

Plant height and evolutionary games

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In plants, investment in height improves access to light, but incurs costs in construction and maintenance of the stem. Because the benefits of plant height depend on which other height strategies are present, competition for light can usefully be framed as a game-theoretic problem. The vertical structure of the world's vegetation, which is inefficient for plant growth, can then be understood as the outcome of evolutionary and ecological arms races. In addition, game-theoretic models predict taller vegetation on sites of higher leaf area index, and allocation to reproduction only after an initial period of height growth. However, of 14 game-theoretic models for height reviewed here, only one predicts coexistence of a mix of height strategies, a conspicuous feature of most vegetation. We suggest that game-theoretic models could help account for observed mixtures of height strategies if they incorporated processes for coexistence along spectra of light income and time since disturbance.

Potential height is an important aspect of the ecology of a plant species [1–3]. Potential or maximum canopy height can range from ~5 cm to >50 m and this full range can be found at a single site. The benefit of height is pre-emptive access to light: taller plants shade shorter plants but not vice versa. This competitive advantage depends on relative rather than absolute height. A new species or phenotype that held its leaves slightly higher than those already present would have an advantage in light capture and, all other things being equal, one might expect it to be capable of becoming established in the mixture. This mixture in turn would be open to invasion by species that grew slightly taller still, and so on. The benefit of height cannot be understood by considering a single strategy in isolation, because it is frequency dependent or game theoretic.

Frequency dependence means that height cannot be understood only by reference to what is physiologically or structurally possible. Much discussion of limits to height proceeds as if natural selection will inevitably drive plants to the tallest height that can be achieved in an environment [4]. This is not so. Selection towards greater height depends on how much benefit is to be obtained, as well as on the costs or feasibility of achieving it. Questions important to ecologists arise. How do competition and physiology interact in shaping the maximum height present in vegetation? What leads to the coexistence of species at a wide range of heights? And, is the mixture of heights to be understood mainly in terms of maximum potential height, or rather in terms of other height-related

traits, such as the pace of vertical growth and duration at a height? Here, we review what has been learnt from game-theoretic models for plant height.

The game-theoretic approach

Evolutionary game theory (Boxes 1,2) provides a formal logical procedure for investigating interactions between strategies [5] when competitive success depends on the frequencies of strategic traits. Biological strategies are construed as phenotypes, meaning that genetic inheritance (Box 3) and gene–environment interactions are not discussed (Box 1). Situations are called games when the viability of a strategy depends upon what strategies are being ‘played’ by competitors. The fundamental question is whether a given existing strategy or mixture of strategies can exclude alternate strategies from establishing (i.e. ‘invading’). Potential invading strategies can be thought of as rare mutants within the existing population, or as initially rare species colonizing from elsewhere. The question asked is whether they can increase if initially rare. A strategy or strategy mixture that cannot be invaded is called an evolutionarily stable strategy (ESS or ESS mixture). So an ESS (if one exists, Box 3) provides a prediction about what we might expect to observe in communities in which both natural selection and colonization from elsewhere can potentially introduce a wide range of alternative strategies. The prediction depends on the traits and processes that the model represents as being decisive in competition and coexistence (Box 1). In this way, game-theoretic models and their predictions are a tool for understanding processes driving the long-term evolution of phenotypes [6,7].

Game-theoretic treatments of plant height

We have found 14 ESS treatments of traits that influence competitive asymmetry via shading in plants. In each model, a game is played between individuals competing for light. The treatments can be grouped (Table 1) according to the focal trait that varies between strategies. Some treatments enable foliage height to vary. Others vary traits such as leaf angle or specific leaf area (SLA: leaf area/leaf mass) that modify the shading power of individuals at a fixed height. In a third group, height growth varies through time, through biomass allocation. Critical assumptions listed in Table 1 are those that bring about frequency dependence and influence the predictions. Five main themes emerge from this compilation of existing models.

Theme 1: benefits and costs of height

Competition for light is asymmetric [8,9] such that taller individuals obtain a disproportionate share. Competing

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Box 1. Game theory and the evolutionarily stable strategy

Evolutionary game theory [53] provides a formal, logical framework for investigating traits whose success is frequency dependent [54], that is, where the success of a strategy depends on which other strategies are present. Consider a mixture or coalition of strategies. Strategies are defined in terms of some trait or behavior, such as height, and refer to phenotypes rather than genotypes (Box 3). The resident population comprises all strategies with a positive population density. In the single species case, there is one strategy at saturating density. When population densities equilibrate, the coalition is said to have ecological stability.

The characteristic thought experiment is to introduce a novel strategy, at low density, into the mixture of strategies already present. The question is whether novel strategies can increase from rarity. The novel strategies introduced can be thought of as mutants in a within-species situation, or as colonists from elsewhere in a between-species situation. A coalition that excludes any new strategies is called an evolutionarily stable strategy (ESS) mixture [38] (Box 2 for formal definitions; Box 3 for some limitations of ESS approaches). An ESS

constitutes a prediction of which strategies can sustain populations in the face of potential competitors, and of how many can coexist, under the circumstances assumed for a particular game [55]. Thus, the predictions are relevant to both questions of microevolution within species, and the assembly of a multi-species community through competitive filtering. By varying the circumstances in the game, differential predictions can emerge in relation to climate zones or site factors [56].

When the interest is principally in height differences between species and in the coexistence of mixtures of height, then strategies can be described in terms of characteristic asymptotic heights. But a strategy might also refer to a decision rule; for example, a degree of etiolation depending on the red:far-red ratio that plants use as an early signal of competing neighbors [57]. In this way, the game-theory approach could be used to investigate plasticity of height as well as pre-programmed height strategies. ESS models can also incorporate multiple strategy dimensions. We have not found height-related ESS treatments that incorporate plasticity or multiple strategies.

individuals increase their relative fitness both directly and indirectly by intercepting more light. Directly, increased light interception increases photosynthesis, although there are diminishing returns because of the shape of the photosynthetic light response curve and the decline in light interception with increasing layers of leaf. Indirectly, intercepting more light increases the relative fitness of an individual even if the light energy cannot be used efficiently, by making the resource unavailable to its neighbors. Consequently, strategies that are taller [10–12], larger [13], mature later (and hence are larger) [14–16] or have greater shading power (flatter leaf angle [17] or higher SLA [18]) displace strategies with less shading power in ESS models for shading-related traits (Table 1).

If taller strategies displace shorter strategies, why does selection or competition not drive heights infinitely upwards? Progressive invasion by ever larger strategies

is restricted by costs. Height incurs costs as past investment in stems for support, as continuing maintenance costs for the stems and vasculature, as disadvantages in the transport of water to height and as increased risk of breakage [4,19–22]. For example, in the models by Givnish [11] and Iwasa *et al.* [12] the proportion of biomass invested in leaf decreases with height. In the treatments for age and size at maturity [14–16], the cost is deferred reproduction. A taller strategy will not invade when the cost of the additional increment, expressed as a decrease in expected reproductive output, outweighs the potential decrease because of shading by competitors.

Theme 2: frequency dependence and shifts along environmental gradients

The benefits of height depend on the abundance of other strategies present, whereas costs are incurred regardless. Consequently, the degree of interaction between strategies

Box 2. Formal definitions for an ESS in a static game

In a set of r species, let u_i be the strategy of i^{th} spp. Then $\mathbf{U} = [u_1, \dots, u_r]$, which is the strategy vector for the community. Similarly, let x_i = population density of i^{th} spp, then $\mathbf{X} = [x_1, \dots, x_r]$, which is the population density vector for the community. Species are evolutionarily identical if they have the same strategy choices ($u \in \mathbf{U}$) and the same consequences from choosing them. The fitness of any strategy (v) in an evolutionarily identical set can then be described using a single fitness generating function (G function), incorporating interactions with all other strategies present (Eqn I):

$$G(v, \mathbf{U}, \mathbf{X}) = G(v, u_1, \dots, u_r, x_1, \dots, x_r) = f(v) - \sum_{i=1}^r f(v, u_i, x_i) \quad \text{[I]}$$

The G function is formulated to provide the rate of population change for strategy v in the community. If $G(v, \mathbf{U}, \mathbf{X}) = 0$, then the population of the species with strategy v is at equilibrium. Substituting u_i for v , the population dynamics of each species can be described as (Eqn II):

$$\dot{x}_i = \frac{\partial \mathbf{X}}{\partial t} = x_i(t) \cdot G(u_i, \mathbf{U}, \mathbf{X}) \quad \text{[II]}$$

An ecologically stable equilibrium (ESE) occurs at \mathbf{X}^* if there exists

σ such that for $1 \leq \sigma \leq r$ (Eqn III):

$$G(x_i^*, \mathbf{U}, \mathbf{X}^*) = 0 \quad \text{for } i = 1, \dots, r; \quad \text{[III]}$$

$$x_i^* > 0 \quad \text{for } i = 1, \dots, \sigma; \quad \text{and } x_i^* = 0 \quad \text{for } i = \sigma + 1, \dots, r$$

A coalition vector \mathbf{U}_c is then defined as the vector of σ strategies that have positive equilibrium density, whilst \mathbf{U}_m is the remnant vector of $r - \sigma$ strategies with $x_i^* = 0$. Then \mathbf{U}_c is an evolutionarily stable strategy (ESS) at an equilibrium point \mathbf{X}^* if, for all $i > \sigma$ and $\mathbf{U}_m \in \mathbf{U}$, \mathbf{X}^* is an ESE [38]. That is to say that the population vector is immune to perturbations regardless of the strategies that are present in the remnant vector.

An ecologically stable community can be identified as an ESS if it satisfies the ESS maximum principle [38,55], which states that, if $G(v, \mathbf{U}, \mathbf{X})$ is the G function for a community, and if \mathbf{U}_c is an ESS, $G(v, \mathbf{U}_c, \mathbf{X}^*)$ must take on a maximum with respect to v at u_1, \dots, u_σ , and that this maximum must be zero. In other words, the fitness of any strategy not present in the coalition must be negative. Sometimes, this criterion can be solved analytically across the full range of possible ESSs, even in an n -strategy game (e.g. Geritz *et al.* [42] for seed mass). But if not, then a proposed ESS can be tested by calculating the G function for all absent strategies. If the game is approached via simulation of a time process, rather than analysis for equilibrium, the relevant test is whether the mutant strategy dies out over a short time course [58].

Box 3. Some limitations on game theoretic approaches to evolutionary outcomes

Game-theoretic approaches consider competition among phenotypes and explicit genetic treatment is absent. The set of potential strategies includes all phenotypes considered evolutionarily feasible [6,7]. Implicitly, it is assumed that all credible invading strategies either already exist somewhere, or can be generated by mutation and recombination.

Not surprisingly, this approach has created tension with those interested in short-term evolutionary dynamics and population genetics (overview by Marrow [59]). The ESS approach can be inadequate when the details of inheritance are important, as under heterozygote advantage, or for tracing gene frequency change among known alleles that are already present in the population. But over longer periods, new genes arise by mutation and it is unhelpful to regard the range of potential phenotypes as restricted by the current genetic structure [60].

Another drawback of ESS models is that, under certain circumstances, particular ESS strategies might be unattainable. The rapidly emerging field of adaptive dynamics [61–63] emphasizes the evolutionary trajectory of strategies in an expanded formulation of a frequency-dependent game. In some fitness landscapes, an ESS might not be convergent stable or might result in an evolutionary branching point [61]. In other cases, there might be no ESS predicted, with either random or cyclic trait shifts (different strategies becoming predominant temporarily but then being invaded by one of the other strategies) [13].

ESS models, expanded game-theoretic treatments and genetic models each shed light on different aspects of the evolutionary process [59]. For coexistence of plant height strategies, much can be learnt from ESS models without addressing issues of inheritance.

is mediated by vegetation properties, such as stand leaf area index (LAI: leaf area/ground area). In high-LAI environments, the disadvantage of being the least-tall strategy is greater. Thus, there is greater benefit for increasing height and the ESS for average height increases with site LAI [11,12,23]. This prediction is supported [24], although the empirical data are surprisingly sparse. Under frequent disturbance (e.g. tropical grasslands), increased competition for light can be manifested strategically as an increased rate of height growth, or under lower disturbance frequency as increased ultimate height. Physiologically, the same conditions that are conducive to higher LAI (i.e. warm, high rainfall and nutrient-rich soils) are those that are conducive to greater height growth. However, the driving evolutionary mechanism causing increased height in high LAI environments is likely to be competition. Unfortunately, this has received limited attention in recent debates about the limits to height growth [4,22,25–27].

Theme 3: 'bang-bang' strategies

In dynamic or differential games, the strategy is a process over time rather than a trait at a moment in time. Makela [28] considered a game involving allocation to stem versus foliage growth in trees. Success in competition for light depends on allocation to stem (height), whereas reproduction depends on the productive part of the plant (foliage area). The ESS in this game is a 'bang-bang' strategy: first a period of allocation directed towards maximizing height growth, then a changeover to allocation towards maximizing reproduction (see also [10]). Such a changeover has been observed in annuals, with a similar but more gradual transition observed for forest tree species [10,29]. With increasing uncertainty about survivorship or the duration of good growth conditions, the ESS shifts from a strict switching time to one in which strategies involving bet hedging, or iteroparity (multiple reproductive events) are selected for [30,31].

A bang-bang prediction also arises for allocation first to vegetative and only later to reproductive growth [30], and for a partly similar reason. Vegetative growth yields compound interest. Therefore, early reinvestment of all photosynthate into vegetative growth yields greater final return than does progressive diversion to reproduction.

However, whereas the bang-bang strategy for vegetative growth before reproduction maximizes reproductive output, the ESS bang-bang strategy for height growth before reproduction does not. Investment in the support structures for height does not increase absolute returns via compound interest – it only avoids returns being decreased by overshadowing competitors.

The dynamic game describing a race for light can be thought of as a series of static games. Strategies for allocation between stem and foliage [32], and between above and belowground growth [33], which maximize the rate of height growth, have been identified in particular scenarios. In each case, there is a single winning strategy, but this is only for maximizing height gain. Models have not yet been formulated for describing how other strategies might persist without seeking to reach the top of the canopy.

Theme 4: competitive outcomes and the 'tragedy of the commons'

The 'tragedy of the commons' [34] is a general principle of resource use. In a system in which resources are finite and access is unrestricted, the most competitive strategy is to maximize personal use of the resource. But this ESS outcome will not maximize community-wide utility from the resource – rather it will tend toward overexploitation of the resource, to the detriment of the community as a whole. This concept has been adapted to describe members of biological communities competing for resources [14–18,35–37]. All strategies would benefit from less competition, but the tragedy of the commons enables strategies that use more resources to intrude. The ESS is for a larger or taller or later maturing denser shading (more resource wasting) strategy than the cooperative strategy that would maximize overall production from the strategy mixture. More generally, this result emerges as a fundamental difference between population (group) and individual based optimization. The population solution seeks to maximize success of the assemblage as a whole, whereas an ESS focuses on the success of individual strategies with respect to alternate strategies [38]. The upshot is that communities (or species) should not be expected to maximize productivity [10,35,36]. That terrestrial vegetation growing in productive locations has tall stems is not a triumph of biological productivity.

Table 1. Summary of ESS^a models for height^b

Focal trait ^b	Critical assumptions	Prediction ^c	Data	Refs
Static games for height and light interception				
Average foliage height in herbs	Photosynthesis per unit leaf area increases with relative height owing to better light conditions Proportion of biomass in leaves decreases with height	SS → ESS height increases with average cover	Yes	[11]
Average foliage height	Photosynthesis is proportional to light levels, which decline logarithmically with height down a canopy Support cost per unit leaf area increases nonlinearly with height	SS → foliage height increases with LAI, and decreases with an increase in cost per height increment and crown depth SM → when the canopy of each morph is thin enough, infinite layers can coexist	No	[12]
Body size (e.g. foliage height)	Competition is size asymmetric. Competitive interactions translate into size-dependent competitive coefficients in population dynamics Basal mortality rate increases linearly with size	Under symmetric competition, SS of smaller body size is possible. As degree of competitive asymmetry increases, multiple SMs become possible ^d	No	[13]
Average foliage height under grazing	Introduces grazing to model of Givnish [11]. There is a sigmoidal increase in the chance of mortality owing to grazing with height	SS → ESS for foliage height 'jumps' from high to low as grazing pressure reaches a critical level	No	[50]
Biomass allocation among foliage, vertical stems and horizontal stems	A plant can allocate biomass to horizontal stems (H), vertical stems (V) or foliage (F) Light capture is a function of an individual's relative height Photosynthetic capacity increases with F, but asymptotes owing to self shading. Self shading is reduced by H	SS → allocation to H, V and F varies with the density of individuals and canopy openness Allocation to V increases with stand density Allocation to H increases in closed habitats to decrease self-shading	No	[23]
Other static games for light interception				
Light extinction coefficient (K) (~leaf angle)	The competitive effect of neighbors on the target plant is determined by K (~leaf angle), and the degree of self shading	SS → K will be close to 1 (flat leaf angle) unless self shading is high, in which case it decreases with LAI. The ESS results in lower canopy productivity than does a cooperative optimal strategy	No	[17]
SLA distribution within the canopy	Leaf biomass and nitrogen mass are constant at different heights in the canopy, but invaders can shift their SLA at any height and thus alter LAI Light attenuation increases with LAI	SS → ESS values for SLA distribution (and hence LAI) are higher throughout the canopy than is the value that optimizes whole-stand productivity	No	[18]
Time strategies for reproductive versus vegetative growth				
Growth strategy (temporal allocation of biomass to trunks and photosynthetic parts)	Trees reproduce at maturity. Fitness is proportional to the condition of the photosynthetic part of the tree at maturity Growth rate of immature tree depends on its relative height Proportional allocation to stem increases linearly with height. Game starts in a uniform, even-aged stand	SS → the ESS for growth is to adopt a bang-bang strategy, with a period of maximal height growth preceding a period of no height growth	No	[28]
Age and size at Maturity (e.g. flowering time in annuals)	The optimal strategy for maximizing individual fitness (lifetime allocation to reproduction) is a bang-bang strategy: individuals switch from devoting all resources to growth to devoting all resources to reproduction Competition for resources is size dependent	SS → the ESS is always to mature later, and at a larger size, than at the age that would maximize fitness of the population rather than the individual	No	[14–16]
Time-strategies for allocation to height versus foliage and (sometimes) versus other activities such as spread or roots				
Tree height in a dense single species stand	Fitness is proportional to stem wood production (~stem diameter), which increases with light, but decreases linearly with tree height because of increasing maintenance costs Excess wood production (after foliage and stem maintenance) is allocated between height and diameter only Model only applies after canopy closure (maximum LAI)	SS → tree height in even-aged stands increases until a critical height is reached, after which all excess wood production is diverted to diameter increase Height is related to basal diameter for all trees of sub-critical height	Yes	[10]
Growth strategy (time function of biomass allocation to trunks and photosynthetic parts) for a sapling waiting for gap formation	More foliage enables greater production under a closed canopy, but a larger trunk enables a gap to be occupied more successfully Reproductive fitness of a sapling following gap formation increases exponentially with relative height Reproductive fitness is integrated over all possible gap formation times	SS → saplings allocate more, in the latter stages of growth, to their photosynthetic parts, if there is a stronger advantage in having a larger trunk in gaps; or to trunks, if there is a high probability of gap formation or mortality	No	[40]
Root:Shoot allocation	Either light or nutrients limit growth, which is determined by root:shoot allocation in a given environment Fitness is a linear function of root:shoot allocation along a light limited or nutrient limited curve	SS → the ESS for root:shoot allocation occurs at the intersection of the nutrient limited and light limited growth curves, such that both resources are equally limiting	No	[33]

^aAbbreviations: ESS, evolutionarily stable strategy; LAI, leaf area index (m^2/m^2); SLA, specific leaf area ($mm^2 mg^{-2}$); SM, strategy mixture; SS, single strategy.

^bIn each model, a game is played between individuals competing for light. The treatments are grouped according to the focal trait that varies between strategies. Some treatments enable foliage height to vary. Others vary traits, such as specific leaf area (SLA: leaf area/mass) or leaf angle, which modify the shading power of individuals at a fixed height. In a third group, height growth varies through time through biomass allocation.

^cIn each treatment, a 'mutant' strategy that differs only in the focal variable competes against the 'residents' in a game for light. The winner is the strategy with the highest payoff, measured as biomass or reproductive output. An ESS arises when no mutant strategy can have a greater payoff than the resident strategy or strategy mixture. In all treatments except those by Iwasa *et al.* [12] and Law *et al.* [13], the games predict a single strategy ESS rather than a mixture (coalition) of strategies.

^dThe predictions from this model emerge from an adaptive dynamics framework (Box 3), rather than a classic ESS formulation of the game. The predicted stable SMs are governed by modified criteria to the other ESS models cited.

Rather, it is the inefficient outcome of an arms race between plants competing for light [39]. If ecosystems were truly cooperative organizations, vegetation would be a thin skin of green near the ground, without expenditure on stems detracting from the production. Not surprisingly, the most productive food systems on Earth (crops) comprise strategies with minimal investment in height [10]. However, these require ongoing artificial selection to maintain an otherwise evolutionarily unstable strategy.

Theme 5: ESS mixtures

A striking feature in most vegetation types is coexistence of species at a range of heights. Only one ESS model directly enables multiple height strategies to coexist. Iwasa *et al.* [12] showed that, provided costs of maintaining leaf at a given height rise with height in an accelerating manner, leaf area should be spread through a continuous range of heights. It can easily be imagined that this strategy mixture could be contributed by many species of different heights, although Iwasa *et al.* left open the possibility of a single species with a deep canopy. This model successfully represents obvious features of forest canopies: the top foliage height is taller in environments that support a greater LAI, and lower in environments where the costs of achieving a given height are greater. The model also makes a less obvious prediction, that there should be a continuous spread of height strategies through the range of heights. To see why, imagine that there is a gap in the height distribution. The height immediately below the gap would have the same gain as the strategy immediately above the gap, but a lower cost. The gap in the height distribution would therefore violate the principle that all coexisting strategies should have equal net gain at an ESS.

Most models fail to address the broad spread of species along the height strategy–axis evident in almost all vegetation (all but two in Table 1 predict a single-strategy ESS). One reason is that most models consider what strategy works best in the presence of a general competitive milieu that is itself unresponsive. For example, the treatments by King [10] and Sakai [40] apply only under a closed canopy, whereas the treatments by Givnish [11] and Sakai [23] apply only to herbaceous vegetation. This helps us to understand what the outcome should be in a given height zone, but can only be a first step towards understanding the full height mixture at a site. A second reason might be that some games do not meet specific requirements for coexistence. For example, Hikosaka and Hirose [17] and Schieving and Poorter [18] fixed the height and leaf mass of individuals, allowing only leaf angle and SLA (respectively) to vary. There might indeed be a single ESS state under some of these constrained conditions.

Conditions for a mixture of strategies

The model by Iwasa *et al.* remains the only one that explicitly predicts a mixed strategy ESS for height, but, recently, a second more general treatment for body size has predicted strategy coexistence. In a two-species game, Law *et al.* [13] showed that, if interactions between species are size asymmetric, and the basal mortality rate increases with body size (for height this might be due to windthrow,

buckling or age), then several stable strategy mixtures are possible. Although the mortality assumption might not be met in many instances, a similar result would emerge if we assumed larger strategies had reduced recruitment rates.

Law *et al.*'s treatment supplements previous findings from ESS treatments for seed mass [41–44] on the general features required for ESS coexistence of a mixture of strategies along a trait spectrum. These are:

- A pre-emptable resource to be subdivided, such as light, or regeneration sites; or something similar to a total allowable leaf area that corresponds to subdividing the light;
- An internal scale within the resource, for example from full light down to compensation point light;
- A hierarchical subdivision between species such that some species are competitively superior in obtaining the resource;
- A tradeoff such that strategies dominant in the competitive hierarchy require a higher base level of the entity to persist.

The last criterion is crucial because it prevents the most competitive strategies from occupying all of the resource. Based on these four criteria, we propose several height-related spectra along which multiple-strategy ESS mixtures should be possible (Table 2).

Future directions

Iwasa *et al.*'s model seems to be the firmest foundation for future work. It makes predictions about upper and lower heights and accounts for a mixture of strategies in between. It is ripe for further development along several directions.

First, although the model predicts a continuous spread of leaf area through heights, it says nothing about the circumstances under which variety should be contributed by many species rather than by one tall species with leaves at many heights. Various factors could increase the chance that a low-height species was more competitive in the lower canopy than were lower leaves of a tall species. A different leaf type, suitable for lower light environments, might more readily be contributed by a separate species than by plasticity within a single species. The marginal costs of deploying leaves by low lateral branches from a tall stem might exceed the costs of a stem that reached only to the height in question. Investigating such possibilities seems interesting and empirically tractable.

A second challenge is to incorporate time processes. A tall strategy does not enter vegetation full grown – it has to begin small. Taller strategies must therefore be successful at growing up through shorter strategies, or at growing the fastest following disturbance and reaching the top first, or at outlasting shorter strategies through persistence. A viable strategy would be defined not by height only, but also by shade tolerance, rapid vertical growth or stem persistence, depending on the strategy for reaching full height. Currently, we have little quantification of how these different traits correlate with each other across species [1,45]. In much vegetation, dynamics comprise a race for light following a disturbance that opens the canopy. The game can be considered a series of these races, and a strategy

Table 2. Proposed strategy axes on which ESS mixtures could exist^a

Coexistence spectrum	Resource or entity to be divided in game	Competitive trait	Limit to full utilization of entity by competitive strategy	Refs
Seed mass – seed number output	Space (~ regeneration sites or 'patches')	Seed mass	Larger seed size limits number of seeds produced and hence number of patches that can be occupied	[43,44]
Height – support costs	Light (~ potential photosynthesis)	Foliage height	Greater height requires proportionally greater investment in support structures, limiting the maximum supportable leaf area for taller species	[10–12]
Height – mortality	Light (~ potential photosynthesis)	Foliage height	Basal mortality increases with height, limiting the population density of the larger species	[13]
Radiation load – water use efficiency	Light (~ potential photosynthesis)	Foliage height or leaf angle	Transpiration per leaf area increases with radiation load thereby limiting the maximum supportable leaf area per unit stem	
Successional status	Time at top of canopy (~ access to high light)	Rate of height growth	Rapid height growth, per unit investment in vertical stem, gives a stem with narrow taper or with low-density wood, hence lower longevity as a structure. Fast-growing species are outlasted by slower species	[3,48]
Shade tolerance	Light (~ potential photosynthesis)	Potential growth rate	High growth rate trades off against tolerance to low resource conditions. Fast-growing strategies that reach the light first cannot survive in the shade	[51,52]

^aReferences supporting the proposed criteria are indicated.

can persist in the game if it captures enough light during each race to make sufficient carbon profit and ensure that it plays in subsequent races. This, rather than 'winning' individual races, will be the criterion for a viable strategy. Succession and species turnover are important components of vegetation dynamics worldwide [46–49], but existing ESS treatments for height do not consider them.

Third, Iwasa *et al.*'s and most other ESS models are conceptual at this stage – few have been connected to empirical data (Table 1). Clearly, of key empirical interest are the tradeoffs that might be responsible for preventing taller species from monopolizing light resources and excluding shorter species (Table 2). If the tradeoffs can be correctly identified and quantified, it should be possible to predict the top height of vegetation and its variation with climate, disturbance and site factors, and also the vertical profile of leaf area. Conversely, data about these outcomes can provide tests of hypotheses about the tradeoffs. Data can stimulate further model development and appreciation of important constraints on plant life history. Determining the strength of frequency-dependent interactions, the partitioning of light across different species in vegetation, measuring the traits of species along potential dimensions of coexistence (Table 2) and calibrating models to changes in climatic conditions or disturbance regimes are all likely to provide valuable stimuli.

In conclusion

An evolutionary perspective reminds us that the benefits of height depend on the total amount of leaf area present per unit area, and on the heights of other strategies. The vertical structure of terrestrial ecosystems, and the large amount of carbon fixed as vertical stems, are outcomes of an evolutionary arms race. ESS models have provided valuable insight to the role of frequency-dependent interactions in reaching this outcome. Recent developments in ESS models for seed mass and theory about ESS mixtures provide stimuli

for extending current ESS models for plant height. Opportunity knocks for rapid development of models accounting for the wide range of heights observed across species in the vegetation of the world.

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