (17)$$

$$C_{Fj} = N_{\text{REQ}i} \times \text{PRICE} - (C_{Gf} \times N_g) \times \text{PRICE} \quad (18)$$

$$C_{Gj} = \frac{C_{\text{TOTAL}} - \text{PRICE}(N_{\text{REQ}i} - C_{Gi} \times N_g)}{1 + \text{PRICE} \times N_g} \quad (19)$$

Variables with the i subscript represent values from the previous step, those with the j subscript represent values for the next step, and C_{Gf} is the amount of C_{Gi} transferred to C_F . Eq. (12) is used to calculate PRICE, Eq. (13) is used to calculate the nutrient deficit, Eq. (14) is used to calculate the amount of nutrients required, and Eq. (15) is used to calculate C_{MIS} when adequate nutrients are not acquired. C_{Gf} is the amount of C_{Gi} that must be allocated to C_F in the j time step in order to optimize carbon utilization (Eq. (16)). Eq. (18) is used to calculate the optimum size of the C_F pool for the next step based on the values of the previous step. The $N_{\text{REQ}i} \times \text{PRICE}$ portion of the equation is the total amount of carbon required to satisfy the nutrient needs from the previous step, and the $(C_{Gf} \times N_g) \times \text{PRICE}$ portion accounts for the reduction of N_{REQ} based on the reduced size of the C_G pool due to C_{Gf} . Equation 18 provides a crucial substitute for C_{Fj} in Eq. (17), so that C_{Gj} can be determined from values derived solely from the i time step (Eq. (19), rationale and/or derivations of Eqs. (15), (18) and (19) can be found in Appendix A). These C pool adjustments allow the tree to convert a sufficient amount of carbon to C_F while still maintaining as large a C_G pool as possible. The second condition requires the plant to adjust the probabilities of the fungi involved in the mutualism, which in the carbon pool adjustment strategy is beyond the tree's capabilities.

2.7. Symbiont selection

In the symbiont selection strategy, the fungal symbiont determines the amount of carbon allocated to each cell. For the symbiont selection simulations, $c_f = 1.5 \times C_{\text{cost}}$, the amount of carbon required to transfer 1.5 units of nutrients. The level of 1.5 units of nutrients per cell was selected because it maximizes the host carbon utilization when the host is associated with the cheapest symbiont, functional type 1, simply due to the definitions of the model parameters. Also, $\text{prob}_f = 1$ for all functional types when $c_f = 1.5 \times C_{\text{cost}}$. The plant host determines the probability of a fungus remaining in the cell based on the N_{ACQ} and N_{REQ} relationship, the p_{cell} value relative to PRICE, and the n_{transfer} for each cell relative to the tree-wide average n_{transfer} value (Table 3). The host's goal is to maximize C_G , and the tree does so by selectively adjusting the symbiont community. If nutrients are acquired at sufficient or excess levels ($N_{\text{ACQ}} \geq N_{\text{REQ}}$) the tree will select against symbionts with $p_{\text{cell}} > \text{PRICE}$, by reducing prob_f to 0; the simulation will attempt colonization in the newly vacant cell in the next step. For beneficial symbioses in this situation, prob_f is considered equal to 1, since the fungi determine c_f .

The PRICE decreases when supply exceeds demand, resulting from selection against costlier symbionts.

If nutrient levels are insufficient ($N_{\text{ACQ}} < N_{\text{REQ}}$), and if n_{transfer} for the cell is less than the average n_{transfer} value for the plot, fungal symbionts will be selected against by reducing prob_f to 0. The PRICE will increase as demand increases, and symbionts that provide inadequate amounts of nutrients are selected against.

In a fourth series of simulations, the symbiont selection and the carbon pool adjustment strategies were combined. For this combined strategy, the tree has an active role in modifying C allocation as well as probabilities of fungi remaining in cells. In these simulations, the tree calculates the optimum adjusted size of the carbon pools based on the previous step. Thus, the tree is able to pre-determine the C_F pool and maximize C_G . Next, the tree selects against the less favorable symbionts, creating vacant cells. Then, colonization occurs on vacant cells until the C_F pool is exhausted rather than utilizing the entire C_{TOTAL} pool. Often, there are vacant cells at the end of each step.

2.8. Selective carbon allocation

In the selective carbon allocation strategy, the tree alters c_f allocation to individual cells based on the performance of the fungi within the cell. The probability of fungi remaining in the cell is determined by prob_f , calculated using the c_f value of the occupied cell. The initial c_f transferred to each cell is initially determined by the fungus as in the symbiont selection strategy as the amount of c_f transferred to newly colonized cells. Adjustments to c_f for each cell are administered in increments of 0.1 C units for the simulations of the selective carbon allocation strategy. The 0.1 increment level was chosen because it allowed for the finest scale carbon allocation adjustments given computational memory limitation.

As in the carbon pool adjustment and the symbiont selection strategies, the relationship between N_{ACQ} and N_{REQ} is the major deciding factor in the selective carbon allocation strategy (Table 3). If $N_{\text{ACQ}} \geq N_{\text{REQ}}$, the tree will increase C_G by increasing c_f to lower priced symbionts and decreasing c_f to the higher priced symbionts, lowering the PRICE. Through successive steps under this condition, prob_f for the higher priced symbionts will decrease such that the fungi will be unlikely to remain in the cell. If $N_{\text{ACQ}} < N_{\text{REQ}}$, c_f will be increased to the cells that have higher than average n_{transfer} values and will be reduced in cells with lower than average n_{transfer} values. The price per unit of nutrients is likely to increase under these situations.

2.9. Environmental conditions

Simulations for all strategies were performed on stable homogeneous environments. Each cell in the simulation had the same environmental conditions in regards to the amounts of inorganically and organically bound nutrients. In all simulations, each cell had a total of 4 units of nutrients. The environmental states that were simulated in the homogenous environments are 0.5:3.5; 0.75:3.25; 1.0:3.0; 1.25:2.75; 1.5:2.5; 2:2; inorganic:organic, respectively.

3. Results

To reach stabilization, the selective carbon allocation simulations went through 6000 discrete time steps and the other simulations underwent 450 discrete time steps. The carbon pool adjustment, symbiont selection, and combined carbon pool adjustment/symbiont selection strategies all reach stable nutrient acquisition levels with stable symbiont communities (Fig. 2). Two hundred replicate simulations were performed for each strategy and environmental condition. Comparisons between strategies

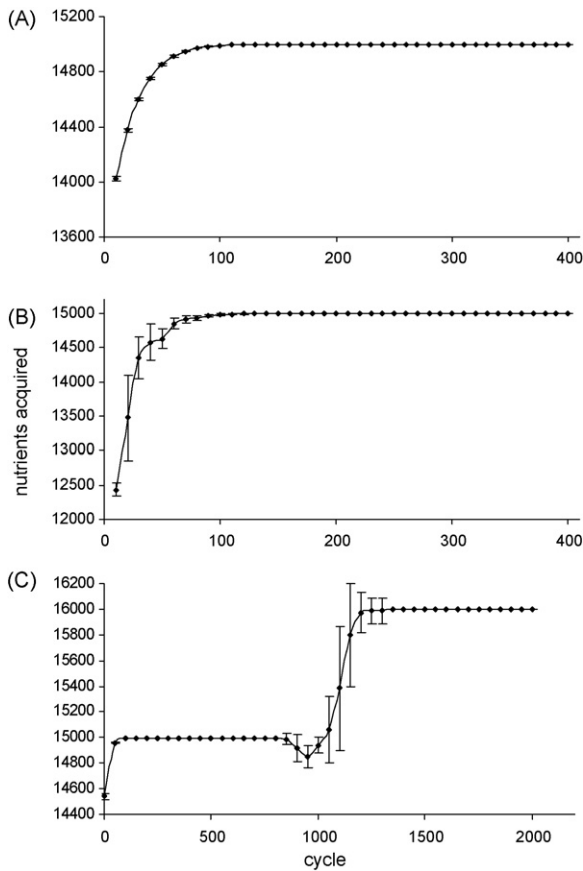


Fig. 2. Nutrient acquisition results of the strategies simulated on a homogeneous environment with 1.5 inorganic units and 2.5 organic units of nutrients in each cell. The optimum condition of 15,000 units acquired occurs after approximately 100 cycles in the carbon pool adjustment strategy (A) and symbiont selection strategy (B). A plateau emerges relatively quickly in the selective carbon allocation strategy, but the second and optimal plateau occurs after approximately 1400 steps (C). Error bars are \pm one standard deviation.

were based on the N_{ACQ} , C_G and C_{MIS} values at the stable plateau regions of the simulation curves. These values represent equilibriums achieved through iterative applications of the host strategies under stable environmental conditions.

When cells contain more than 1.5 units of inorganic nutrients per cell (the point at which the optimum nutrient acquisition can occur without the uptake of any organic nutrients), the results for each strategy do not differ from the results at the 1.5 inorganic nutrient units per cell. The results of the simulations performed in homogeneous environments are summarized in Table 4, and the strengths and weaknesses of individual strategies are summarized in Table 5.

The pool adjustment strategy is unsuccessful if inorganic nutrient availability is low (0.5 and 0.75 units per cell) and the average carbon cost per unit of nutrients is greater than 2.0. In these cases, the equilibrium quantity of nutrients acquired is below the minimum required nutrients (Fig. 3). If inorganic nutrient availability is high (≥ 1.5 units per cell), the pool adjustment strategy achieves the theoretically optimum conditions. At intermediate levels of inorganic nutrient availability (1.0 and 1.25 units per cell), the strategy is successful and is able to minimize C_{MIS} . At high inorganic nutrient availability, the symbiont community is a monospecific, functional type 1 population. Species richness is higher in simulations at low and intermediate inorganic nutrient levels (Fig. 5A). The maintenance of lower priced, yet non-optimum nutrient providing fungi limits the success of this strategy.

The symbiont selection strategy is the best strategy for acquiring nutrients (Fig. 4), but not for maximizing carbon use efficiency, as shown by relatively large quantities of carbon mismanaged (due to acquiring excess nutrients, therefore not optimizing C_G) at low and intermediate inorganic levels. When cell occupancy is below 100% and inorganic nutrient levels are less than 1.0 unit per cell the C_{TOTAL} pool is exhausted by the occupying symbionts. Thus, carbon is only allocated to growth if cells are 100% occupied by fungi and the carbon required to satisfy the symbiont community is less than C_{TOTAL} ; this is the case when inorganic nutrients are greater than 1.0 unit per cell. At equilibrium, the symbiont communities are all monospecific and made up of the optimum fungal functional type for the given environmental conditions (Fig. 5B).

Combining the symbiont selection and the pool adjustment strategies results in optimum carbon use efficiency under all conditions. The results of simulations at inorganic nutrient levels ≥ 1.5 are identical to the results for the symbiont selection strategy operating

Table 4
Plant-level simulation results at the equilibrium plateaus for all strategies in homogenous environments. The nutrient availability is indicated in the $in_{cell}:on_{cell}$ column. More successful strategies acquire a sufficient amount of nutrients ($\geq N_{MIN}$, which is 10,000 units for the simulations) with the lowest C_{MIS} values.

Strategy	$in_{cell}:on_{cell}$	N_{ACQ}	C_F	C_G	C_{MIS}	PRICE	% occupied
Pool adjustment	0.5:3.5	7,498.2	20,000	0	0	2.67	100
	0.75:3.25	9,933.61	20,000	0	0	2.01	100
	1.0:3.0	11,249.6	18,750.4	1249.6	1.4	1.67	100
	1.25:2.75	12,763	17,236.9	2763.1	0	1.35	100
	1.5:2.5	15,000	15,000	5000	0	1	100
Symbiont selection	0.5:3.5	12,498.9	20,000	0	3998.6	1.6	83.3
	0.75:3.25	13,792.9	20,000	0	5499.1	1.45	92
	1.0:3.0	15,000	19,499.9	500.1	5849.9	1.3	100
	1.25:2.75	15,000	17,248.28	2751.72	2585.3	1.15	100
	1.5:2.5	15,000	15,000	5000	0	1	100
Symbiont selection with pool adjustment	0.5:3.5	11,539.4	18,460.6	1539.4	6.2	1.6	76.9
	0.75:3.25	12,245.1	17,754.9	2245.1	0	1.45	82.4
	1.0:3.0	13,043.6	16,956.4	3043.6	0	1.3	87
	1.25:2.75	13,953.5	16,046.5	3953.5	1.3	1.15	93.03
	1.5:2.5	15,000	15,000	5000	0	1	100
Selective carbon allocation	0.5:3.5	11,617.6	20,000	0	2784.7	1.72	81.4
	0.75:3.25	13,027.5	20,000	0	4647.8	1.53	92.1
	1.0:3.0	14,997	19,498	502	5845	1.3	100
	1.25:2.75	13,686.1	17,026	2974	885.9	1.24	100
	1.5:2.5	15,000	15,997.9	4002.1	1064.3	1.07	100

Table 5
Attributes of plant strategies for allocating carbon to roots utilized in the simulations.

Strategy	Strategy description	c_f^*	Strategy strength(s)	Strategy weakness(es)
Carbon pool adjustment	Adjust tree wide carbon pools (C_F and C_G) to maximize C_G and acquire sufficient nutrients	Donor determined	Effective when inorganic nutrients are readily available	Host can not evict cheating symbionts, thus strategy is not effective when inorganic nutrient availability is low All cells receive the same amount of C regardless of symbiont functional type or if cell is vacant
Symbiont selection	Select for favorable symbionts and against "cheating" symbionts	Recipient determined	Effective under all nutrient conditions Rapid organization of symbiont community of favorable functional types and eviction of "cheaters"	Low functional type diversity High C_{MIS} in environments with low inorganic nutrient availability
Selective carbon allocation	Incrementally increase C allocated to favorable symbionts and decrease C allocated to "cheating" symbionts	Mixed recipient and donor determined	Feedback between host and symbionts maintains diverse functional type communities under several environmental conditions	Trade-off between strategy efficiency and magnitude of incremental increases/decreases PRICE higher than in Symbiont Selection strategy and $C_{MIS} > 0$ regardless of nutrient availability

* c_f is the amount of carbon allocated to each cell.

solely. Furthermore, the symbiont communities are all monospecific at equilibrium, and comprised of the same fungal functional types as in the symbiont selection strategy. However, at low and intermediate inorganic nutrient levels, the strategies operating in concert result in lower levels of cell occupancy and thus lower levels of carbon required to maintain the symbiont community. The simulations utilizing both the symbiont selection and the pool adjustment strategies are able to maximize carbon use efficiency at all nutrient levels (Fig. 4).

The selective carbon allocation strategy is also successful at all nutrient levels, and reaches its optimal levels at inorganic nutrient levels ≥ 1.5 units per cell. However, this optimal achieved level is lower than the theoretical optima achieved by the pool adjustment and symbiont selection strategies. Cell occupancy for all

environmental conditions is approximately 90%, and populations of all functional types are maintained (Fig. 5C). The maintenance of populations of higher priced functional types under this strategy increases the price paid for nutrients above the optimum levels reached in the symbiont selection strategy. Under all environmental conditions, this strategy is able to dedicate carbon to growth and reproduction; however, there are also moderate C_{MIS} pools indicating that growth and reproduction are nutrient limited. Functional type community stabilization requires up to 6000 time steps in the selective carbon allocation strategy depending on the environmental condition, thus the dynamics are much slower than the other strategies. This is due in part to the size of the incremental increases and decreases of carbon allocated to each cell. Smaller magnitudes of incremental adjustments require a greater number

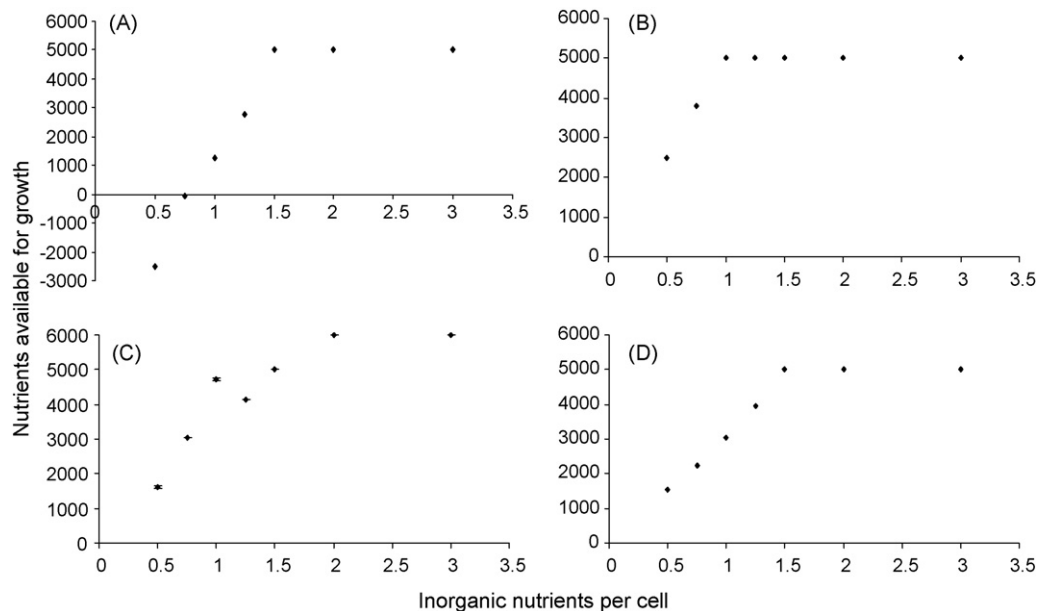


Fig. 3. Nutrients available for growth based on the environmental conditions of a homogenous plot for (A) the carbon pool adjustment strategy, (B) the symbiont selection strategy, (C) the selective carbon allocation strategy, and (D) the combined carbon pool adjustment and symbiont selection strategy. The carbon pool adjustment strategy is insufficient at low levels of available inorganic nutrients (≤ 0.75 units per cell). Note the differences in nutrient acquisition under the symbiont selection strategy (B) and combined carbon pool adjustment and symbiont selection strategy (D) when inorganic nutrient availability is < 1.5 units per cell.

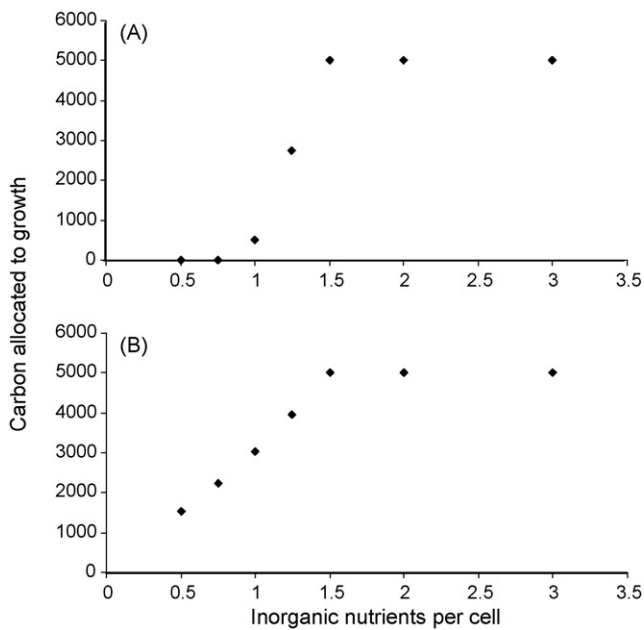


Fig. 4. Carbon allocated to growth based on environmental conditions of a homogeneous plot for (A) the symbiont selection strategy and (B) the combined carbon pool adjustment and symbiont selection strategy. Note that when inorganic nutrient availability is <1.5 , the symbiont selection strategy does not adequately allocate carbon to growth. Although the symbiont selection strategy is able to acquire larger amounts of nutrients (see Fig. 3), the combined strategy utilizes its carbon more efficiently.

of time steps to reach community stabilization. Larger magnitudes reject less favorable functional types more rapidly. However, community stability is rarely achieved since favorable species may be deemed unfavorable if they are unable to reciprocate appropriate quantities of nutrients compared to the increased amount of carbon allocated to them. The community then “resets” to the random initial condition when all functional types are equally present in the community.

4. Discussion

Functional diversity is a potential factor in maintaining highly diverse ectomycorrhizal fungal communities (Bruns, 1995; Cairney, 1999; Kernaghan, 2005; Buée et al., 2007). Experiments investigating the effect of ectomycorrhizal diversity on host productivity suggest that increased functional diversity enhances nutrient uptake in culture (Jonsson et al., 2001; Baxter and Dighton, 2001) and that the availability of nutrients influences the effect (Baxter and Dighton, 2005). Furthermore, nutrient addition has been shown to differently affect root colonization by ectomycorrhizal fungi with distinct life history strategies (Lilleskov and Bruns, 2003). Our simulations clarify the conditions under which to expect the host to maintain functionally diverse symbionts. Only the selective carbon allocation strategy is able to maintain a successful, diverse functional type community and only does so when inorganic nutrient availability is low (Fig. 5, panel C). The carbon pool adjustment strategy also results in diverse functional type communities at low inorganic nutrient availabilities (Fig. 5, panel A), but these do not provide sufficient nutrients to the host (Fig. 3, panel A). The simulations suggest that diverse communities enhance host productivity only if the appropriate functional types are present. Furthermore, the strategy utilized by the host plant greatly affects the ability to maintain associations with the appropriate fungal functional types.

The most effective mutualisms from the host’s perspective (i.e., those with the highest C_G and lowest C_{MS}) utilized strategies func-

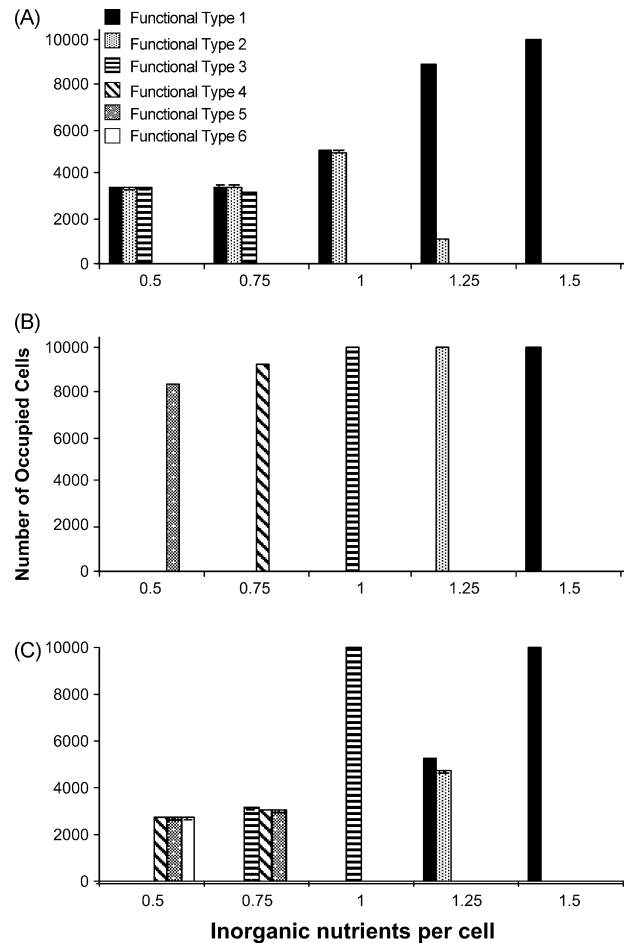


Fig. 5. Functional type community composition under various homogeneous inorganic nutrient availability levels in (A) the pool adjustment strategy, (B) the symbiont selection strategy, and (C) the selective carbon allocation strategy. Pool adjustment never contains the most costly functional types (4–6), symbiont selection results in single functional type communities, and selective carbon adjustment results in communities with favorable functional types more abundant.

tioning at both the whole tree and individual root tip scales. The more basic strategies (pool adjustment and symbiont selection) both function optimally as long as the inorganic nutrient availability is sufficient. The limitations of these strategies are exposed when inorganic nutrient availability is below optimal, and the plant must acquire some amount of organically bound nutrients to satisfy its demands. Natural habitats where this is common include heaths (dominated by ericaceous species) and boreal and temperate forests with well developed organic soil horizons (Schlesinger, 1977). The pool adjustment strategy fails to acquire sufficient nutrients at low inorganic nutrient availability due to its inability to reject lower cost symbionts that do not acquire sufficient quantities of organically bound nutrients. The symbiont selection strategy suffers high levels of C_{MS} because it does not adequately manage plant level carbon pools. This may be less of a disadvantage than the nutrient limitation likely under pool adjustment because trees can allocate more carbon to root symbionts when they grow in high-light locations (Tweig et al., 2007).

Combining the pool adjustment and symbiont selection strategies results in the most favorable, albeit monospecific, symbiont community. But this is expected, since environmental conditions are homogeneous. Given a heterogeneous environment, a tree should maintain several different symbiotic fungal types. As in the symbiont selection strategy, the fungal symbiont determines the amount of carbon it receives, and the tree selects for or against the

symbiont based on the price per unit nutrient paid at each cell. The pool adjustment simply serves to control the total C_F pool, and effectively controls the number of symbiotic associations that are maintained. Since soils are almost universally heterogeneous at fine scales (e.g., Lechowicz and Bell, 1991; Farley and Fitter, 1999), under this strategy we may expect a tree to maintain a more diverse fungal community as soil nutrient heterogeneity increases. However, the amount of soil heterogeneity that will result in a tree maintaining diverse symbionts will of course depend on the relative costs and efficiencies of the available suite of fungi. Environmental heterogeneity may be incorporated into the simulations by defining multiple zones (sets of cells) with different nutrient availabilities. In this manner, simulations would provide hypotheses addressing the (potential) maintenance of diverse symbiont communities across various levels of environmental heterogeneity.

The selective carbon allocation strategy operates at the scale of the single root tip, and like the symbiont selection strategy, the conditions at the whole-plant level influence the outcomes at each root tip. The strategy results in optimal symbiont utilization in regards to nutrient acquisition and maintains diverse symbiont communities in environments with lower mineralized nutrient content. However, since the whole plant carbon pools are not directly managed under this strategy, there is still a sizable C_{MIS} pool when mineralized nutrients are abundant. When inorganic nutrient levels are 1.0 unit per cell, and organic nutrients are 3.0 units per cell, the selective carbon allocation strategy stabilizes with a single fungal functional type (Fig. 5). This result appears out of place when compared to the multiple fungal functional types maintained under environmental conditions containing 0.75 and 1.25 units of inorganic nutrients per cell. The condition arises because the optimum N_{ACQ} occurs at 1.5 units per cell, and fungal functional type 3 is able to provide the ideal price for nutrients given the environmental conditions. The same condition occurs in the symbiont selection strategy and the combined carbon pool allocation with symbiont selection strategy under the same environmental conditions. Therefore, one prediction is that a single fungal functional type should be maintained where an available fungal species provides an ideal price at a given nutrient availability.

Unlike the symbiont selection strategy, the selective carbon allocation strategy cannot be combined with the carbon pool allocation strategy as it is currently applied. The sizes of the carbon pools are adjusted following each step, modifying the available C_F pool for the next step. The modification of the carbon allocated to each root tip is applied in a random order, and to limit the carbon availability to the entire root system via pool adjustment would potentially sanction more beneficial symbionts simply based on the order at which the cell is assessed. However, the selective carbon allocation strategy is able to acquire nutrients in excess of the host requirements under all environmental conditions (Table 4). Plants in full sun, as these simulations are intended to model, are rarely carbon limited but are commonly nutrient limited. Thus, processes that maximize nutrient uptake at the cost of carbon may only rarely reduce the fitness of plants in full sun. Actively managing carbon pools would be more important for shaded seedlings and saplings. However, shaded plants may share common mycorrhizal networks with canopy trees that may ease their carbon deficiency (Simard et al., 1997).

The mutualism strategies presented here facilitate empirical research because they can be characterized through measurable, and therefore experimentally testable, plant and fungal physiological activities. The carbon pool adjustment strategy relates to whole plant carbon allocation and determines how much of the excess carbon pool should be allocated to the root system, in particular to the fine roots, rather than stored for future use by the plant. Therefore, experiments or comparative studies tracing the fate of carbon in the plant under different soil nutrient conditions would be suitable

for testing carbon pool hypotheses. The symbiont selection strategy may operate via selective root turnover, through the rejection of the fungal hyphae at the plant-fungus interface, or by biochemical inhibition of carbohydrate transfer. Thus, symbiont selection experiments should incorporate fine root growth and turnover, multiple potential fungal partners, and a wide range of nutrient availabilities. Selective carbon allocation requires sanctions where less beneficial symbionts receive a smaller portion of the host's carbon (adapted from rhizobia models proposed by Denison, 2000; West et al., 2002; Kiers et al., 2006, see also Nehls et al., 2007). Measuring the carbon exchange between a host and multiple fungal species under the same environmental condition or a single fungus under differing environmental conditions would assess selective carbon allocation potential (as suggested by Kummel and Salant, 2006).

The experiments proposed above (and other potential empirical research) are useful in both testing assumptions of the simulation model and for modifying model strategies and parameters. The mechanisms that underlie the strategies must be identified; moreover, the capabilities of plants and/or fungi to manage carbon flow in symbiosis, as well as the ability to distinguish carbon flow as donor or recipient determined, must be addressed. Host sanctions proportionate to symbiont benefit have been shown in legume-rhizobia symbioses (Kiers et al., 2006), and host control of carbohydrate transfer in ectomycorrhizal symbioses via biochemical pathways has also been demonstrated (Nehls et al., 2007; Nehls, 2008). Differences in mycelial growth rate, fungal biomass and respiration rate may be responsible for differences in cost (sink strength) associated with different fungal symbionts (Rygielwicz and Andersen, 1994; Bidartondo et al., 2001).

5. Conclusions

Biological markets involve at least two interacting partners. In these simulations, one tree interacts with multiple mycorrhizal functional types, at most one per cell, from a 6-member symbiont pool. In previous theoretical biological market applications, the host has the responsibility of selecting its symbiont and the extent to which that symbiont is utilized (Kummel and Salant, 2006). Here, the extent of utilization includes the number of interactions (occupied cells) and the allocation of carbon to each cell. Thus, the plant must employ strategies that can modify both aspects of utilization. In uniform static environments, both symbiont selection and selective carbon allocation strategies (the strategies that make decisions at the single cell level) can organize stable functional type communities that maximize the host's ability to acquire nutrients.

Predictions concerning mycorrhizal communities based on these simulations include a decrease in fungal functional type diversity with decreased carbon input from the host as indicated in both the carbon pool adjustment and selective carbon allocation strategies when inorganic nutrient availability is high. Moreover, plants must invest more carbon with the mycorrhizal symbionts when inorganic nutrients are less abundant. Active control of carbon distribution by plants at the scale of the individual root is required to optimally structure and utilize functional type communities.

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Appendix A

Explanations of select equations.
Eq. (10):

$$C_{MIS} = (N_{ACQ} - N_{REQ}) \times PRICE \quad (9)$$

$$C_{MIS} = (C_{Gj} - C_{Gi}) + (C_{Gj} - C_{Gi}) \times (N_g \times PRICE) \quad (9a)$$

$$C_{Gj} = \frac{C_{Gi} + C_{MIS}}{1 + N_g \times PRICE} \quad (10)$$

Eq. (9a) redefines C_{MIS} in terms of how the pool will be allocated to C_G in the next step: $(C_{Gj} - C_{Gi})$ represents the new carbon allocated to C_G , and $(C_{Gj} - C_{Gi}) \times (N_g \times PRICE)$ reflects the amount of carbon that must be allocated to C_F in order to satisfy the new nutrient requirements based on the C_G pool. Eq. (10) is an algebraic transformation of Eq. (9a) solved for C_{Gj} .

Eq. (15):

$$C_{MIS} = C_{Gi} - \frac{N_{ACQi} - N_{MIN}}{N_g} \quad (15)$$

Eq. (15) calculates C_{MIS} in the case when too much carbon has been allocated to C_G while $N_{ACQ} > N_{MIN}$. C_{MIS} is equivalent to the amount of C_G that could not be supported by the acquired nutrients in the i time step. The $(N_{ACQi} - N_{MIN})/N_g$ term is equivalent to the portion of C_G that was able to be supported in the i time step. If $N_{ACQ} < N_{MIN}$ and $C_G = 0$, the symbiont community is ineffective under the given environmental conditions; since the carbon pool adjustment strategy is unable to select against ineffective symbionts, the strategy has failed.

Eq. (18):

$$C_{Fj} = N_{REQi} \times PRICE - (C_{Gf} \times N_g) \times PRICE \quad (18)$$

Eq. (18) is used to calculate the optimum size of the C_F pool for the next step based on the values of the previous step. The $N_{REQi} \times PRICE$ portion of the equation is the total amount of carbon required to satisfy the nutrient needs from the previous step, and the $(C_{Gf} \times N_g) \times PRICE$ portion accounts for the reduction of N_{REQ} based on the reduced size of the C_G pool due to C_{Gf} .

Eq. (19):

$$C_{Gj} = \frac{C_{TOTAL} - PRICE(N_{REQi} - C_{Gi} \times N_g)}{1 + PRICE \times N_g} \quad (19)$$

$$C_{Gf} = C_{Gi} - C_{Gj} \quad (16)$$

$$C_{Fj} = C_{TOTAL} - C_{Gj} \quad (17)$$

$$C_{Fj} = N_{REQi} \times PRICE - (C_{Gf} \times N_g) \times PRICE \quad (18)$$

$$C_{TOTAL} - C_{Gj} = N_{REQi} \times PRICE - [(C_{Gi} - C_{Gj}) \times N_g] \times PRICE \quad (18a)$$

Eqs. (16) and (18) are listed to explain substitutions for values in Eq. (17), which are represented in Eq. (18a). Eq. (18a) is algebraically solved for C_{Gj} , resulting in Eq. (19).

References

Abuzinadah, R.A., Read, D.J., 1986. The role of proteins in the nitrogen nutrition of ectomycorrhizal plants. 1. Utilization of peptides and proteins by ectomycorrhizal fungi. *New Phytol.* 103, 481–493.

Axelrod, R., Hamilton, W.D., 1981. The evolution of cooperation. *Science* 211, 1390–1396.

Baxter, J.W., Dighton, J., 2001. Ectomycorrhizal diversity alters growth and nutrient acquisition of grey birch (*Betula populifolia*) seedlings in host-symbiont culture conditions. *New Phytol.* 152, 139–142.

Baxter, J.W., Dighton, J., 2005. Phosphorus source alters host plant response to ectomycorrhizal diversity. *Mycorrhiza* 15, 513–523.

Bidartondo, M.I., Elk, H., Wallander, H., Söderström, B., 2001. Do nutrient additions alter carbon sink strength of ectomycorrhizal fungi? *New Phytol.* 151, 543–550.

Bronstein, J.L., 1994. Conditional outcomes in mutualistic interactions. *Trends Ecol. Evol.* 9, 214–217.

Bronstein, J.L., 2001. The costs of mutualism. *Am. Zool.* 41, 825–839.

Bruns, T.D., 1995. Thoughts on the processes that maintain local species diversity of ectomycorrhizal fungi. *Plant Soil* 170, 63–73.

Buée, M., Courty, P.E., Mignot, D., Garbaye, J., 2007. Soil niche effect on species diversity and catabolic activities in an ectomycorrhizal fungal community. *Soil Biol. Biochem.* 39, 1947–1955.

Cairney, J.W.G., 1999. Intraspecific physiological variation: implications for understanding functional diversity in ectomycorrhizal fungi. *Mycorrhiza* 9, 125–135.

DeBellis, T., Kernaghan, G., Bradley, R., Widden, P., 2006. Relationships between stand composition and ectomycorrhizal community structure in boreal mixed-wood forests. *Microb. Ecol.* 52, 114–126.

Denison, R.F., 2000. Legume sanctions and the evolution of symbiotic cooperation by rhizobia. *Am. Nat.* 156, 567–576.

Farley, R.A., Fitter, A.H., 1999. Temporal and spatial variation in soil resources in a deciduous woodland. *J. Ecol.* 87, 688–696.

Gardes, M., Bruns, T.D., 1996. Community structure of a ectomycorrhizal fungi in a *Pinus muricata* forest: above- and below-ground views. *Can. J. Bot.* 74, 1572–1583.

Gibson, F., Deacon, J.W., 1990. Establishment of ectomycorrhizas in aseptic culture: effects of nitrogen and phosphorus in relations to successions. *Mycol. Res.* 94, 166–172.

Hoeksema, J.D., Schwartz, M.W., 2003. Expanding comparative-advantage biological market models: contingency of mutualism on partner resource requirements and acquisition trade-offs. *Proc. R. Soc. Lond. B* 270, 913–919.

Hoeksema, J.D., Kummel, M., 2003. Ecological persistence of the plant-mycorrhizal mutualism: a hypothesis from species coexistence theory. *Am. Nat.* 162, S40–S50.

Johnson, N.C., Hoeksema, J.D., Bever, J.D., Chaudhary, V.B., Gehring, C., Klironomos, J., Koide, R., Miller, R.M., Moore, J., Moutoglou, P., Schwartz, M., Simard, S., Swenson, W., Umbanhowar, J., Wilson, G., Zabinski, C., 2006. From Lilliput to Brobdingnag: extending models of mycorrhizal function across scales. *Bioscience* 56, 889–900.

Johnstone, R.A., Bshary, R., 2008. Mutualism, market effects and partner control. *J. Evolut. Biol.* 21, 879–888.

Jonsson, L.M., Nilsson, M.C., Wardle, D.A., Zackrisson, O., 2001. Context dependent effects of ectomycorrhizal species richness on tree seedling productivity. *Oikos* 93, 353–364.

Kernaghan, G., 2005. Mycorrhizal diversity: cause and effect? *Pedobiologia* 49, 511–520.

Kiers, E.T., van der Heijden, M.G.A., 2006. Mutualistic stability in the arbuscular mycorrhizal symbiosis: exploring hypotheses of evolutionary cooperation. *Ecology* 87, 1627–1636.

Kiers, E.T., Rousseau, R.A., Denison, R.F., 2006. Measured sanctions: legume hosts detect quantitative variation in rhizobium cooperation and punish accordingly. *Evol. Ecol. Res.* 8, 1077–1086.

Koide, R., Elliot, G., 1989. Cost, benefit and efficiency of the vesicular arbuscular mycorrhizal symbiosis. *Func. Ecol.* 3, 252–255.

Kummel, M., Salant, S.W., 2006. The economics of mutualisms: optimal utilization of mycorrhizal mutualistic partners by plants. *Ecology* 87, 892–902.

Lechowicz, M.J., Bell, G., 1991. The ecology and genetics of fitness in forest plants. II. Microspatial heterogeneity of the edaphic environment. *J. Ecol.* 79, 687–696.

Lilleskov, E.A., Bruns, T.D., 2003. Root colonization dynamics of two ectomycorrhizal fungi of contrasting life history strategies are mediated by addition of organic nutrient patches. *New Phytol.* 159, 141–151.

Molina, R., Massicote, H., Trappe, J.M., 1992. Specificity phenomena in mycorrhizal symbioses: community-ecological consequences and practical implications. In: Allen, M.F. (Ed.), *Mycorrhizal Functioning: An Integrative Plant-Fungal Process*. Chapman and Hall, New York, pp. 357–423.

Nehls, U., 2008. Mastering ectomycorrhizal symbiosis: the impact of carbohydrates. *J. Exp. Bot.* 59, 1097–1108.

Nehls, U., Grunze, N., Willmann, M., Reich, M., Küster, H., 2007. Sugar for my honey: carbohydrate partitioning in ectomycorrhizal symbiosis. *Phytochemistry* 68, 82–91.

Noë, R., Hammerstein, P., 1994. Biological markets: supply and demand determine the effect of partner choice in cooperation, mutualism and mating. *Behav. Ecol. Sociobiol.* 35, 1–11.

Read, D.J., Perez-Moreno, J., 2003. Mycorrhizas and nutrient cycling in ecosystems—a journey towards relevance? *New Phytol.* 157, 475–492.

Roiiloa, S.R., Alpert, P., Tharayil, N., Hancock, G., Bhowmik, P.C., 2007. Greater capacity for division of labour in clones of *Fragaria chiloensis* from patchier habitats. *J. Ecol.* 95, 397–405.

Roughgarden, J., 1975. Evolution of marine symbiosis—a simple cost-benefit model. *Ecology* 56, 1201–1208.

Rygiewicz, P.T., Andersen, C.P., 1994. Mycorrhizae alter quality and quantity of carbon allocated below ground. *Nature* 369, 58–60.

Sachs, J.L., Mueller, U.G., Wilcox, T.P., Bull, J.J., 2004. The evolution of cooperation. *Q. Rev. Biol.* 79, 135–160.

Schlesinger, W.H., 1977. Carbon balance in terrestrial detritus. *Ann. Rev. Ecol. Syst.* 8, 51–81.

Schwartz, M.W., Hoeksema, J.D., 1998. Specialization and resource trade: biological markets as a model of mutualisms. *Ecology* 79, 1029–1038.

Simard, S.W., Perry, D.A., Jones, M.D., Myrold, D.D., Durall, D.M., Molina, R., 1997. Net transfer of carbon between ectomycorrhizal tree species in the field. *Nature* 388, 579–582.

Simms, E.L., Taylor, D.L., 2002. Partner choice in nitrogen-fixation mutualisms of legumes and rhizobia. *Integr. Comp. Biol.* 42, 369–380.

Simms, E.L., Taylor, D.L., Povich, J., Shefferson, R.P., Sachs, J.L., Urbina, M., Tausczik, Y., 2006. An empirical test of partner choice mechanisms in a wild legume-rhizobium interaction. *Proc. Roy. Soc. B: Biol. Sci.* 273, 77–81.

Smith, S.E., Read, D.J., 1997. *Mycorrhizal Symbioses*, 2nd ed. Academic Press, San Diego, USA.

Stuefer, J.F., DeKriib, H., Daring, J.H., 1996. Exploitation of environmental heterogeneity by spatial division of labour in a clonal plant. *Func. Ecol.* 10, 328–334.

Tannenbaum, E., 2007. When does division of labor lead to increased system output? *J. Theor. Biol.* 247, 413–425.

- Trappe, J.M., 1977. Selection of fungi for ectomycorrhizal inoculation in nurseries. *Annu. Rev. Phytopath.* 15, 203–222.
- Twieg, B.T., Durall, D.M., Simard, S.W., 2007. Ectomycorrhizal fungal succession in mixed temperate forests. *New Phytol.* 176, 437–447.
- West, S.A., Griffin, A.S., Gardner, A., 2007. Evolutionary explanations for cooperation. *Curr. Biol.* 17, R661–R672.
- West, S.A., Kiers, E.T., Simms, E.L., 2002. Sanctions and mutualism stability: why do rhizobia fix nitrogen? *Proc. R. Soc. Lond. B* 269, 685–694.
- Wilkinson, D.M., Sherratt, T.N., 2001. Horizontally acquired mutualisms, and unsolved problem in ecology? *Oikos* 92, 377–384.