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On strategies of plant behaviour: evolutionary games of habitat selection, defence, and foraging

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ABSTRACT

Background: Strategies of habitat selection, defence, and foraging depend critically on population density and the frequency of alternative strategies: they are evolutionary games. Although commonly modelled in studies of animal behaviour, they are less frequently used to provide insights into the behaviour of plants. A 'review' and analysis of how these universal strategies apply to plants should help motivate further development of plant evolutionary games.

Questions: Should plants practise density-dependent habitat selection? Do games of plant defence depend on demography and habitat quality? How similar are games of competition for nutrients and light?

Methods and models: Assessments of eco-evolutionary dynamics with computer simulations (habitat selection), evolutionary invasion analysis (defence), and *G*-functions (foraging).

Results: Selection gradients for pre-emptive habitat selection are steeper than those for passive dispersal and yield an advantage that increases with population density. The evolutionarily stable defence level in a homogeneous environment is proportional to the ratio of survival by mature versus immature plants. In heterogeneous environments, investments in herbivore defence depend on habitat quality and are resolved by habitat selection. Games of competition for both nutrients and light predict Tragedies of the Commons in which size, density, and investment in tissue that does not directly contribute to fitness depend on the source of competition.

Conclusion: Much of the dynamic feedback between the ecology of plants and their evolution can be understood with models of three universal processes: habitat selection, safety and defence against enemies, and foraging for nutrients and other resources. The specifics of models may differ among taxa, but not the underlying density and frequency dependence of their eco-evolutionary strategies.

Keywords: adaptive landscape, defence, evolutionarily stable strategies, evolutionary game theory, habitat selection, height in trees, nutrient foraging, Tragedy of the Commons.

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INTRODUCTION

How tall should a tree be? As a best response curve, a focal individual need only be some-what taller than its neighbours, say $v* = u + \theta$, where u is the height of neighbouring trees, θ is an amount needed to be out of the shade and in the sunlight, and $v*$ is the best response to the height of others. In this simple example, trees would be under selection to achieve infinite height in a never-ending arms race of runaway selection. But trees experience increasingly unacceptable costs to height such as maintaining non-productive tissues and vascular transport systems. Eventually, a height is reached where the benefits of being taller than neighbours no longer exceed the costs. At that point, the arms race ends and the canopy height of the forest is established. It is a rather bizarre eco-evolutionary game where the optimal height of a tree depends largely on the height of its neighbours and the inherent costs of height imposed by the physical environment.

Foraging for light by plants in the simple form described above and in much more sophisticated models (Dybzinski *et al.*, 2011) illustrates some of the fundamentals of foraging games common to all organisms. Height in trees is both a form of the Tragedy of the Commons (Hardin, 1968) – overinvesting to gain access to a common resource – and a form of interference competition. Interference is a foraging game built on spite. If an individual is a bully, paying a cost to deprive another access to a resource, then the bully can recoup its losses via increased resource accessibility or through a higher relative fitness than the deprived individual.

The density and frequency dependence implicit in competition for light and nutrients dictate that foraging must be modelled as an evolutionary game. So, too, must strategies of habitat selection and defence. Early seed germination that pre-empts the use of resources or space by other individuals can be favoured by natural selection whenever 'waiting' for optimal conditions reduces the probability of resource ownership. Selfish freeloaders can 'parasitize' the defensive strategy of others. Although the games may appear different, each one emerges through reciprocal feedbacks between ecology and evolution (e.g. Pelletier *et al.*, 2009; Alberti, 2014). In some games, the feedbacks can be modelled and solved explicitly. In others, it can be more efficient to use computer simulation. The challenge, in each instance, is to seek solutions that yield fundamental insights into each strategy.

We begin our search for those insights by simulating comparisons between pre-emptive habitat selection and passive dispersal. Next, we demonstrate how evolutionary invasion analysis can predict optimal strategies for constitutive and induced plant defences. We illustrate how theories of habitat selection that optimize the trade-off between protection against herbivores and competitive ability yield plant strategies of 'defence in space'. We show how fitness-generating functions predict the Tragedy of the Commons with models of below-ground games played by roots and above-ground games of stem height. We conclude with a discussion on the importance of evolutionary games, and their explicit feedback between ecology and evolution, to our understanding of plant evolutionary strategies.

HABITAT SELECTION

We compare two extreme modes of habitat selection: (1) ideal pre-emptive habitat selectors (Shmida and Ellner, 1984; Pulliam, 1988; Pulliam and Danielson, 1991) that occupy the best sites first, versus (2) passive dispersers that occupy sites at random. Passive dispersal typifies so-called physical transport systems [such as dispersal by wind and water (Roughgarden *et al.*, 1987)]. Ideal

pre-emption assumes, as population size increases, that sites within a given habitat are occupied in rank order from highest to lowest fitness opportunities. Mean fitness declines with density. Passive dispersers will expect to achieve the mean fitness of the habitat as a whole. It follows that the fitness of an individual practising passive dispersal will exceed that of ideal pre-emption only if the fitness of the best unoccupied site dips below the weighted average. Thus, if we rank sites by fitness, we should be able to predict the sequence of site occupation with density and the optimal strategy of habitat use for different distributions of site quality (Rosenzweig, 1987; Morris, 1994). Note, as we do so, that we are explicitly assessing course-grained (Levins, 1962) habitat selection where individuals occupy a site for life. Other models (e.g. Gersani *et al.*, 2001; O'Brien and Brown, 2008; McNickle and Brown, 2012, 2014) apply to fine-grained habitat selection as practised by roots seeking nutrients.

The optimal strategy of each mode of habitat selection is revealed by its density-dependent global invader strategy landscape (Apaloo *et al.*, 2009; Morris, 2011). These valley-like invasion landscapes display the fitness that an individual using a particular strategy (the choice of which habitat to reside in) can expect when it is played against all possible competing strategies (expressed as alternative habitat choices). An individual already using the best strategy will be unable to achieve higher fitness by adopting any alternative strategy; its fitness is thus the minimum (floor) of the invasion landscape.

In the case of pre-emptive habitat selection, the invasion landscape emerges from the expectation that an individual always moves to the unoccupied site yielding highest fitness ['the best response dispersal dynamics' (Křivan *et al.*, 2008) – an unbeatable strategy (Hamilton, 1967)]. As these best sites become occupied, the invasion landscape sinks and changes shape with increasing population size. As it does so, it reveals the full set of density- and frequency-dependent dynamic strategy states (DSS) of habitat selection as well as the evolutionarily stable strategy when the population exists at equilibrium. The valley floor specifies the best strategy (proportion of individuals in each habitat) at every possible population size. The steepness and height of valley walls specify the difference in fitness (selection gradient) between that strategy and others.

Invasion landscapes for plant habitat selection

In order to draw and explore the shapes of invasion landscapes, we simulate habitat selection by an asexual semelparous (e.g. annual) species. We imagine that the species occupies an environment of constant size composed of two habitats that either comprise the entire environment or are embedded within non-suitable substrate. Habitats contain a fixed number of sites such that each site supports only the first individual to occupy it. Subsequent individuals occupy an alternative site based on either pre-emptive selection (choose the best of the remaining sites) or passive dispersal (occupy one of the remaining sites at random). Site quality (represented by the discrete population growth rate, λ) follows either a normal or Poisson distribution that is unique to each habitat.

The simulation begins with 1000 random draws for each site from the frequency distribution describing fitness in each habitat (400,000 values for cases where there are 200 sites in each habitat; see www.evolutionary-ecology.com/data/3041Appendix.pdf). The mean of these random draws for each site yields its expected fitness. We allow the population size and number of individuals in each habitat to vary. We then calculate the fitness that one additional individual can expect under each scenario of habitat selection, and draw the three-dimensional invasion landscapes.

Figure 1 illustrates the fitness expectations of the two modes of habitat selection when the high-quality habitat (2) has twice as many sites as the other (1) in an environment with unsuitable matrix. The landscape for pre-emptive habitat selectors is mostly symmetrical (Fig. 1A), that for random use less so. The DSS of pre-emptive habitat selection changes rapidly from a habitat-2 specialist at low population size to a generalist using both habitats (Fig. 1A). Fitness is lower, and selection gradients less steep, when individuals settle into sites of a habitat at random (compare Fig. 1A with 1B). In this case, the landscape changes asymmetrically from a pure habitat-2 specialist towards 70% occupation of habitat 2 at higher population sizes. Unlike pre-emptive habitat selection that yields high rewards for habitat choice at all population sizes, biased occupation of one or the other habitat for random use has only small fitness consequences at low population sizes. The valley walls become steeper and higher at high population sizes for both strategies because individuals packed into one or the other habitat gain substantial fitness by dispersing their offspring.

We evaluate which of the two modes of habitat selection is more fit, and whether or not one mode can overtake the other, by graphing the fitness difference between them (Fig. 1C). The fitness advantage of ideal pre-emptive habitat selection increases rapidly at low to moderate population sizes, and increases more slowly thereafter (Fig. 1C). Since the pre-emptive mode always yields higher fitness, and since the difference increases with population size, random use is most likely to displace the pre-emptive strategy at low population size and only if site pre-emption incurs a fitness cost.

Symmetrical invasion landscapes emerge for both strategies when the unsuitable matrix disappears and the habitats are equal in size (Fig. 2). The DSS of pre-emptive habitat selection again changes rapidly from a habitat-2 specialist (at population size = 2) to a generalist using both habitats. Selection gradients, and thus the probability of observing the DSSs in a real population, are also steeper and higher for a given strategy at high population sizes than they are at low population size. Fitness in the bowl-shaped random use landscape is lower than for any strategy of pre-emptive habitat selection (compare Fig. 2B with 2A). The best 'random' strategy nevertheless mirrors that of pre-emption.

The valley walls of the pre-emptive invasion landscape are steepest, and the valley floor more complex, when the distribution of sites expressing different qualities are clumped according to a Poisson distribution (Fig. 3A). Here, small changes in population size can have large effects on the fitness achievable by individuals that disperse to the best habitat. Nevertheless, the same general patterns of a bowl-shaped random-use landscape, and a more-or-less piecewise linear fitness-difference landscape, are retained (Fig. 3B, C). Each invasion landscape thus confirms our expectation that random use can invade and displace site pre-emption only if the weighted average fitness yields positive population growth, and if the fitness of the last occupied site by pre-emptive individuals is less than the weighted mean quality.

We can estimate the cost of failing to select the best site available, and the feedback onto strategies through changes in population size, by calculating the fitness difference that a single pre-emptive habitat selector should expect if it moves away from the ESS. Movement of a few individuals to the 'wrong' habitat at low population size can cause a large change in the proportion of individuals occupying habitat 2. The change in strategy thus entails a relatively high fitness cost (Fig. 4). The cost is also relatively high in dense populations because the slopes of the selection gradients increase with density. The cost of erring in site selection, and thus eco-evolutionary feedback onto the habitat-selection strategy, is lowest at intermediate population sizes. It also tends to be lower for individuals that move from
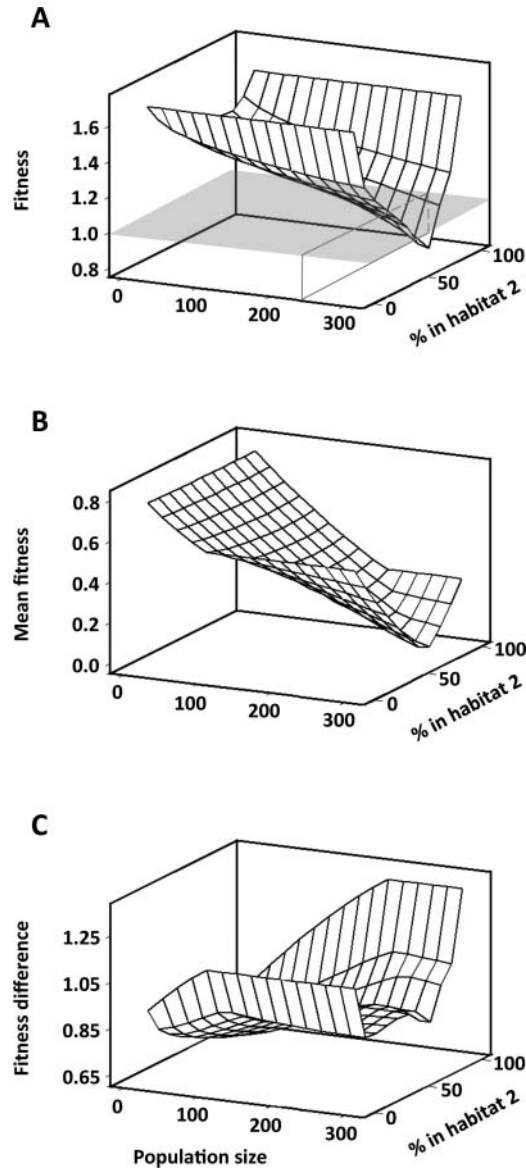
Fig. 1. Global invasion landscapes for ideal pre-emptive habitat selection (A), random use (B), and the difference between pre-emption and random habitat use (C), when the environment includes unsuitable matrix and when there are more sites in high- than low-quality habitat. The intersection of the horizontal (shaded) and vertical planes with the invasion landscape in (A) yields the evolutionarily stable strategy of ideal pre-emptive habitat selection. Site quality is normally distributed. Parameter values for habitat 1: number of sites = 100, mean site quality = 1.1, standard deviation in site quality = 0.2; parameter values for habitat 2: number of sites = 200, mean site quality = 1.15, standard deviation in site quality = 0.2, unsuitable matrix = 100 sites with zero fitness.
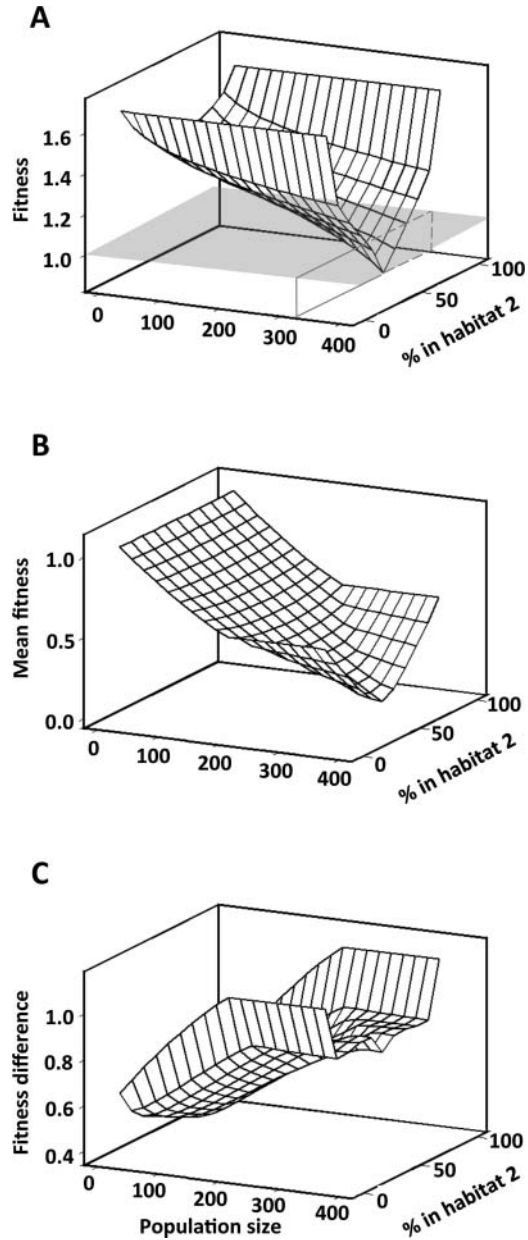
Fig. 2. Global invasion landscapes for ideal pre-emptive habitat selection (A), random use (B), and the difference between pre-emption and random habitat use (C). The intersection of the horizontal (shaded) and vertical planes with the invasion landscape in (A) yields the evolutionarily stable strategy of ideal pre-emptive habitat selection. Site quality is normally distributed. Parameter values for habitat 1: number of sites = 200, mean site quality = 1.1, standard deviation in site quality = 0.2; parameter values for habitat 2: number of sites = 200, mean site quality = 1.15, standard deviation in site quality = 0.2.
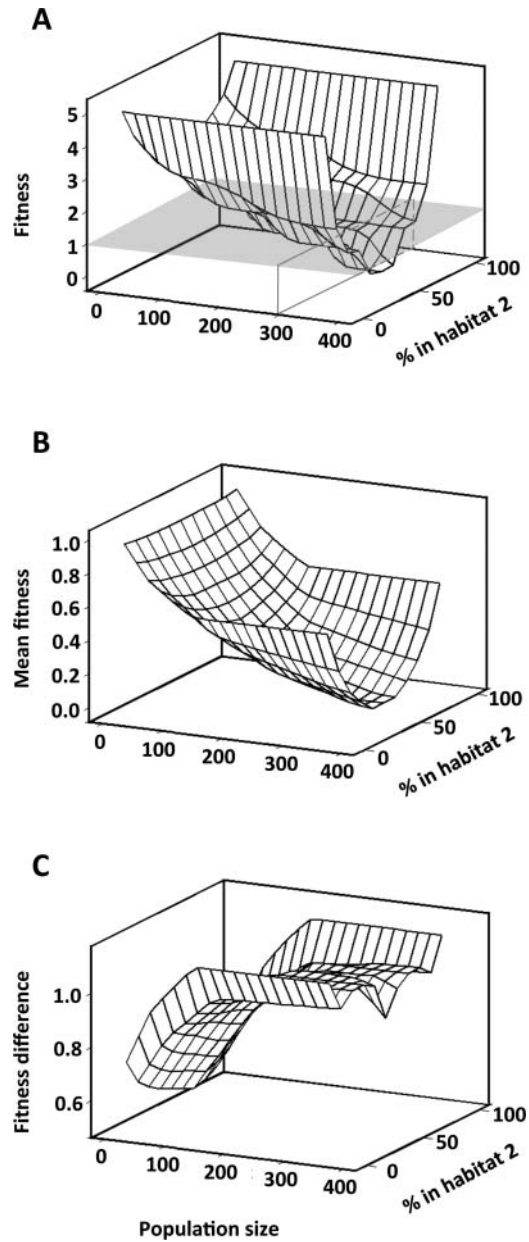
Fig. 3. Global invasion landscapes for ideal pre-emptive habitat selection (A), random use (B), and the difference between pre-emption and random habitat use (C), when site quality fits a Poisson distribution. The intersection of the horizontal (shaded) and vertical planes with the invasion landscape in (A) yields the evolutionarily stable strategy of ideal pre-emptive habitat selection. Parameter values for habitat 1: number of sites = 200, mean site quality = 1.1; parameter values for habitat 2: number of sites = 200, mean site quality = 1.15.
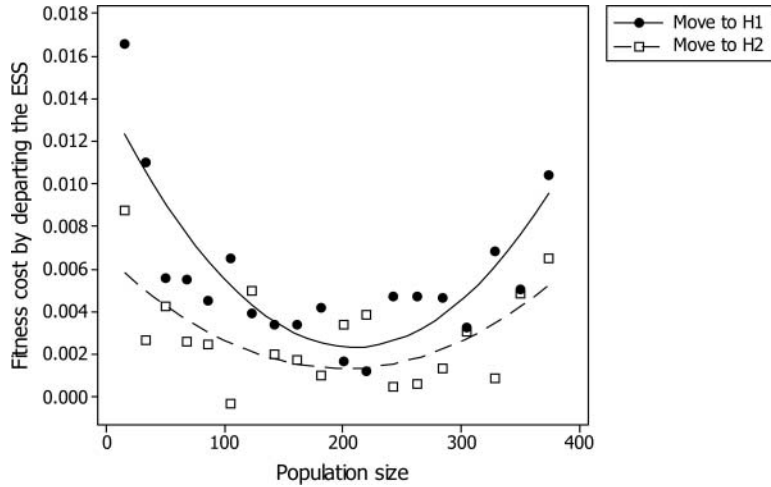
Fig. 4. The fitness cost associated with a single individual leaving the evolutionarily stable strategy of habitat selection at different population sizes. The cost is high at low population sizes because movement of a single individual has a relatively large effect on the proportion of individuals living in each habitat. The cost is also high at high population sizes because the slopes of the selection gradients increase with density (e.g. Fig. 1). Parameter values for habitat 1: number of sites = 200, mean site quality = 1.1, standard deviation in site quality = 0.2; parameter values for habitat 2: number of sites = 200, mean site quality = 1.15, standard deviation in site quality = 0.2. Curves fitted by quadratic regression.

the poorer to the better habitat (Fig. 4). These rather important patterns teach us that the switch from pre-emptive habitat use to random use is much more involved than simply assessing the mean fitness of the two strategies at different population sizes.

DEFENCE AGAINST ENEMIES

Assessing more than mean fitness is especially important when evaluating traits associated with defence. Plants respond to danger by myriad interacting constitutive and induced strategies (Åström and Lundberg, 1994) that often yield repeated convergent suites of traits (Agrawal, 2011). One solution is to become undetectable, or nearly so. Invisibility can be achieved by coloration, form and shape, and also by simply blending into a vast number of similar individuals.

Plant defence as a game

We illustrate the optimum level of defence in response to ecological variation in herbivory by reviewing an optimization model developed by Åström and Lundberg (1994). We then extend Åström and Lundberg's (1994) analysis in order to assess whether the optimal strategy is evolutionarily stable.

The model evaluates situations when the plant evolves a fixed level of defence in response to a similarly fixed risk of herbivory. The model would be different for induced defences that depend on the variance in risk, not just the mean value [if the variance is zero, then induced and constitutive defence solutions converge (Åström and Lundberg, 1994)]. If we project

population density, N, in discrete time steps from time t to $t + 1$ (for convenience we imagine yearly), then the growth rate of a plant population subject to herbivory can be described by:

$$N_{t+1} = (1 - p)(s_a + s_j B(D, N))N_t + p(s_a + s_j B(D, N))N_t D. \qquad (1)$$

In equation (1), population growth rate is determined by yearly survival rate, s_i, and per capita fecundity, B. Mature reproducing plants (adults) survive at rate s_a and plants that have not yet reached reproductive maturity (juveniles) survive at rate s_j. Annual plants become an important special case when $s_a = 0$. The parameter p is the probability of attack, $0 \leq p \leq 1$, and represents the ecological context for eco-evolutionary feedbacks in this model. The defence level, D, varies between zero and 1. When $D = 0$, zero resources are invested in defence; when $D = 1$, a maximum amount is invested, constrained by some minimum reserve for maintenance and growth.

Per capita fecundity in the model is under both ecological and evolutionary control and is both negatively density-dependent and negatively affected by investments in defence (D). We assume that investments in defence compromise fecundity. Biomass growth rate, survival, competitive ability, nutrient acquisition, and other crucial traits are likely involved in the feedback between ecology and evolution, but we choose to build a general model with simple and uncomplicated assumptions. The expression for per capita fecundity is:

$$B = (a - \beta D - cN), \qquad (2)$$

where a is maximum fecundity, β scales the defence investment into reduced fecundity, and c is the strength (slope) of density dependence.

In a completely safe environment with no risk of herbivory ($p = 0$), the right-most term of the right-hand side (RHS) of equation (1) also becomes zero. Population growth is then only dictated by the remaining parts of the RHS, which is a fixed growth rate reduced by the factor βD, the investment in defence. If the risk of herbivory is zero, then D should be zero. If, on the other hand, $p = 1$, attack is certain and only the right-most term of equation (1) contributes to population growth. If $D = 0$, there will be no population growth at all. Some level of defence is required for the population to increase.

To determine the value of defence investment, D, that maximizes per capita population growth (fitness), divide both sides in equation (1) by N_t (so the RHS equals per capita population growth rate). Calculate the first derivative of that fitness expression with respect to D, set the derivative equal to zero (to ensure that it represents the extreme point of the fitness function with respect to D), and solve for D – the optimal defence level. The optimal defence level at this stage is a function of all parameters, including population density, N, which also depends on ecological circumstances. In agreement with the results of Åström and Lundberg (1994), one can conclude quite intuitively that increased risk, decreased defence cost, and increased maximum fecundity (that can at least partially compensate for the trade-off with investment in defence) all contribute to an increased optimal defence level.

Åström and Lundberg's (1994) analysis revealed an interesting life-history twist, namely the demographic importance of the ratio between the survival of mature and immature individuals. The optimal defence level (D^*) is proportional to the ratio of adult to juvenile survival – the larger that ratio, the higher the optimal defence level: $D^* \propto (s_a/s_j)/2$ (see Åström and Lundberg, 1994, for details). Thus, annual plants are expected to have lower defence levels than perennials. This aspect of the model agrees with the observation that increased adult longevity in woody plants is associated with higher defence levels (Loehle, 1988; Zangerl and Bazzaz, 1992).

We wish to know whether Åström and Lundberg's (1994) solution is evolutionarily stable. We thus extend the model with an evolutionary invasion analysis (e.g. Otto and Day, 2007) to determine whether the optimal solution (i) is attainable through gradual adaptive trait evolution (Eshel and Sansone, 2003) that includes, implicitly, the potential for phenotypic plasticity, and (ii) cannot be invaded and replaced by some alternative strategy value. Equation (1) serves both purposes by considering how the optimal value of plant defence is influenced by density and frequency dependence (ecology), and how the level of plant defences affects equilibrium population size.

Figure 5 displays the evolutionary analysis as a pairwise invasibility plot (Geritz *et al.*, 1998). For resident strategy values below approximately 0.6, mutant strategy values higher than the resident have positive fitness (indicated by the + sign in Fig. 5). For resident strategy values higher than approximately 0.6, mutant strategy values less than the resident have positive fitness. This eco-evolutionary optimum is thus both ESS (evolutionarily stable strategy) and convergent stable.

We complete the full eco-evolutionary analysis in Fig. 6 by plotting the equilibrium population density calculated from equation (1) against various defence investment levels (D). The optimal and evolutionarily stable defence level is indicated in the figure by a black dot. In this example, the peak of the equilibrium population density coincides with the eco-evolutionary solution. The evolutionarily stable solution (the black dot) fully matches the optimal ecological solution (maximum equilibrium population density).
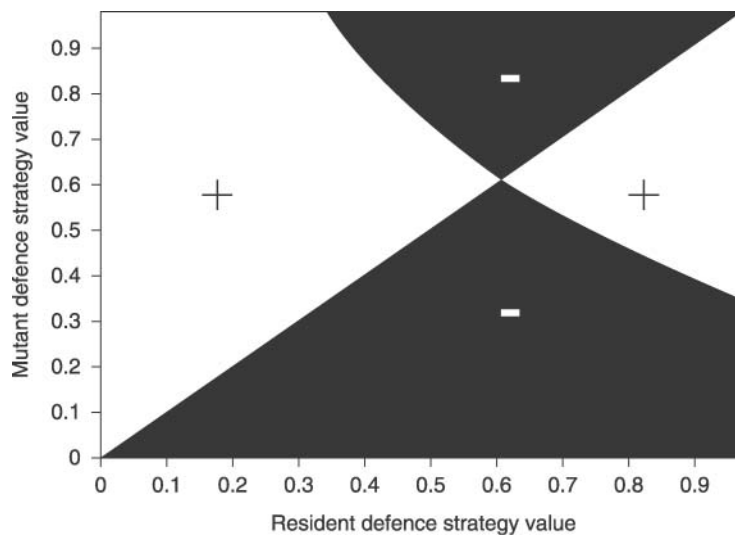
Fig. 5. The pairwise invasibility plot (Geritz *et al.*, 1998) for the defence game based on the model given by equation (1). Fitness is equal for the resident and the mutant strategies along the diagonal. Towards the left of the figure, strategy values of the mutant have higher fitness than the resident (indicated by + sign). Therefore, any mutant deviating from the resident with a higher defence level will be able to invade. Towards the right of the figure, values below the diagonal have higher fitness than the resident. Therefore, lower defence levels in the mutant are favoured. Eventually, the system comes to rest at a defence value around 0.6, i.e. corresponding to approximately slightly more than half of the maximal amount of resource available for the defence. The parameter values are: $s_a = 0.6$, $s_j = 0.3$, $a = 10$, $\beta = 5$, and $c = 0.75$.
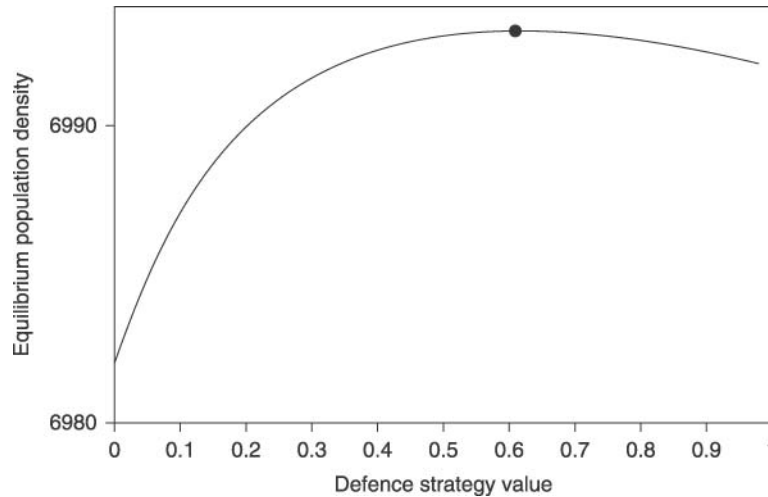
Fig. 6. The equilibrium population density as a function of the level of defence invested. The function has a maximum at an intermediate level of defence investment. That maximum corresponds to the optimal and evolutionarily stable defence level. Therefore, in this case acquiring the optimal defence solution through gradual adaptive evolution also maximizes population density. That is not necessarily the case in all systems (see text). Parameter values are as in the legend to Fig. 5.

In our example, the strategy that is adaptive to individuals maximizes population density. However, the eco-evolutionary solution need not match the 'best for the population' ecological solution (Kokko, 2011; Lundberg, 2013). Adaptive evolution can, under many different circumstances, lead to an extreme 'tragedy' of evolutionary suicide where strategies that are adaptive to individuals nevertheless cause extinction of the entire population (Parvinen, 2005; Morris and Lundberg, 2011). The adaptive evolution of individual strategies does not guarantee the well-being of the population or species.

Plant defence in space

Defence games, whether prey are mobile or not, take place in spatially complex arenas where an individual's best strategy depends on the strategies of neighbours. These strategies will depend in turn on ecological events dictating competitive ability, the probability of being detected by herbivores, and if detected, the probability of being damaged or eaten. Ecological determinants of population density affect the probability of detection in two ways: high plant density may attract herbivores, but there may be safety in numbers; high population density also increases competition and therefore the affordability of the defence.

We illustrate one possible outcome of a density-dependent trade-off between competitive ability and herbivore defence in Fig. 7. Here, we assume two habitats of different qualities from the point of view of the plants. Competition reduces fitness as density increases. Suppose now that two strategies can be played – being defended or not being defended. The undefended strategy generally gains competitive advantage, and equally so in both habitats. This competitive advantage plays out fine as long as the population density is reasonably high because there is safety in numbers. If detected, susceptibility is high, but the per capita probability of encounter with enemies is low. When population density is low, however, the
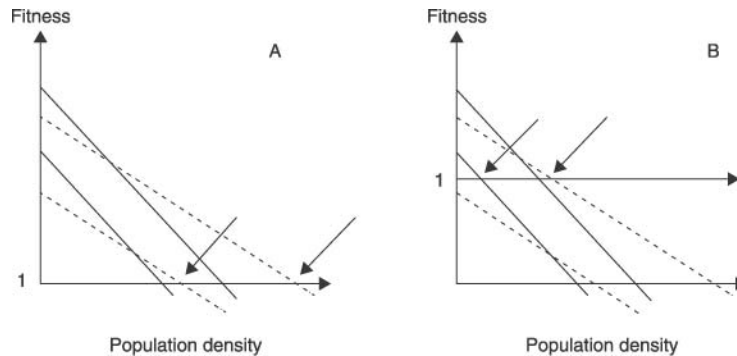
Fig. 7. (A) Fitness in two habitats as linear functions of population density. The upper pair denotes defended (solid line) and undefended (dashed line) individuals in the better habitat (higher fitness). The lower pair denotes fitness in the poorer habitat, again for defended and undefended individuals. At low population densities, the defended strategy is superior to (has higher fitness than) the undefended one. At equilibrium (arrows; fitness equals 1 in both habitats), the undefended strategy is superior in both habitats. (B) If the environment is made poorer overall such that all fitness functions are shifted downward (or the x-axis upward), then at equilibrium the defended strategy becomes superior in the poorer habitat whereas the undefended strategy remains superior in the better habitat.

probability of encountering herbivores will often be much higher, and undefended plants will have low fitness. Therefore, at low densities in both habitats, the defended strategy is superior, whereas at high densities the undefended strategy has the upper hand (Fig. 7A).

Imagine, at equilibrium (fitness equal to 1), that the undefended strategy populates both habitats according to an Ideal Free Distribution (Fretwell and Lucas, 1969). We now alter the ecological conditions such that the resources in the two imaginary habitats are considerably lower and thus sustain much lower population densities (Fig. 7B). In the richer habitat, the situation remains the same: defend yourself at low densities, and at high density rely on safety in numbers to beat the competition by being undefended. In the poorer habitat, however, equilibrium population density is now very low, making safety in numbers untenable: the trait optimum switches to being defended.

NUTRIENT FORAGING GAMES

The eco-evolutionary feedbacks between population size and adaptive strategies emerge strongly as plants compete below ground for nutrients or above ground for light. Optimal root production or optimal height depends on the density and strategies of neighbours.

Below-ground competition in plants as a game

Root production by plants provides a classic example of how a Tragedy of the Commons can occur through density and frequency dependence (Gersani *et al.*, 2001; Laird and Aarssen, 2005; Schenk, 2006). The roots of an individual plant result both in the harvest of unexploited nutrients, together with those that otherwise would have been harvested by the roots of others. The former adds to the collective harvest of all neighbouring plants, whereas the latter simply represents 'stealing' from one's neighbour (a kind of pilfering). In non-cognitively deciding how much to invest in roots, the individual plant sees both of these

sources of nutrient harvest – adding to the collective and stealing from the collective – as benefits, and it will invest accordingly. However, this now becomes a foraging game, as it incentivizes neighbours to increase their root production to steal back what otherwise would be lost. As a consequence, the neighbourhood of plants will overproduce roots beyond the collective optimum and suffer a collective reduction in seed yield or in surplus nutrients available for reproduction.

We couch this Tragedy of the Commons from root competition as an eco-evolutionary game by extending a model of Gersani *et al.* (2001) to include population size and dynamics. Let the per capita growth rate of a focal individual be given by:

$$G(v, u, N) = \frac{v}{v + u(N-1)} H(r) - cv - d, \tag{3}$$

where v is the root proliferation of the focal individual, u is the per plant root proliferation of neighbours, r is the sum of all roots in the neighbourhood ($r = v + (N-1)u$), N is the number of plants comprising a neighbourhood of competitors, c is the per unit cost of root production, and d is some mortality or loss rate expressed in units of nutrients harvested. The function $H(r)$ describes the total amount of nutrients harvested within the neighbourhood as a function of total roots. We assume that H increases monotonically and at a diminishing rate with respect to r (Gleeson and Fry, 1997). A given individual's share of the combined nutrient harvest, H, is directly proportional to its contribution to the total root mass.

Just like the herbivore defence fitness function that we solved before, we find potential evolutionary solutions, u^*, by taking the derivative of G with respect to v, setting this equal to 0, and then evaluating at $v = u^*$. The necessary condition for the evolutionarily stable root production is:

$$\frac{1}{N}\frac{\partial H}{\partial r} + \frac{(N-1)}{N}\frac{H}{r} = c, \tag{4}$$

where the left-hand side (LHS) represents the benefit to the plant of producing more roots and the RHS represents the cost. The benefit of producing roots represents a weighted average of the marginal benefit of more roots and the average benefit of roots. The marginal benefits and costs are explicitly ecological. The marginal benefit is weighted by the focal individual's fraction of the population, while the average benefit is weighted by the proportion of the neighbourhood comprised of other plants.

Because of diminishing returns to total harvest from total root production, the average nutrient uptake per root will always be higher than the marginal uptake. Thus at u^* the total root production, $r = u^*N$, will increase as N goes from 1 to ∞, even as the root production per plant, u^*, declines with N. Furthermore, per capita growth rate declines as density goes from one plant to many. This decline occurs not only because the plants must share the nutrient harvest, but also because the plants overproduce roots beyond the value that would maximize collective profit. Collective profit is maximized if the collective production of roots, r, balances marginal uptake with marginal costs. Ideally, the collection of plants should behave as just one plant to maximize collective profit. However, restrained root production is not evolutionarily stable and can be invaded by 'cheaters' (Hamilton, 1967; Morris *et al.*, 2001), and as all plants respond in kind the inevitable Tragedy of the Commons ensues as the ESS.

The equilibrium population size occurs when per capita growth rate (or net profit per plant) is zero. Setting $G = 0$ and rearranging gives:

$$\frac{H}{r} = c + \frac{d}{u}. \tag{5}$$

Equation (5) is in implicit form since the population size of plants influences total root production, r, the individual root production, u, and total nutrient harvest, H. But several general results emerge. If H is a smoothly decelerating function that reaches an asymptote at R (total available nutrients for harvest), then N^* can never be greater than R/d. The equilibrium neighbourhood density of plants will decrease with c and even more rapidly in d, and will increase with uptake capacity of a unit of roots.

Root competition is largely symmetric in the sense that each root regardless of source has similar access to the nutrients within its neighbourhood. On a per root basis, a larger plant does not necessarily have an advantage over a plant with a smaller root mass, or vice versa. Not so with stems and leaves competing for light. Competition for light is highly asymmetric where the taller or leafier individual captures a disproportionate amount of the light (Wilson, 1988; McNickle and Dybzinski, 2013). A number of models have examined this asymmetry (Koch *et al.*, 2004; Kokko, 2007) and conclude that such asymmetric competition results in diverting resources away from reproduction and seed production and towards stem tissue, whose sole purpose is to reduce and/or preclude shading by neighbours.

Competition in plants as a game of height

We can model the asymmetric competition for light in much the same way as we did for roots by making one's share of the collective resource harvest proportional to a power α of a plant's root production where $\alpha > 1$. For symmetric competition simply let $\alpha = 1$. This generalizes the previous fitness function to be:

$$G(v, u, N) = \frac{v^\alpha}{v^\alpha + u^\alpha(N-1)} H(r) - cv - d. \tag{6}$$

In solving for the necessary conditions for the evolutionarily and ecologically stable solutions to this eco-evolutionary game, we get the following conditions for u^* and N^*, respectively:

$$\frac{1}{N}\frac{\partial H}{\partial r} + \frac{\alpha(N-1)}{N}\frac{H}{r} = c. \tag{7}$$

There is a remarkable simplicity and similarity to the case of symmetric competition in roots, except that the average nutrient uptake (second term on the LHS) has been magnified by the asymmetry, α. Compared with when competition is symmetric, we see a greater weighting towards pre-emption (the second term on the LHS) and this weighting towards pre-emption increases with α. In fact, it can result in a near runaway selection for what might seem like utterly counterproductive values of 'r' save for the fact that as a game all plants must exaggerate their investment in stems and leaves, and respond in kind to remain in the game. Furthermore, it can be shown that this race for light, with its emphasis towards stem and leaves, results in a smaller equilibrium population size and so N^* declines with the magnitude of the asymmetry α. Hence, below-ground competition (symmetric: $\alpha = 1$)

should select for smaller and more abundant plants than competition for light ($\alpha \gg 1$). It is not surprising then that extreme competition for light results in a few large trees where the majority of the nutrients and carbon go into growing and maintaining a stem and leaves.

We can consider a limiting case by assuming that essentially all of the resources get harvested ($H = R$ and $dH/dr = 0$). This is now simply a game of pilfering. We can explicitly solve for per plant root investment and resulting equilibrium population size.

$$N^* = \frac{-R(\alpha - 1) + \sqrt{R^2(\alpha - 1)^2 + 4\alpha Rd}}{2d}, \tag{8}$$

$$r^* = \frac{R - dN^*}{c}. \tag{9}$$

In this extreme case, u represents investment in non-productive tissues such as height and woody stem. Hence collective yield and population size would be maximized by $u = 0$ and $N^* = R/d$. But, there is strong selection to pre-empt the resources of one's neighbours. So as the number of neighbours increases, collective investment in non-productive tissue increases also. The equilibrium population size of plants declines with the asymmetry. As α goes from 0 towards ∞, we see N^* go from $(R/d)^{0.5}$ to 1, and total investment in non-productive tissue goes from $r^* = (R - \sqrt{Rd})/c$ to R/c. As competition for light becomes increasingly asymmetric, we expect to see fewer and larger 'trees'.

DISCUSSION

We chose to model three universal properties: the needs for habitat, safety, and nutrients. Our models reveal not only that the properties are the products of evolutionary games, but also that the games frequently create a Tragedy of the Commons in which individual advantage comes at the expense of reduced population growth rate. It is nevertheless informative to explore the degree to which strategies of space use, for example, are independent of, complementary with, or antagonistic to those associated with defence, foraging for nutrients, and competing for light. If the strategies are independent of one another, then the metaphor of an adaptive landscape poses markedly divergent 'watersheds' that direct each strategy upwards to its adaptive peak (or downwards to the valley bottom of its invasion landscape). Complementary strategies march arm-in-arm along a single adaptive slope, while antagonistic strategies can tumble helter-skelter through a pock-marked landscape where the fitness gains by one strategy are invariably matched by the losses of another. For instance, high resource availability may result in a high plant density that increases the value of site pre-emption, leads to low plant defences, and over-investment in stems, leaves, and roots. The negative covariance between plant defences and the intensity of the Tragedy of the Commons for nutrients would have opposite feedbacks on plant population size and habitat selection – lower defence permits higher densities, while over-investment in roots, stems, and leaves encourages lower densities, and higher rates of herbivory. In sum, directed versus undirected seed dispersal (habitat selection), directed or undirected vegetative growth (site selection within habitats), plant defences, and investment in roots, stems, and leaves in response to nutrient foraging games, likely become co-adapted.

We can imagine cases that fit each scenario. In rich environments, our models suggest that habitat selection alone can provide sufficient defence against enemies by dilution, crypsis, mimicry, and cooperatively sharing information about risks (Danell *et al.*, 1991; Pearse *et al.*, 2013). Here, the strategies are complementary. In poor environments, however, two few individuals share the risk, and there is no option other than for each individual to invest in its own defence.

Opportunities for antagonistic strategies are compounded when we add competition for nutrients to the panoply of eco-evolutionary games. Foraging games are frequently dominated by a Tragedy of the Commons where yields gained by pre-emptive resource harvest, and losses accrued by waiting, cause adaptive individuals to invest more than they otherwise should. Optimal foraging for nutrients and light is often less about reaching the highest fitness possible than it is about making the best of a bad deal. Though traits may differ, all plant taxa share producer–scrounger games, games of resource and space pre-emption, arms races, and resource pilfering games. We simply see them differently because we become mesmerized by proximal traits such as the haustoria of root parasites, floral mimicry in orchids, the massive root systems of prairie plants, and the majesty of gallery forests. Yet, natural selection does not. Selection remains the same while the taxa-specific traits vary.

Such frequency- and density-dependent selection can and often does promote multiple strategies and their associated biodiversity. When we contemplate the stability of those co-existing strategies and taxa, we must also recognize that the ecological and evolutionary stability of our models more typically represent attractors for selection than inevitable stable solutions. Landscapes identifying ecological and evolutionary stability rise, fall, twist, and shift shape with the exigencies imposed by organisms living in stochastic environments. Sometimes, as in games of defence associated with varying densities of habitat selectors, a mixed strategy emerges that is contingent on population density (defend at low density, hide at high density). Either a pure hide or pure defend strategy could nevertheless evolve if the population density is stable through time and space.

We acknowledge that each game is likely to influence other density- and frequency-dependent processes external to our models. Copious production of wind-dispersed seeds may enhance arrival on the best sites for germination and growth, but only if the ensuing parent–offspring conflict is resolved in favour of adults. Competition and defence strategies will be compromised by conflicting demands associated with pollination and reproduction. Although 'complete' eco-evolutionary models would include these and other effects and interactions (e.g. Falster and Westoby, 2003), our simplified versions provide substantial fodder to be digested by theory and empirical testing.

Our models of competition for light and nutrients, for example, highlight an inherent peril of density- and frequency-dependent evolution. Adaptive evolution by individuals often creates a Tragedy of the Commons where self-interest causes all individuals to be less efficient than they otherwise would be. In extreme cases, self-interest causing the tragedy leads to resource collapse and population extinction (Rankin *et al.*, 2007). Resolution of the tragedy typically occurs through one or more of four routes: exclusion, cooperation, coercion, and diminishing returns (Morris *et al.*, 2001; Rankin *et al.*, 2007). Plants practise each mechanism at multiple scales. Clones produced through selfing, tillers, suckers, rhizomes, and stolons allow single genotypes to monopolize local resources. Modular structure enables plants to simultaneously exploit a variety of local opportunities while sharing interest in the total production of offspring. Spatial dispersion limits herbivory (e.g. Danell *et al.*,

1991; Hjältén *et al.*, 1993). But, in the end, the Tragedy of the Commons played by terrestrial plants in their roots, stems, and leaves may be the unintentional and wonderful source of invertebrate and vertebrate biodiversity through foliage height diversity, greater amounts of overall plant tissues, and more varied forms of plant tissues distributed more broadly in time and space.

As we contemplate a human-dominated planet and global climate change, the processes of adaptation will remain the same. To anticipate these changes to ourselves and the other denizens of this planet, we will need to heed the lessons that plants can teach us about eco-evolutionary games.

REFERENCES

Agrawal, A.A. 2011. Current trends in the evolutionary ecology of plant defence. *Funct. Ecol.*, **25**: 420–432.

Alberti, M. 2014. Eco-evolutionary dynamics in an urbanizing planet. *Trends Ecol. Evol.*, **30**: 114–126.

Apaloo, J., Brown, J.S. and Vincent, T.L. 2009. Evolutionary game theory: ESS, convergence stability, and NIS. *Evol. Ecol. Res.*, **11**: 489–515.

Åström, M. and Lundberg, P. 1994. Plant defence and stochastic risk of herbivory. *Evol. Ecol.*, **8**: 288–298.

Danell, K., Edenius, L. and Lundberg, P. 1991. Herbivory and tree stand composition: moose patch use in winter. *Ecology*, **72**: 1350–1357.

Dybzinski, R., Farrior, C., Wolf, A., Reich, P.B and Pacala, S.W. 2011. Evolutionarily stable strategy carbon allocation to foliage, wood, and fine roots in trees competing for light and nitrogen: an analytically tractable, individual-based model and quantitative comparisons to data. *Am. Nat.*, **177**: 153–166.

Eshel, I. and Sansone, E. 2003. Evolutionary and dynamic stability in continuous population games. *J. Math. Biol.*, **46**: 445–459.

Falster, D.S. and Westoby, M. 2003. Plant height and evolutionary games. *Trends Ecol. Evol.*, **18**: 337–343.

Fretwell, S.D. and Lucas, H.L., Jr. 1969. On territorial behavior and other factors influencing habitat distribution in birds. *Acta Biotheor.*, **14**: 16–36.

Geritz, S.A.H., Kisdi, E., Meszena, G. and Metz, J.A.J. 1998. Evolutionarily singular strategies and the adaptive growth and branching of the evolutionary tree. *Evol. Ecol.*, **12**: 35–57.

Gersani, M., Brown, J.S., O'Brien, E.E., Maina, G.M. and Abramsky, Z. 2001. Tragedy of the commons as a result of root competition. *J. Ecol.*, **89**: 660–669.

Gleeson, S.K. and Fry, J.E. 1997. Root proliferation and marginal patch value. *Oikos*, **79**: 387–393.

Hardin, G. 1968. The tragedy of the commons. *Science*, **162**: 1243–1248.

Hjältén, J., Danell, K. and Lundberg, P. 1993. Herbivore avoidance by association: vole and hare utilization of woody plants. *Oikos*, **68**: 125–131.

Hamilton, W.D. 1967. Extraordinary sex ratios. *Science*, **156**: 477–488.

Koch, G., Sillett, S., Jennings, G. and Davis, S. 2004. The limits to tree height. *Nature*, **428**: 851–854.

Kokko, H. 2007. *Modelling for Field Biologists and Other Interesting People*. Cambridge: Cambridge University Press.

Kokko, H. 2011. Directions in modelling partial migration: how adaptation can cause a population decline and why the rules of territory acquisition matter. *Oikos*, **120**: 1826–1837.

Křivan, V., Cressman, R. and Schneider, C. 2008. The ideal free distribution: a review and synthesis of the game-theoretic perspective. *Theor. Pop. Biol.*, **73**: 403–425.

Laird, R.A. and Aarssen, L.W. 2005. Size inequality and the tragedy of the commons phenomenon in plant competition. *Plant Ecol.*, **179**: 127–131.

Levins, R. 1962. Theory of fitness in a heterogeneous environment. I. The fitness set and adaptive function. *Am. Nat.*, **96**: 361–373.

Loehle, C. 1988. Tree life history strategies: the role of defenses. *Can. J. For. Res.*, **18**: 209–222.

Lundberg, P. 2013. On the evolutionary stability of partial migration. *J. Theor. Biol.*, **321**: 36–39.

McNickle, G.G. and Brown, J.S. 2012. Evolutionarily stable strategies for nutrient foraging and below-ground competition in plants. *Evol. Ecol. Res.*, **14**: 667–687.

McNickle, G.G. and Brown, J.S. 2014. An ideal free distribution explains the root production of plants that do not engage in a tragedy of the commons game. *J. Ecol.*, **102**: 963–971.

McNickle, G.G. and Dybzinski, R. 2013. Game theory and plant ecology. *Ecol. Lett.*, **16**: 545–555.

Morris, D.W. 1994. Habitat matching: alternatives and implications to populations and communities. *Evol. Ecol.*, **8**: 387–406.

Morris, D.W. 2011. Adaptation and habitat selection in the eco-evolutionary process. *Proc. R. Soc. Lond. B: Biol. Sci.*, **278**: 2401–2411.

Morris, D.W. and Lundberg, P. 2011. *Pillars of Evolution*. Oxford: Oxford University Press.

Morris, D.W., Lundberg, P. and Ripa, J. 2001. Hamilton's rule confronts ideal-free habitat selection. *Proc. R. Soc. Lond. B: Biol. Sci.*, **268**: 291–294.

O'Brien, E.R. and Brown, J.S. 2008. Games roots play: effects of soil volume and nutrients. *J. Ecol.*, **96**: 438–446.

Otto, S.P. and Day, T. 2007. *A Biologist's Guide to Mathematical Modeling*. Princeton, NJ: Princeton University Press.

Parvinen, K. 2005. Evolutionary suicide. *Acta Biotheor.*, **53**: 241–264.

Pearse, I.S., Hughes, K., Shiojiri, K., Ishizaki, S. and Karban, R. 2013. Interplant volatile signalling in willows: revisiting the original talking trees. *Oecologia*, **172**: 869–875.

Pelletier, F., Garant, D. and Hendry, A.P. 2009. Eco-evolutionary dynamics. *Phil. Trans. R. Soc. Lond. B: Biol. Sci.*, **364**: 1483–1489.

Pulliam, H.R. 1988. Sources, sinks, and population regulation. *Am. Nat.*, **132**: 652–661.

Pulliam, H.R. and Danielson, B.J. 1991. Sources, sinks, and habitat selection: a landscape perspective on population dynamics. *Am. Nat.*, **137**: 169–184.

Rankin, D.J., Bargum, K. and Kokko, H. 2007. The tragedy of the commons in evolutionary biology. *Trends Ecol. Evol.*, **22**: 643–651.

Rosenzweig, M.L. 1987. Density-dependent habitat selection: a tool for more effective population management. In *Modeling and Management of Resources Under Uncertainty* (T. Vincent, Y. Cohen, W.J. Grantham, G.P. Kirkwood and J.M. Skowronski, eds.), pp. 98–111. Berlin: Springer.

Roughgarden, J., Gaines, S. and Pacala S. 1987. Supply side ecology: the role of physical transport processes. In *Organization of Communities Past and Present* (J.H.R. Gee and P.S. Giller, eds.), pp. 491–518. Oxford: Blackwell Scientific.

Schenk, H.J. 2006. Root competition: beyond resource depletion. *J. Ecol.*, **94**: 725–739.

Shmida, A. and Ellner, S. 1984. Coexistence of plant species with similar niches. *Vegetatio*, **58**: 29–55.

Wilson, J.B. 1988. Shoot competition and root competition. *J. Appl. Ecol.*, **25**: 279–296.

Zangerl, A.R. and Bazzaz, F.A. 1992. Theory and pattern in plant defense allocation. *Am. Nat.*, **132**: 363–391.