**INTRODUCTION**

Biotic interactions among plants and other taxa influence plant fitness, and this influence depends on both the density of organisms and the frequencies of the different types of organisms that interact (De Deyn & Van der Putten 2005; Bever et al. 2010; Johnson 2011; Thorpe et al. 2011). These biotic interactions include competition for resources (Grime 1979; Tilman 1982; Wilson 1988; Gasper & Jackson 1997; Novoplansky 2009), attack by enemies (e.g. herbivory, disease) (Oksanen 1990; van der Heijden et al. 2008; Agrawal 2011; Johnson 2011; de Kroon et al. 2012) and investment in a diverse set of mutualisms (Hockesma & Bruna 2000; Denison et al. 2003; Bshary & Bronstein 2004; Kiers & Denison 2008; Archetti et al. 2011). Along with the abiotic environment, these biotic interactions shaped – and continue to shape – the ecology and evolution of plants. This web of biotic interactions may be viewed as an evolutionary game, and here, we review the game theoretical approaches that have been applied to questions in plant ecology. First, however, we will explain the way in which the contribution of evolutionary game theory is unique among the conceptual tools employed by plant ecologists.

Models of plant strategies differ widely depending on the system under study, the question asked, or the mechanisms of interest. However, most models of plant strategies share some general features that we outline here. (1) First, models typically assume or solve for some optimal strategy or trait value that maximises plant fitness (Fig 1a). The idea is that low investment in a trait can present a cost in the form of some missed opportunity, whereas high investment in a trait can present a cost in terms of resources that are allocated to the trait beyond what is necessary. (2) Models also capture the effects of some external factor that affects plant fitness either negatively (e.g. enemy attack, resource competition) or positively (e.g. facilitation, mutualism) (Fig 1b). Nearly all models that seek to identify plant strategies include these two basic features.

![Figure 1](image-url) Many models have nested combinations of four factors depending on whether they are density-independent (a, b), density-dependent (c–d) or density- and frequency-dependent (a–d). (a) An optimal strategy is assumed. (b) Some external factor is included (e.g. neighbours, nutrients, enemies, mutualism) that impacts plant fitness either positively or negatively. For simplicity, we show linear relationships. (c) Density-dependent models include population density which can have positive or negative effects. (d) Frequency-dependent models allow the strategies used by neighbouring plants to have impacts on the focal plant’s fitness. These are often negative (dashed), but might be positive in some regions of parameter space (e.g. hump-shaped solid). All four of the factors depicted in this Figure (a–d) may interact to influence fitness.
Game theoretical models include these two features (Fig 1a, b), but also generally include two additional ecological interactions. (3) Population density might alter the success of any given strategy either positively or negatively (Fig 1c). Pollination provides an example of positive density-dependence when success is contingent on a high density of conspecifics (Allison 1990). Alternatively, competition provides an example of negative density-dependence when per capita resource capture declines with increasing plant density (Westoby 1984). (4) The frequency of other strategies used by the neighbours of a focal plant might influence the fitness achieved by the focal plant (Fig 1d). For example, the success of an insect-pollinated focal plant might depend on the frequency of other floristic traits or alleles in a physiological self-incompatibility system that exists in the population (Marshall & Folsom 1991). Similarly, competition may be influenced by the strategies (e.g. height, root length density) used by neighbours (Novoplansky 2009; Mommer et al. 2010; Thorpe et al. 2011). Our observation is that these four features are common among game theoretical models in plant ecology; (1) an optimal strategy value (Fig 1a), (2) an external biotic factor limits fitness (e.g. competition, enemy attack or mutualism), (3) population density explicitly alters focal plant fitness (Fig 1c) and (4) neighbour strategies explicitly influence focal plant fitness (Fig 1d). In contrast, only the first two features are common among non-game theoretical models in plant ecology.

Theoretical ecologists distinguish fitness effects from three types of processes (Roughgarden 1971): (1) density-independent, (2) density-dependent and (3) frequency-dependent. On the basis of the generalities identified above, we argue that density-independent, density-dependent or frequency-dependent models fall into nested combinations of the four relationships described above. First, density-independent models are the simplest, and envision that there is an optimal trait and some external factor (Fig 1a, b), but plant fitness is modelled as if it is independent of the presence or traits of neighbours. Second, a density-independent model can be made density-dependent by allowing fitness to depend upon the number of individuals interacting (e.g. Fig. 1a–c), but such models assume that all individuals use the same strategy. Third, a density-dependent model can be made frequency-dependent by relaxing this assumption and specifically allowing alternative strategies to interact and influence each other’s fitness (Fig 1a–d). As we review below, many models in plant ecology are explicitly built upon a density-independent framework, with the effects of density- and frequency-dependence only implicitly included. The potential pitfall of this implicit approach is that it allows the modeller to bias the model behaviour according to preconceived ideas about the effects of density- and frequency-dependence that may or may not be correct.

As we review below, explicitly including these important ecological processes in game theoretical models often produces drastically different hypotheses about plant strategies that—if true—have important implications for our understanding of plant ecology.

In the following section, we provide a brief non-mathematical summary of important game theoretical concepts. The rest of the review is broken into three sections that focus on models of competition, enemies and mutualisms respectively. Throughout, we emphasise that a game theoretical perspective is already implicitly embedded, even if not explicitly modelled in many schools of plant ecology and that plant ecologists already have many points of contact with game theory. We conclude each section by highlighting empirical and theoretical gaps in our understanding of the evolutionary games in plant ecology.

**Game theory essentials for the plant ecologist**

Books have been written about evolutionary game theory (Smith 1982, Weibull 1997, Vincent & Brown 2005), and a number of concise, yet still lengthy articles have summarised its major themes and mathematics (Riechert & Hammerstein 1983; Abrams et al. 1993; Vincent et al. 1993; Falster & Westoby 2003; McGill & Brown 2007; Apaloo et al. 2009; Ripa et al. 2009). Such detail is beyond the scope of our essay, and here, we restrict our brief, non-mathematical summary to those concepts that are immediately relevant for the application of game theory to plant ecology and that are often glossed over in its more general treatments.

The concept of the Evolutionarily Stable Strategy (ESS) is central to game theory in ecology. An ESS is a strategy employed by a community in dynamic equilibrium that resists a challenge (or an ‘invasion’ in the theoretical ecology sense) from any new strategy that is introduced or invades at low density (Riechert & Hammerstein 1983; Vincent & Brown 2005; Apaloo et al. 2009). These strategies can be thought of as peaks on an adaptive landscape, where alternative strategies have lower fitness and thus evolution or community assembly is constantly driven towards the ESS peak (Fig. 2). Although some traits are adaptive, it is important for ecologists to recognise that others might not be adaptive. Despite the singular ‘strategy’ in the term ESS, an ESS solution may be comprised of a single strategy or a diversity of strategies (Fig. 3). The idea is that both evolution and community assembly tend to drive communities towards an ESS as suboptimal strategies are replaced, a tendency that is termed convergence stability (Apaloo et al. 2009; Ripa et al. 2009; Pintor et al. 2011). Game theorists typically define ‘fitness’ as the per capita population growth rate of a strategy, which can take on any value – positive or negative – depending on the context and
would equal zero at equilibrium (i.e. the population is no longer growing or shrinking) (Vincent & Brown 2005).

Game theoretical analyses in plant ecology typically present a relevant model of a plant strategy, along with its ESS solution, which describes in ecological terms the strategy that will resist any challenge (e.g. Oksanen 1990; Augner et al. 1991; Gersani et al. 2001; Dybzinski et al. 2011). Most studies also demonstrate convergence stability of that solution, which ensures the ESS can be reached from any colonising strategy and from any direction, through evolution, species introductions or plasticity (Apaloo et al. 2009; Ripa et al. 2009).

The use of the word ‘Strategy’ in the term ESS contains a potentially useful ambiguity that is also, unfortunately, potentially confusing in plant ecology. The useful ambiguity embraces the fact that plant traits are sometimes genetically fixed, sometimes plastic or most often a combination of both (Sultan 2000; de Kroon et al. 2009). Game theoretical models are equivocal in this regard, and it is up to the plant ecologist to interpret the model predictions through the lens of biological reality to determine the degree to which the traits that comprise the ESS are fixed or plastic. Confusion can arise because this determination is seldom made very boldly, and authors may assume one thing while readers may assume another.

Game theory is often associated with behaviour, but it need not be, and evolutionary game theory can apply equally to fixed or plastic traits. The main difference between models of fixed and plastic traits is that they have different implications for the mode and tempo of plant community dynamics. A community comprised of individuals with fixed traits will have to cycle through generations for natural selection, acting on either extant variation or the immigration and mutation of new types, to arrive at the ESS from arbitrary starting conditions. In contrast, if a trait is plastic, a community may rapidly arrive at the ESS from arbitrary starting conditions as each individual assesses and responds to its environment in ecological time.

Like almost every model in ecology and evolution, evolutionary game theory assumes that evolution is an equilibrial process. However, the danger is that this can undermine the credibility of game theoretical analyses in the eyes of a modern ecologist, who knows that the discipline’s early assumptions of equilibrium have been thoroughly rejected. Indeed, there is substantial evidence suggesting that systems in ecology rarely reach equilibrium (Caswell 1978; Deangelis & Waterhouse 1987), and we want to be clear that our view is that evolution by natural selection is no exception. Countless stochastic and context-dependent processes can shift through time and space, causing disturbances that prevent a system from ever reaching equilibrium.

However, species with traits produced and maintained by natural selection undoubtedly exist. How then should we sensibly model this process? We suggest that there is an underappreciated distinction between an equilibrial state and an equilibrial process. A system may never reach an equilibrial state and yet still be driven by an equilibrial process. That is, natural systems can still move towards an ever shifting equilibrium even if stochastic processes and shifting context dependency make it unlikely that an equilibrial state will be reached. Further, this stochasticity can be incorporated into models if it is desirable to explicitly ask questions about stochasticity. For the purposes of this paper, it is perhaps sufficient to recognise that the equilibrium requirements of game theoretical explanations of evolved strategies are no more stringent than any other explanation of evolved strategies – all such explanations require relatively consistent, but not necessarily continuous, selection pressure that rises above the stochasticity of real systems over long time periods.

Having reviewed the essential concepts of an ESS, convergence stability, the relevance of game theory for both fixed and plastic traits and assumptions regarding equilibrium, we now examine the existing game theoretical literature in plant ecology for understanding plant interactions with competitors, enemies and mutualistic partners.

RESOURCE COMPETITION AND ALLOCATION

Plants often compete for limiting resources, such as light, water and soil nutrients (Grime 1979; Tilman 1982; Wilson 1988; Casper & Jackson 1997). We define resource competition as a negative interaction between individual plants mediated by a limiting resource that, once intercepted by a particular individual, is not available to other individuals. Following the emphasis in the literature, we will focus on strategies for tissue allocation (e.g. allocation to height, leaves or roots), and due to the differences in resources and strategies above- and belowground, we discuss shoot and root competition separately.

Aboveground competition for light

Height-structured competition for light is the original (Givnish 1982) and perhaps least controversial example of game theory in plant ecology (Oksanen 1990; Givnish 1995; Falster & Westoby 2003). The following simple thought experiment illustrates its dynamic: Imagine a crowded stand of uniformly sized plants growing at approximately the same rate. As the plants grow close to one another, the advantage gained by a slightly taller plant is asymmetrical: the taller plant secures light with which to conduct photosynthesis and simultaneously deprives its neighbours of that light. The winners are thus determined by the frequencies of height strategies in the community. At geological time scales, this is the arms race that has raised the descendants of a humble alga upon the stupendous stilts of the giant redwoods. At diurnal time scales, this is the process that causes plastic plants to elongate their stems when they sense shifts in the red to far-red ratio of light caused by taller neighbours (Ballare et al. 1991; Dudley & Schmitt 1996; Murphy & Dudley 2007). However, allocation to height is not without costs, most conspicuously in the resources used to build a stem, which might otherwise have been used for reproduction, and less conspic-

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urally in risks associated with being taller, such as wind throw, xylem cavitation or increased herbivory (Oksanen 1990; Ryan & Yoder 1997).

This thought experiment highlights the importance of frequency-dependence in height-structured competition. In terms of absolute height, the tallest tree in a forest has no more access to light than does a diminutive herb in a nearby clearing. Instead, competition for light depends on relative height, and the most competitive height for a plant is just barely above that of its neighbours, which affords it an advantage in light capture but also minimises the costs associated with height (Givnish 1982; Oksanen 1990; Ballare et al. 1991; Falster & Westoby 2003; Murphy & Dudley 2007). This relativity in the success of different strategies depending on which strategies are interacting is a key component of evolutionary game theory. It is worth noting that similar game-theoretical height-structured competition may occur among plants competing for pollinators, where the highest presentation is rewarded with the greatest pollination success.

Except as an pre-adaptation to fire or herbivores (Oksanen 1990), plant allocation to height is an arms race or – as it is increasingly termed – a Tragedy of the Commons (TOC) (Givnish 1982, 1995; Falster & Westoby 2003). If individual plants could somehow ‘agree’ not to engage in height-structured competition and instead formed communities that were short sheets of ground-level foliage (as is approximately the case among stands of close relatives (Givnish 1982; Anten & During 2011)) or if plants could somehow punish neighbours that attempted to grow taller (e.g. Givnish 1982), each plant would have more photosynthate to devote to other processes such as reproduction (King 1990). Indeed, the green revolution that has been credited with increasing crop seed and fruit yields worldwide was largely achieved by artificially selecting dwarf varieties of crop plants, which do not engage in an aboveground TOC (Brown 2001). These gains in fruit and seed yield illustrate how this TOC can come at an absolute cost to plants. However, natural selection cannot produce such agreeable dwarf strategies because once a ‘cheater’ grows taller; it gains an asymmetrical advantage in resource capture that outweighs the cost. Thus, all else equal, game theoretical analyses consistently predict increasing ESS height or ESS allocation to height under conditions that support higher plant densities, faster growth rates or both (Givnish 1995; Falster & Westoby 2003), whereas plants of shorter stature dominate poorer sites (Givnish 1982).

Although hardly a surprise in itself, the nuanced, game-theoretical explanation is perhaps surprising. Ecophysiological approaches to understanding plant height are density-independent and focus on proximate biophysical limits, such as hydraulic constraints (e.g. Ryan & Yoder 1997) or mechanical limitations (Niklas 2007). Conventional ecosystem approaches to understanding plant height are also density-independent and focus on abiotic correlatives, such as temperature (e.g. Way & Oren 2010) or atmospheric ozone (e.g. Wittig et al. 2009). Although appropriate within certain spheres of inquiry, these approaches omit the reason why allocation to height is selected. In contrast, a game theoretical approach to understanding height is explicitly density-dependent and frequency-dependent and explains height’s fundamental cause what drives species adapted to fertile sites to grow tall are the dire consequences of not keeping up with neighbours that cast deep shade (Givnish 1982; Iwasa et al. 1985; Falster & Westoby 2003). If nature is red in tooth and claw, so too is it shady under stem and branch.

Above, we focussed on tissue allocation to stem height. However, there is also a game-theoretical literature concerning the ESS strategies of leaf angle, leaf mass and leaf area index (LAI; cumulative leaf area per ground area) across environmental gradients and under different assumptions about self- vs. non-self-shading (Hikosaka & Hirose 1997; Schieving & Poorter 1999; Anten & Hirose 2001; Anten 2002; Anten & During 2011). Here, the consistent and general finding is also a TOC in which leaf physiology and morphology is predicted to be a compromise between a strategy that maximises the net photosynthetic return of the individual and a strategy that diminishes the net photosynthetic return of neighbours via shade. Under conditions where individuals hold light-interminating territories and most photosynthesize is produced using light coming from overhead (e.g. forest canopies), the TOC is minimised and leaf physiology and morphology is predicted to maximise the net photosynthetic return of the individual. However, when the foliage of different individuals is interleaved and/or significant photosynthate is produced using light that arrives at steep angles, competitive interindividual shading is predicted to reduce absolute net photosynthetic return of the individual (a TOC) by increasing specific leaf area (Schieving & Poorter 1999), LAI (Anten & Hirose 2001; Anten 2002) or horizontal leaf angle (Hikosaka & Hirose 1997).

Belowground competition for resources

Similar to models of optimal plant height, game theoretical models of active root investment (hereafter, simply ‘root density’) predict a TOC in root production (King 1990; Zhang et al. 1999; Brown 2001; Gersani et al. 2001; Craine 2006; O’Brien et al. 2007; O’Brien & Brown 2008; Dybzinski et al. 2011). The explanation is similar in each case: in the absence of competition (i.e. when the problem is properly framed as density-independent), the optimal root density is just enough to prevent leaching of any limiting belowground resources from the system. However, a plant that produced the minimal root density would be potentially susceptible to a challenge by a strategy that increased its root density beyond the minimum, allowing the challenger to pre-empt the resource supply. The situation is analogous to height-structured competition for light and highlights the frequency-dependent nature of competition; being taller is an advantage above-ground and having greater root density is an advantage below-ground against competitors that are shorter or have less root density respectively.

Greenhouse pot experiments have demonstrated a belowground TOC via the plastic behaviour of roots grown alone vs. with competitors (Maina et al. 2002; Mommer et al. 2010; Semchenko et al. 2010). In some cases, plants grown alone produced less per capita root mass with more per capita allocation to fecundity, whereas the plants that grew in competition produced more per capita root mass with less per capita allocation to fecundity. Many of these studies (e.g. Gersani et al. 2001; O’Brien et al. 2005) have been criticised on methodological grounds and future work should take care to avoid these methodological problems (see Laird & Aarsen 2005; Schenk 2006; Hess & de Kroon 2007; Semchenko et al. 2007 for detailed discussion of these methodological pitfalls). Furthermore, other studies found no evidence (Murphy & Dudley 2007; Semchenko et al. 2007; Cahill et al. 2010) or ambiguous evidence (O’Brien et al. 2005) of a belowground TOC via root plasticity. Clearly more data are needed to explore this hypothesis. It is also true that all experimental studies of a belowground TOC to date have focussed on competitive root allocation. 548 G. G. McNickle and R. Dybzinski Review and Synthesis
Models of plant allocation with respect to competition

There are some similarities between non-game theoretical and game theoretical models of plant strategies for competition. (1) Models find some optimal level of allocation either to aboveground or belowground tissues. That is, low allocation to tissues associated with resource capture can be costly in terms of missed foraging opportunities, whereas high allocation can be costly because it wastes resources on unnecessary tissue production (Fig. 4a). (2) Models also assume that increasing resource levels (e.g. full sun > shade, nutrient-rich soil > nutrient-poor soil) have a positive effect on plant fitness (Fig 4b). Thus, under this density-independent framework, the only effect of neighbours is through changes to resource levels (shade, nutrient depletion). That is, neighbours cast shade, or cause a reduction in soil nutrients, and so a focal plant that does not respond to neighbours is simply smaller or less fecund because it lost some resources. This density-independent framework is the simplest necessary to capture plant responses to competitors, and indeed this may be all the relevant processes in some systems (e.g. Givnish 1982).

However in other systems, density- and frequency-dependence may become important and game theoretical models can extend this framework to incorporate these processes. Such models still find (1) optimal tissue allocation (Fig 4c), and (2) the idea that higher levels of resources have positive effects on plant fitness (Fig 4d) – although the inclusion of density- and frequency-dependence causes a TOC that alters these curves from the density-independent version. Two additional variables are included; (3) first, plant growth is almost always negative density-dependent (Fig 4e), and allocations strategies should be expected to change as a function of the density of plants. (4) Second, frequency-dependence is included by recognising that neighbours employ a variety of strategies, and that different strategies can have different effects on the focal plant’s fitness (Givnish 1982, 1995; Gersani et al. 2001; Dybzinski et al. 2011). For aboveground competition, this effect is size asymmetrical – shorter neighbours have almost no effect on light interception of the focal plant, while taller neighbours can have extremely negative effects by casting shade on the focal plant (Fig 4f – dashed). Without this frequency-dependent effect, the optimal height of a plant is as close to 0 as is possible (Fig 4a). Alternatively, for belowground competition, this effect is size symmetrical – each increment of root length density leads to an increment of nutrient acquisition and this produces a monotonically increasing negative effect on a focal plant from neighbours with higher root length density strategies (Fig 4f – solid). This frequency- and density-dependence is common in many plant systems, and is captured in game theoretical models of optimal allocation.

Future directions

(1) One relatively new area of plant ecology where game theory may provide insight is in plant allocation responses to elevated atmospheric CO2 (eCO2). The leaf-level responses to eCO2 are well understood (Norby & Zak 2011), but the allocation responses have been notoriously difficult to understand (Körner et al. 2007) and might benefit from a game theoretical viewpoint. For example, the model of Dybzinski et al. (2011) predicts an increase in ESS allocation to fine roots in response to increased leaf-level nitrogen use efficiency, a phenomenon that occurs under eCO2 (Norby & Zak 2011). A stand that was formerly at ESS under ambient atmospheric CO2 will no longer be at ESS under eCO2 and thus will be susceptible to a challenge from a strategy with greater fine root density.

One hypothesis is that resource availabilities (e.g. light, nitrogen, water) are sufficiently variable that plants have evolved a plastic response that maintains competitive superiority under varying conditions. Thus, as leaves increase their nitrogen use efficiency under eCO2, plants may assess and respond to pre-empt competitors by increasing fine root density to the new ESS. Alternatively, if plants lack sufficient plasticity to remain at ESS under eCO2, then one would predict turnover in community composition as better competitors under the new conditions colonise and replace the old resident species.

(2) How prevalent are TOC allocation strategies, and what conditions favour plastic vs. fixed allocation strategies? The mixed support for a plastic TOC in the literature suggests that our understanding of belowground TOCs is incomplete. Thus, it would greatly aid the development of models to have more data concerning when and which species exhibit above- or belowground TOCs. Similarly, it would greatly aid the development of experiments to
have models that explore more detailed hypotheses about when a plastic TOC is or is not expected.

**ENEMY DEFENCE**

The enemies of plants can dramatically impact individual fitness (Agrawal 2011; Johnson 2011; Karban 2011), and these fitness impacts can influence community and population dynamics (Johnson & Agrawal 2005; Viswanathan et al. 2008; Agrawal 2011). We define an enemy as any organism that benefits from an interaction that is, on balance, harmful to plants. Herbivores, parasites and diseases fall under our definition of plant enemies, and in this section, we review game theoretical models of plant defence against enemies. Many of the existing game theoretical models have focused on plant–herbivore interactions, and more specifically, most models have asked: what is the optimal level or type of defence plants should employ against herbivores? Thus, we will limit our discussion to plant defences against herbivores and point out that plant–pathogen and plant–disease interactions are important (van der Heijden et al. 2008; Bever et al. 2010; Rasmann et al. 2011; de Kroon et al. 2012) and understudied by game theorists.

When viewed in isolation (i.e. as density-independent), the problem of plant defence against herbivores is a straightforward optimisation based on the potential costs of the herbivore vs. the costs of the defence (Coley et al. 1985; Endara & Coley 2011). How might density- and frequency-dependence play into a plant’s optimal defence strategy? Because plants compete with their neighbours for limiting resources, and because herbivores may select hosts based on their defence levels (Oksanen 1990; Augner et al. 1991; Augner 1994; Viswanathan et al. 2007), a strategy used by an individual that is a net cost to its neighbours will potentially be a net benefit to itself. For example, because many herbivores are mobile and selective for at least part of their lifecycle (Tuomi et al. 1994), a plant with a higher defence strategy than a neighbour may be able to deflect herbivores onto those neighbours. This produces the direct benefit of minimising enemy attack, and potentially an indirect benefit through reduced competitive ability of attacked neighbours. Thus, the goal of plant defences might be conceptualised partly as an attempt to minimise attack and partly as an attempt to deflect herbivores onto neighbours (e.g. Oksanen 1990; Augner et al. 1991) resulting in a TOC for the evolution of defence. As focal and neighbour plants simultaneously attempt to deflect potential enemies onto each other, and because they may differ in the strategies they use for defence, the analysis of the problem becomes frequency-dependent, or game theoretical (Oksanen 1990; Augner et al. 1991; Augner 1994; Tuomi et al. 1994; Augner 1995; Augner & Bernays 1998; Broom et al. 2005).

Game theoretical and non-game theoretical models of defence often have several features in common: (1) They seek to find an optimal level of defence; that is, low defence levels are costly because of herbivore damage, whereas high levels are costly because they are higher than is necessary to defend against attack (Fig. 5a). (2) Models must also include the fact that herbivore damage is costly to plant fitness (Fig. 5b). These first two features are not specific to game theoretical models and represent the minimum conditions necessary to predict a plant's best defence strategy. For example, the resource availability hypothesis posits that fast-growing species may invest less into defence because they are more able to replace tissues lost to herbivory, whereas slow-growing species have less capacity to replace tissues and must invest in defence (Coley et al. 1985; Endara & Coley 2011).

Game theoretical models add to this existing theory by exploring the consequences of explicitly including interactions among different strategies. This still includes the idea that (1) there is an optimal defence strategy (Fig. 5c) and that (2) herbivory is costly (Fig. 5d) – though as above, the ESS shifts compared with a density-independent model. Game theoretical models add two more parameters, (3) including the potential negative effects of the competitive interactions between alternative plant strategies that occur with increasing population density (Fig. 5e). That is, negative density-dependence can influence the resources plants have available to invest in defence and alter the ESS level of defence. (4) the strategy used by a neighbour can now influence the probability of attack of the focal plant (Fig. 5f). For example, growing next to a relatively undefended neighbour might be advantageous because mobile and selective herbivores might attack the neighbour. Alternatively, growing next to a highly defended neighbour might be bad because mobile and selective herbivores would attack the focal plant. Explicitly including density- and frequency-dependence into models is what sets game theoretical models (E.g. Oksanen 1990; Augner et al. 1991; Tuomi et al. 1994; Broom et al. 2005) apart from
from non-game theoretical models (e.g. Coley et al. 1985; Endara & Coley 2011).

A basic hypothesis of these game theoretical models for optimal defence strategies is that the success of a given strategy might depend on which other strategies co-occur. This need not be true in all systems, in which case non-game theoretical models are adequate. However, when frequency-dependence does occur, game theoretical models will be necessary to capture the relevant ecological interactions. A clear empirical example of the importance of alternative plant strategies for defence in shaping ecological outcomes is a series of papers by Viswanathan et al. (2005, 2007, 2008) that investigated the consequences of sequential attack by flea beetles (Psylliodes affinis) and tortoise beetles (Plagiometronia clarata) feeding on bittersweet nightshade (Solanum dulcamara). Bittersweet nightshade has an inducible response to both beetles, but each herbivore induces a different and apparently mutually exclusive response (Viswanathan et al. 2007). Moreover, once each defence is induced, it appears that the plant cannot switch its defence strategy, which is maintained through the growing season (Viswanathan et al. 2005). Thus, when a flea beetle is the first to attack a plant, it induces one type of chemical defence (Viswanathan et al. 2007) that decreases the future occurrence of either beetle. Alternatively, initial attack by tortoise beetles induces a completely different type of chemical defence (Viswanathan et al. 2007) that has no impact on future occurrence of either beetle. In other words, this plant-herbivore system produces a situation where individuals within a bittersweet nightshade population may employ different strategies for herbivore defence.

Thus, we might hypothesise that there would be a strong relationship between the types of herbivores and the types of plant defence strategies that occur. Indeed, an experiment that manipulated the frequency of plant strategies in common garden plots (all flea beetle induced, all tortoise beetle induced or mixture) demonstrated strong frequency-dependence of the types of plant defence strategies for the structure of the herbivore community throughout the growing season (Viswanathan et al. 2008). The two beetles differ greatly in their mode of feeding, and the authors have also shown strong frequency-dependent effects of herbivore type and abundance on damage to plants based on the plant defence strategy (Viswanathan et al. 2005). Furthermore, the herbivores experience frequency-dependence depending on the types of defence strategies expressed in the population (Viswanathan et al. 2008).

Density-independent models cannot make predictions about these types of frequency-dependent effects because they do not include them in the model. Instead, the S. dulcamara examples illustrate that certain questions or systems require models which explicitly capture frequency-dependent effects. As the S. dulcamara example illustrates, such frequency-dependence can have cascading effects on population and community dynamics and has broad implications for our understanding of these dynamics. This single empirical example does not mean that frequency-dependence will always be important; for example, non-mobile or non-selective herbivores that have little opportunity to switch hosts based on plant defence levels may represent a truly density-independent scenario where a game theoretical approach would not be necessary. However, the results described above are sufficient to make the point that frequency-dependence can have strong impacts in the ecology and evolution of plant and herbivore species, and that for these systems non-game theoretical models would get the wrong answer.

Future directions

(1) One of the biggest open questions in the field of plant-herbivore interactions is why do different plants differ in the type and level of defence (Johnson 2011)? One potential answer is that this is driven by frequency-dependent processes. Understanding frequency-dependent interactions among plants with different strategies for defence will necessitate moving away from studying (or assuming) single strategy systems and instead experimentally manipulating systems with multiple strategies (e.g. Johnson & Agrawal 2005; Viswanathan et al. 2005, 2008). For example, do the costs and benefits of defence for a plant with one type of defence shift as a function of the presence or absence of other strategies? And how does this shape plant or herbivore population and community dynamics?

(2) Increasingly, the role of pathogens, especially in soil, has been recognised as an important determinant of plant population and community organisation (van der Heijden et al. 2008; Bever et al. 2010; Rasmann et al. 2011; Schnitzer et al. 2011; de Kroon et al. 2012, Johnson et al. 2012). Game theoretical models have largely been silent on plant–pathogen interactions, although verbal models are often implicitly game theoretical (e.g. de Kroon et al. 2012). We suggest that the development of more explicitly quantitative hypotheses that incorporate density- and frequency-dependence into theories of plant–pathogen interactions would generate testable hypotheses in this field.

**Mutualisms**

Mutualistic associations between plants and other taxa can affect plant fitness, and these fitness impacts may alter population growth, community structure and ecosystem function (van der Heijden et al. 1998; Hoeksema & Bruna 2000; van der Heijden et al. 2008; Archetti et al. 2011). We define mutualism as any interaction between partners, where the interaction benefits both individuals by producing a positive fitness outcome for each. This definition therefore includes a diverse group of taxa, including nitrogen fixing bacteria (van der Heijden et al. 2008), arbuscular and ecto-mycorrhizal fungi (van der Heijden et al. 1998; Hoeksema et al. 2010), free living rhizosphere bacteria (Kuzyakov 2002; Denison et al. 2003; Kiers & Denison 2008), a diverse group of pollinators (Marshall & Folsom 1991; Fenster et al. 2004) and seed dispersers (Howe & Smallwood 1982). This enormous variation in taxa and types of activities involved in the interaction has made generalizations difficult, and much of the existing literature has been focussed on simply defining the nature of the types of games that might be applicable to mutualisms or understanding when and how it is even possible that mutualisms might evolve (Trivers 1971; Axelrod & Hamilton 1981; Bshary & Bronstein 2004; Brown & Vincent 2008; Archetti et al. 2011). As a result, specific models are rare, but based on the structure of models for competition (Fig. 4) and enemies (Fig. 5) we offer a suggestion for the basic parameters and structure such models might take.

Many models of plant mutualisms make use of biological markets theory, which envisions the mutualism as a continuous game of trading resources between individuals that differ in how efficiently they can capture each resource (Schwartz & Hoeksema 1998; Bshary & Bronstein 2004; Archetti et al. 2011). The simplest form of a biological markets model is density-independent
(e.g. Hocksema & Bruna 2000). In these models, there are two general features: (1) There is some optimal level of investment into the mutualistic association that maximises the returns on trade with the mutualistic partner (too low and the plant misses out on resources or services that they cannot easily acquire themselves, while too high and they risk overpaying for the traded resource, Fig. 6a) and (2) that investment from mutualistic partners have a net positive effect on the fitness of the focal plant (Fig. 6b) – though a mutualism-parasitism continuum (Hocksema et al. 2010) could also be captured if necessary. This model structure, combined with parameters about resource availability, makes predictions about when plants should gather resources themselves, vs. when they should engage in trade with their mutualistic partner.

When they are important, density- and frequency-dependent considerations can be merged with these conventional ideas. Although specific models are rare, we suggest the following general framework. A game theoretical model would produce a situation where there is (1) still some optimal level of investment into mutualistic trade by a focal plant (Fig. 6c) and (2) where investment from the mutualistic partner produces a net benefit to the focal plant (Fig. 6d) – though, as always the inclusion of density- and frequency-dependence changes the optimal strategy. As above, game theory would add two more parameters related to frequency and density-dependence. (3)

<table>
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<th>Density-independent</th>
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<td>(a) Focal plant’s mutualism strategy</td>
<td>(c) Focal plant’s mutualism strategy</td>
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<td>(b) Density of mutualists</td>
<td>(d) Density of mutualists</td>
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<td>(e) Population density</td>
<td>(f) Alternative neighbor mutualism strategies</td>
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**Figure 6** Many existing models of plant investment into mutualisms are density-independent (a, b), however, following the general model framework of Fig. 1, we suggest some basic relationships that could introduce frequency- and density-dependence into these models (c–f). Curves are perturbations and represent a hypothetical slice through multidimensional space in which values for companion panels are held fixed as shown (dash-dot line for a & b; Evolutionarily Stable Strategy dashed line for c–f). (a & c) Relationship between mutualism investment strategy and fitness. (b & d) Relationship between mutualistic partner density and focal fitness. (e) relationship between population density and focal fitness. (f) relationship between neighbour strategies and focal plant fitness. See text for more detailed description of relationships.

Density-dependence will also play a role in the optimal strategy for investment into mutualisms. We suggest that for mutualisms density-dependence will take the form of some hump-shaped relationship, where increasing population density has positive effects at low densities, switching to negative effects at higher population densities (Fig. 6e). We expect such a relationship because in many cases the mutualistic partners of plants often cannot exist without plants, and vice versa, so low plant density often will also mean a low density of mutualistic partners leading to suboptimal plant performance (e.g. van der Heijden et al. 1998; Burrows & Pfleger 2002). However, as plant population density increases past some critical threshold, competition for mutualistic partners becomes limiting and produces a shift to negative density-dependence (E.g. Allison 1990; Kunin 1997). (4) We suggest that frequency-dependence would manifest itself through competition for access to mutualistic partners among plants using different strategies producing a TOC. Specifically, this would become important where mutualistic partners are able to choose plants that offer more reward for the partnership such that increasing investment by neighbours would have a negative effect on the focal plant by pre-empting access to mutualisms (Fig. 6f). For example, there is considerable evidence that pollinators preferentially pollinate plants that offer the most nectar (Pyke 1978; Lefebvre et al. 2007) or that foraging animals may disperse seeds that are in the largest or most nutritious fruits (Howe & Smallwood 1982). This pre-emption of mutualistic services through frequency-dependent processes is probably most important for mobile mutualists (e.g. seed dispersers, pollinators) and can have dramatic effects on plant fitness, yet it is not captured in density-independent models. This means that many models potentially severely underestimate plant investment into mutualisms. These effects are often observed in data, and theoretical descriptions of mutualisms will only be enhanced by explicitly including density and frequency-dependence into theory.

However, even immobile mutualistic partners may influence plant performance leading to frequency-dependent effects. A basic hypothesis of this type of game theoretical model for investment into mutualisms suggests that the success of any given plant strategy would depend on the strategies used by its neighbours. For example, van der Heijden et al. (1998) performed a number of experiments on microcosm plant communities where the number and type of arbuscular mycorrhizal fungi (AMF) species was manipulated (zero AMF, one AMF species or four AMF species). In one experiment, successful growth of eight of the eleven plant species studied was strongly tied to the presence of at least one AMF species. Further, among these eight species of plants different plant species benefitted from different AMF species suggesting species specific strategies for association between plants and AMF. Alternatively, the non-mycorrhizal species of plant in this experiment performed best in the zero AMF treatment and poorest when any AMF were present. In short, the success of plant strategies was strongly tied to the frequency of other plant strategies available. For example, being a non-mycorrhizal plant is a very effective strategy in an AMF free environment but becomes less successful when the frequency of plants engaging in AMF associations increases (van der Heijden et al. 1998). In field experiments, strong positive links between manipulated AMF diversity and plant species diversity are commonly observed (van der Heijden et al. 1998; Burrows & Pfleger 2002; Hocksema et al. 2010). Together, these suggest strong frequency-dependent effects on community composition.

As for competition and herbivory, theory that is density-independent cannot make any predictions about the frequency-dependent...
effects described above. Instead, the study of van der Heijden (1998) highlights that specific plant taxa often benefit from specific mutualistic taxa, and that the success of any given plant species can depend on the strategy used by the other plant species around it (e.g. the non-mycorrhizal species succeeded only when there were no AMF present, whereas the success of the mycorrhizal plant species depended on which types mycorrhizal fungi were present). We suggest that a game theoretical approach to the study of mutualisms would make markedly different predictions about the optimal strategy for investing into mutualisms, and for the overall fitness benefits obtained by any individual. Specifically, game theoretical models might predict a TOC for investment into mutualistic partnerships that produces a higher level of investment into mutualisms compared with non-game theoretical models. This occurs when mutualistic species preferentially associate with plants that offer them the highest reward, driving an arms race or a TOC for investment into mutualisms.

Future directions

(1) Most of the literature we have reviewed on plant mutualisms treats the problem generally. This is not surprising given the great diversity of taxa that form mutualisms with plants. However, the field would benefit from the development and testing of specific models for specific mutualisms. For example, how does investment into alternative traits that attract pollinators influence competition for access to pollinators? How do plants choose among and invest in a diverse set of potential mycorrhizal partners when their neighbours are also competing for access to those same partners?

(2) Is there any evidence for a TOC in investment by plants to mutualists? We hypothesise that when mutualists are selective and mobile, this should occur. However, no one, to our knowledge, has

DISCUSSION

Plant ecologists recognise the importance of density-independent, density-dependent and frequency-dependent processes (De Deyn & Van der Putten 2005; Bever et al. 2010; Johnson 2011; Thorpe et al. 2011). Yet, many theories are built upon an explicitly density-independent framework, while density-dependence and frequency-dependence are only implicitly considered. This is perhaps unsurprising since many of theories in plant ecology pre-date much of the formal development of evolutionary game theory (Smith 1982; Weibull 1997; Vincent & Brown 2005). Furthermore, ‘starting simple’ is a reasonable scientific strategy: understand the simplest and perhaps most important variables before building in additional complexity. However, few ideas in science represent an end point. We have shown how game theory can take classic ideas (e.g. optimal tissue allocation, optimal enemy defence and optimal investment into mutualism), and build in density- and frequency-dependence using game theory to make novel predictions (Figs 4–6). When these processes are important, this produces more ecologically realistic models that we believe offer enhanced understanding and predictive power for plant ecologists.

In a similar way, the studies that we have reviewed are unlikely to represent end points in the theoretical understanding of plant ecology. Indeed, these models cry out for further development in at least two respects. First, the studies that we reviewed tended to

treat plant–plant interactions as a game influenced by static external factors (e.g. competitors, enemies or mutualisms). Biotic interactions in past models were largely viewed as static external factors that influence plant–plant interactions, but are not reciprocally influenced through co-evolution. Although this approach recognises the importance of density- and frequency-dependence for plants, it is almost certainly still too simplistic. Plant enemies and mutualistic partners are not static external factors; they are dynamic entities subject to both density- and frequency-dependence themselves and to co-evolution with plants. As we gain an understanding of how density- and frequency-dependence influence plant–plant interactions, models of co-evolution (e.g. Ripa et al. 2009; Pintor et al. 2011) between plants and the taxa that interact with them will be a worthy future goal. Second, the studies that we reviewed tended to permit only a single-ESS solution for a given set of environmental factors. As Falster & Westoby (2003) point out, most plant communities, which persist at a given set of environmental factors, are quite diverse, containing many species and many strategies for competition, enemy defence and mutualism. This contrasts sharply with simple models that often produce single-ESS solutions for one type of biological interaction (Augner et al. 1991; Gersani et al. 2001). Again, it is reasonable to begin with simple models and expand as empirical results inform the development of future theory, but models that represent multiple-ESS solutions (e.g. Vincent & Brown 2005; Ripa et al. 2009; Pintor et al. 2011) will be a step forward.

Our goal here was to provide a simple introduction to how game theory can contribute to our understanding of plant ecology. Following an emphasis in the literature, we focussed on three fundamental biotic interactions and showed how game theory can be used to build in more ecological realism. However, we do not wish to give the impression that our review circumscribes all that game theory may contribute to plant ecology in the future. Indeed, many more plant traits than just allocation to tissue, defence and trade with mutualistic partners might be influenced by density- or frequency-dependent processes, and game theoretical models could be made to better understand any of them.

CONCLUSION

Game theory produces very different predictions from conventional ideas in plant ecology, and can be especially important when frequency-dependent processes occur. First, game theoretical models of plant–plant competition extend conventional ideas that plants should allocate biomass to the organs that collect whichever resource is limiting (a density-independent framework), to account for the fact that plants interact with a diverse set of height, leaf and root strategies that also affect fitness (a density- and frequency-dependent framework). Second, game theoretical models of plant–herbivore interactions extend conventional ideas about optimal herbivore defence (a density-independent framework) to account for the fact that defector herbivores onto one’s neighbours may not only prevent damage, but may remove competition (a density- and frequency-dependent framework). Finally, game theoretical models of plant–mutualism interaction might extend conventional ideas about optimal investment into mutualisms or partner choice (a density-independent framework), into a sort of bidding war, where plants must compete for access to trades with potential mutualistic partners (a density- and frequency-dependent framework). By extending existing ideas to account for density- and
frequency-dependence, game theory provides an exciting new frontier in the study of plant ecology.

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REFERENCES


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